Determinants of Data Deficiency in the impacts of alien bird species

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Abstract

Aim

To identify the factors that influence the availability of data on the negative impacts of alien bird species, in order to understand why more than 70% are currently classified as Data Deficient (DD) by the Environmental Impact Classification of Alien Taxa (EICAT) protocol.

Location

Global.

Methods

Information on factors hypothesised to influence the availability of impact data were collated for 344 alien bird species (107 with impact data and 237 DD). These data were analysed using mixed effects models accounting for phylogenetic non-independence of species (MCMCglmm).

Results

Data deficiency in the negative impacts of alien birds is not randomly distributed. Residence time, relative brain size and alien range size were found to be strongly related to the availability of data on impacts.

Main conclusions

The availability of data on the negative impacts of alien birds is mainly influenced by the spatial and temporal extents of their alien ranges. The results of this study suggest that the impacts of some DD alien birds are likely to be minor (e.g. species with comparatively long residence times as aliens, such as the common waxbill (Estrilda astrild) and the Java sparrow (Padda oryzivora)). However, the results also suggest that some DD alien birds may have damaging impacts (e.g. species from orders of alien birds known for their impacts to biodiversity but with comparatively small alien ranges, such as the New Caledonian crow (Corvus moneduloides)). This implies that at least some DD alien birds may have impacts that are being overlooked. Studies examining the traits that influence the severity of alien bird impacts are needed to help to predict which DD species are more likely to impact upon biodiversity.

Key words: Data deficient, biological invasion, alien birds, range size, residence time, brain size.

Introduction

In recent years, there has been much debate regarding the implications of biological invasions for native biodiversity (see Sax & Gaines, 2003; Briggs, 2013; Russell & Blackburn, 2017). However, there is no doubt that alien species can have severe negative impacts upon native biodiversity. For example, they have been shown to pose a threat to the existence of 27% of mammals, birds, reptiles and amphibians worldwide (Bellard et al., 2016a), and to represent the most common threat associated with vertebrate extinctions, having been implicated in approximately two-thirds of all such extinctions since AD1500 (Bellard et al., 2016b). Recent studies also demonstrate that alien species are contributing to the global homogenisation of biodiversity. For example, alien invasions have substantially altered the global distribution of terrestrial gastropods (snails and slugs), the distribution of which is now shaped primarily by global trade relationships and climate (Capinha et al., 2015).

Despite the well-known and substantial impacts of some alien species, there is a lack of systematic and quantitative data on alien species impacts in general (Kumschick et al., 2015; Hoffmann & Courchamp, 2016; Wilson et al., 2016; Kumschick et al., 2017). Birds are amongst the best-studied animal groups, but alien birds are no exception to this rule. A recent global review of alien bird impacts on native biodiversity, undertaken using a new protocol developed to quantify and categorise the impacts of alien species (the Environmental Impact Classification for Alien Taxa (EICAT); Hawkins et al., 2015), could not find any impact data for 296 of 415 species (> 70%) with known alien populations (Evans et al., 2016). These species were therefore classified as Data Deficient (**DD**) by the EICAT method. (Note that our usage of **DD** here differs from that of the IUCN Red List (http://www.iucnredlist.org), which relates to species extinction risk: “A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status.” (IUCN, 2016)). Two other recent studies of the global impacts of alien birds (Baker et al., 2014; Martin-Albarracin et al., 2015) also found data for a relatively small number of species (33 and 39 respectively), and concluded that we need more information on their impacts.

The limited data that are available reveal significant variation in the severity of the environmental impacts attributable to alien birds. For example, in New Zealand, the alien population of the mallard (*Anas platyrhynchos*) could be on the verge of causing the extinction of the Pacific black duck (*A. superciliosa*) through hybridisation (Guay et al., 2010), but as far as we are aware, the impacts of the alien Australian magpie have not resulted in declining populations of any native species (Morgan et al., 2006). While it is possible that a lack of data on the impacts of an alien bird species stems from the fact that it has no impacts, it would be unwise to assume so. We would therefore expect there also to be variation in the severity of impacts associated with **DD** alien bird species. As far as we are aware, the reasons why we may be lacking data for some alien bird species but not others have yet to be examined, and as such, drivers of data deficiency regarding their impacts represent a gap in our understanding of biological invasions. An obvious question therefore, is are there factors that determine whether alien birds have been subject to research in order to assess their impacts as invaders? Identifying these factors would help us to understand why some species have not been studied, and what the implications of data deficiency might be for the prevalence of alien bird impacts more widely.

There are at least three broad reasons why we might lack data on the impacts of alien birds. First, species perceived by scientists or the general public to have severe impacts may attract research, whilst species perceived to have negligible impacts on biodiversity may remain unstudied. A recent examination of bias in invasion biology found that alien species with documented impacts are more frequently studied than alien species with no documented impacts (Pyšek et al., 2008). Similarly, Evans et al. (2016) found a greater number of studies on the impacts of alien bird species that had more severe documented impacts (but see Kumschick et al., 2017). Given the scarce resources allocated to conservation (Joseph et al., 2009), the prioritisation of research towards those species that are perceived to cause the most damage is to be expected. In this case, **DD** species would tend to be those with low perceived impacts; whether or not a bird species was **DD** would potentially be related to the severity of its impacts, depending on the accuracy of those perceptions.

Second, some species may be more amenable to study because of their availability. For example, there will have been greater opportunity to study species with longer residence times (*sensu* Wilson et al., 2007), by dint of their longer existence as aliens. Such species have also had more time to cause impacts, which may prompt research. Species with larger alien ranges and those introduced to a broader range of locations may be encountered and studied more frequently, simply because they are more widespread. Furthermore, widespread species are likely to have had more opportunities to impact biodiversity due to the breadth of habitats they may encounter. As species with more severe impacts are more frequently researched, we may therefore have more information about widespread species. Similarly, generalist species (as determined by their dietary and habitat preferences) may be more readily studied because they are likely to utilise or occupy and impact upon a broader variety of habitats (*sensu* Carrascal et al., 2008; Reif et al., 2015). Larger brain size relative to body mass (an indicator of enhanced behavioural flexibility) has been linked to increased abundance in UK farmland birds (Shultz et al., 2005), and has been found to enhance survival amongst birds and mammals introduced to novel environments (Sol et al., 2007; Sol et al., 2008); thus large-brained birds may also be encountered more regularly. Large-brained birds have also been found to have higher levels of urban tolerance, with more of these species (compared to birds with smaller brains) being able to breed successfully within city centres (Maklakov et al., 2011). This brings large-brained birds into direct contact with human population centres, which may also increase their exposure to research.

In contrast, species may be encountered less frequently when they occur in remote, inhospitable or politically unstable regions of the world, where their impacts are difficult to record, where there is a lack of capacity (funding/knowledge/political will) to undertake research, or from locations where existing studies may be harder to locate. Two recent studies examining geographic bias in invasive species research (Pyšek et al., 2008; Bellard & Jeschke, 2015) found that the majority of studies on a broad range of taxonomic groups are being undertaken in the more developed regions of the world. Similarly, over 50% of the impact data uncovered by Evans et al. (2016) related to invasions within mainland North America, Australia and Europe, with the fewest data for those within Africa and South America (7.2% combined). A related study by Martin-Albarracin et al. (2015) found that most alien bird impact data were available for invasions within Europe, with little for those within Africa and South America. Evans et al. (2016) also found that amongst orders of alien birds, comparatively more impact data were available for Psittaciformes (parrots), possibly because the majority of alien parrot species were within North America. These results are congruent with those from a recent study examining reasons for data deficiency amongst species listed on the IUCN Red List, which found that IUCN **DD** terrestrial mammal species tend to occupy highly specific, remote habitats (Bland et al., 2015). Here, we would expect **DD** alien species to be those with smaller alien ranges, specific dietary and habitat preferences and relatively small brains. They would also tend to have been introduced more recently and to fewer new locations, and be established in less developed, more remote and inaccessible regions of the world. In such cases, whether or not a bird species was **DD** would potentially be unrelated to the severity of its impacts where it occurs.

Third, some species may be easier or more preferable to study, due to their specific characteristics. For example, large-brained species may receive greater research attention because they possess interesting traits relating directly to their enhanced intelligence (e.g. Lefebvre et al., 2002; Emery & Clayton, 2004; Sol et al., 2005; Maklakov et al., 2011; Lefebvre et al., 2013). Certain orders of large-brained birds (primarily Corvids (crows and allies) and Strigiformes (owls)) have been found to be associated with more severe impacts (Evans et al., 2016). This may be due to their enhanced intelligence and behavioural flexibility, which enables them to exploit the available resources in their new surroundings more effectively (in the case of crows and owls, through predation). As species with more severe impacts tend to be more frequently studied, we may therefore have more impact data for large-brained alien birds. In support of this, in their global reviews of the impacts of alien birds, Baker et al. (2014) and Martin-Albarracin et al. (2015) found large-brained birds to be associated with more severe impacts.

Conspicuous species may also be more amenable to study because they have a higher detection probability (*sensu* McCallum, 2005). For example, nearly 90% of the impact data found by Evans et al. (2016) were for species from five orders (Passeriformes (perching birds), Psittaciformes, Galliformes (gamebirds), Anseriformes (ducks, geese and swans) and Columbiformes (pigeons and doves)). Similarly, the majority of the impact data compiled by Martin-Albarracin et al. (2015) came from four of the same five orders. Many of the species amongst these orders are large-bodied and conspicuous. Evans et al. (2016) also found that amongst all orders with impact data, comparatively more data were available on the impacts of Psittaciformes, but fewer for Passeriformes. Parrots tend to be relatively large, colourful and noisy whereas, by comparison, many perching birds are small and inconspicuous (although many have distinctive songs). Large-bodied bird species have also been found to have more severe impacts in Europe (Kumschick et al., 2013), and as high-impact species attract research, we may know more about larger-bodied birds. These results reflect those from a study of data deficiency amongst IUCN Red List species, where Bland et al. (2012) note that amongst terrestrial mammals, **DD** species tend to be small-bodied. Taken together, these studies suggest that **DD** species would tend to have smaller brain and body sizes, and to be less conspicuous. Again, whether or not a bird species was **DD** would potentially be unrelated to the severity of its impacts.

Here, we test a range of hypotheses (H) better to understand why impact data is available for some alien bird species, whilst others remain **DD**. Based on the factors discussed above and the results of previous studies, we expect to find proportionally more **DD** species amongst those species which: (H1) have alien ranges within less developed regions of the world; (H2) are small-bodied and less conspicuous; (H3) have smaller relative brain sizes; (H4) are specialists; (H5) have small alien ranges; (H6) are present in fewer biogeographic realms; and (H7) have shorter residence times.

Methods

Data

A list of 415 alien bird species, comprising 119 species with impact data and 296 **DD** species, was taken from Evans et al. (2016); as far as we are aware, this represents the most comprehensive global dataset on the impacts of alien birds. For this study, impact data were identified through a literature review, with **DD** species being those for which no impact information was found (for more information on the literature review methodology, see Evans et al., 2016). Our analysis was restricted to those alien birds for which we had a complete dataset for all predictor variables described below – a total of 344 species (107 with impact data and 237 **DD**).

We assembled data on the following variables to test each of the seven hypotheses listed in the Introduction:

H1: We used the Human Development Index (HDI) to test whether **DD** species tend to have alien ranges within less developed regions of the world. The HDI (downloaded from http://hdr.undp.org/en/2015-report on 21 November 2016) is a country-level, composite measure of achievement in three key aspects of human development: being educated, having a long and healthy life and maintaining a decent standard of living. Here it is used as a proxy for the research potential of a country. A list of countries occupied by each alien bird species was extracted from the Global Avian Invasions Atlas (GAVIA) (Dyer et al., 2016), and the highest country HDI score was taken for each species. This provided us with a measure of the potential exposure of a species to research. Data on the impacts of alien populations of the Christmas white-eye (*Zosterops natalis*) relate only to the Cocos (Keeling) Islands, which currently does not have a published HDI. The Cocos (Keeling) Islands is a territory of Australia, so the HDI score for Australia was applied for this species.

H2: We tested whether **DD** species tend to be smaller-bodied using data on adult body mass (g), extracted from the recently published amniote life-history database (Myhrvold et al., 2015). Missing data for ten species were taken from Sekercioglu (2012).

To determine whether inconspicuous species are more likely to be **DD**, we tested whether **DD** species are less likely to belong to families of birds which we considered to be conspicuous based on their broad taxonomic characteristics. We selected three families of alien birds which we considered to be inconspicuous, primarily because they comprise small to medium sized birds (Estrildidae (waxbills, munias and allies), Fringillidae (true finches) and Thraupidae (tanagers)) (*n* = 55), and three families which we considered to be conspicuous, because they generally comprise species that are large, colourful and have loud and distinctive calls (Psittacidae and Psittaculidae (true parrots) and Phasianidae (pheasants and allies)) (*n* = 92).

H3: To test whether **DD** species have smaller relative brain sizes, data on this trait (measured as the residuals of a log–log least-squares linear regression of brain mass against body mass) were taken from Sol et al. (2012). Using data that have been adjusted for body mass takes into account allometric effects, as larger species tend to have larger brains due to their size alone (Sol et al., 2005). Data were not available for 86 species, so for those species we estimated relative brain size using data from species from the closest taxonomic level within the Sol et al. (2012) dataset. Thus, brain size data for 47 species were calculated by taking an average for species from the same genus, 22 by taking an average for species from the same family, and 17 by taking an average for species from the same order.

H4: To test whether data deficiency is related to measures of habitat specialism, we followed Kumschick et al. (2013) and calculated the number of the following broad habitat types occupied by each species in its 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 habitat preferences were extracted from BirdLife International (2017). To test whether **DD** is related to measures of diet specialism, we used proportionate data on the major food types consumed by a species taken from Sekercioglu (2012). These data were used to calculate a Simpson's Diversity Index (SDI) for each species, where $D = \sum(n/N)^2$ (n = proportion of food types utilised by a species; N = maximum number of possible food types). SDI values range between 0 and 1, with lower scores indicating more diversity (generalism) in a species dietary preferences. A worked example for the Mandarin duck (*Aix galericulata*) is provided in the Supplementary Material: Appendix 1, Table A1.

H5: We used data on alien range sizes (km^2) from GAVIA (Dyer et al., 2016) to test whether **DD** species have smaller alien range sizes.

H6: We used data from GAVIA (Dyer et al., 2016) on the number of eight biogeographic realms (Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, Oceanic, Palearctic and Antarctic) occupied by each species, to test whether **DD** species are present as aliens in fewer biogeographic realms.

H7: We used data on residence time (the length of time (in years) since the first record of introduction for an established alien bird species) from GAVIA (Dyer et al., 2016) to test whether **DD** species have been introduced more recently. Details on the methods used to calculate alien range sizes, number of biogeographic realms occupied and residence time are given in Dyer et al. (2016).

Analysis

The presence or absence of impact data for each of the 344 alien bird species was analysed as a binary response variable (0 = absence of impact data; 1 = presence). To test whether there is phylogenetic signal in data deficiency, we first downloaded 100 randomly selected phylogenetic trees (Hackett backbone) incorporating all 344 species from Birdtree.org (http://birdtree.org/subsets/). The caper package (Orme et al., 2013) in R was used to determine the strength of the phylogenetic signal using the D statistic developed by Fritz & Purvis (2010). We compared the distribution of our binary trait across the tips of the 100 phylogenetic trees for two null models – a Brownian motion model of trait evolution and a random trait distribution model (generated by shuffling species tip values). D = 0 is the expected result under Brownian motion, whilst D = 1 infers a random distribution of data deficiency with respect to the phylogeny. We found a phylogenetic signal in data deficiency (D = 0.78, with the probability of D resulting from either Brownian phylogenetic structure or no phylogenetic structure both being 0).

This necessitates using an analytical method that incorporates phylogenetic structure in the data.

We used the MCMCglmm package (Hadfield, 2010) to create linear mixed models using Bayesian Markov Chain Monte Carlo methods to account for correlated random effects arising from phylogenetic relatedness. We used a probit link function and included phylogenetic covariance between species as a random effect, setting flat, largely uninformative priors. To ensure adequate model convergence and mixing, we ran the models for 1000000 iterations with a burn-in of 2500 iterations, which maintained effective sample sizes for all estimated parameters at > 1000.

Data for all predictor variables were log transformed, with the exception of habitat breadth, number of realms occupied and HDI score. HDI score data were not normally distributed and could not be normalised by log transformation. Here, we divided the data into four categories of Low (HDI score of 0 – 0.549), Medium (0.550 – 0.699), High (0.700 – 0.799) and Very High (0.800 and above), following the four formal HDI categories adopted by the United Nations Development Programme (see http://hdr.undp.org/en/composite/HDI).

The car package (Fox and Weisberg, 2011) was used to calculate variance inflation factors for all variables, to check for the potential effects of multicollinearity. We also used hierarchical partitioning (Chevan & Sutherland, 1991; Mac Nally, 1996), implemented using the hier.part package (Walsh and Mac Nally, 2013), to determine the extent to which each predictor variable was independently related to the response variable, relative to the effects of other variables analysed.

For multivariate analysis, we included only variables that demonstrated significant relationships ($P < 0.05$) during univariate analysis. Following an initial run of the multivariate model, iterative model simplification was undertaken by removing the least significant variable and rerunning the model, and repeating the process until the multivariate model contained only variables with significant terms ($P < 0.05$).

To examine the effect of conspicuousness on the availability of impact data, the actual and expected distributions of impact data availability across alien bird families were analysed using a contingency tables test (chi-squared test of independence).

All statistical analyses were undertaken using RStudio version 0.99.893 (R Core Team, 2016).

Results

Univariate analysis revealed positive relationships between impact data availability and all predictor variables except diet breadth (Table 1). There were strong positive relationships ($P < 0.01$) between data availability and alien range size, relative brain size, habitat breadth, HDI, number of biogeographic realms occupied and residence time. The distribution of species with and without impact data for these variables is shown in Figure 1. There was also a weak positive relationship between data availability and body mass (Table 1). Using the car package, we found no evidence of significant collinearity between variables (all variance inflation factors < 3; Supplementary Material: Appendix 1, Table A2).

Following model simplification, multivariate analysis indicated that birds with impact data tend to have longer residence times than **DD** species (163.1 versus 85.4 years, on average), larger relative brain sizes (mean residual = 0.24 versus –0.21 for **DD** species) and larger alien ranges (1,017,337km^2 versus 51,393km^2 for **DD** species) (Table 2). The reduced model also indicated that we are more likely to have impact data for alien bird species that occupy more biogeographic realms as aliens (average number of realms occupied = 2.57 versus 1.48 for **DD** species), and that occupy a broader range of habitats in their native ranges (average number of habitats occupied = 3.83 versus 3.19 for **DD** species), although these relationships were weaker (Table 2). The positive univariate relationships between data availability and HDI and body mass were not recovered when controlling for other predictors. During model simplification the deviance information criterion (DIC) did not increase by > 2. Hierarchical partitioning also identifies relatively strong independent effects of alien range size, residence time and relative brain size on the availability of impact data (Supplementary Material: Appendix 1, Table A3). Relatively large joint contributions of alien range size and number of realms occupied may arise because these two variables are correlated with each other (Pearson's product-moment correlation: $r = 0.63$, $df = 342$, $P = < 0.001$).

Data availability was also non-randomly distributed with respect to conspicuousness. More impact data were available for alien species from conspicuous bird families and less for species from inconspicuous families (Table 3).

Discussion

Information on the environmental impacts of alien birds is not available for over 70% of species globally. However, data deficiency is not randomly distributed amongst alien birds. Three variables demonstrated consistent, strong positive relationships with impact data availability in both univariate and multivariate analysis: data deficient alien birds tend to have shorter residence times, smaller relative brain sizes and smaller alien range sizes. These results suggest that data deficiency amongst alien birds is influenced by all three of the factors proposed in the Introduction: the severity of their impacts (perceived or real), their availability for research, and their specific characteristics.

Residence time was found to be the strongest predictor of impact data availability (Figure 1, Table 2) (based on DIC values produced during univariate analysis: Table 1). This is likely to be because it influences a species availability for research. Residence times vary substantially amongst alien birds. For example, the Seychelles fody (*Foudia sechellarum*) and Guanay cormorant (*Phalacrocorax bougainvillii*) have both had recorded alien populations for < 10 years, and are **DD** (Evans et al., 2016) whilst alien populations of the common pheasant (*Phasianus colchicus*) and the red junglefowl (*Gallus gallus*) date back approximately 1000 and 1500 years, respectively (Dyer et al., 2016), and their impacts are comprehensively recorded (Evans et al., 2016). The effect of residence time may reflect the time it takes for the impacts of an established alien species to be noticed and quantified – this could well be the case for species that invade remote environments away from human populations. It may also reflect the lag time between the arrival of an alien species and its establishment, spread and the eventual onset of impacts (*sensu* Crooks, 2005). That said, Aagaard & Lockwood (2014) studied invasion lags amongst 17 alien bird species, and found that lag times were relatively short (ranging from 10 to 38 years). If we could generalise based on this study, given an average residence time for **DD** alien birds of 85.4 years, it suggests that while recent alien bird arrivals may require monitoring for the onset of impacts, **DD** alien bird species with long residence periods may indeed have negligible impacts (unless they have restricted alien ranges and therefore have yet to be noticed). For example, the common waxbill (*Estrilda astrild*) and Java sparrow (*Padda oryzivora*) are both **DD**, and have residence times of over 300 years, larger than average alien ranges (422,399km^2 and 864,438km^2 respectively) and alien populations in developed regions of the world including North America and Europe (Dyer et al., 2016). It is certainly conceivable that these species have low environmental impacts.

With regards to the intrinsic characteristics of alien bird species, the trait with the strongest effect on impact data availability was relative brain size (Table 2). Bird species with large brains, relative to their body mass, have been shown to be more successful at establishing in novel environments, which is argued to be due to their enhanced ecological flexibility (Sol et al., 2005). Large-brained birds have also been shown to possess higher levels of urban tolerance and to be more successful at establishing within urban environments due to their propensity for innovative behavior (Maklakov et al., 2011). Parrots account for most of the 30 species with the largest brains in our dataset ($n = 25$), and are conspicuously successful at establishing in large urban centres (Butler, 2005; Menchetti & Mori, 2014; Pârâu et al., 2016). For example, rose-ringed parakeets (*Psittacula krameri*) have established breeding populations in major urban areas across ten European countries, with a conservative European population estimate of more than 85,000 individuals (Pârâu et al., 2016). Other Psittaciform species with established alien populations in large cities include monk parakeets (*Myiopsitta monachus*) in New York, red-breasted parakeets (*Psittacula alexandri*) in Singapore, red-crowned parrots (*Amazona viridigenalis*) in San Diego, and rainbow lorikeets (*Trichoglossus haematodus*) and little corellas (*Cacatua sanguinea*) in Perth. This proximity to human populations may be driving research into the impacts of parrot species, and may also be one of the reasons why we have proportionately more impact data for parrots than any other order of alien birds (Evans et al., 2016). In this case, data deficiency would relate to availability for study and the possession of interesting traits, but would be unrelated to the severity of a species impacts. Indeed, while we have proportionately more information on the impacts of alien parrots, their impacts tend to be less severe than those caused by alien birds from other orders (Evans et al., 2016).

Nevertheless, there is also some evidence that relatively large-brained species may be more likely to have environmental impacts. Approximately two-thirds (*n* = 23) of the species with more severe impacts identified by Evans et al. (2016) (those causing declining populations, population extirpations or species extinctions) were large-brained, and of the five species allocated to the most damaging EICAT impact category (**MV**), four were large-brained: the great horned owl (*Bubo virginianus*), barn owl (*Tyto alba*), Australian masked-owl and great kiskadee (*Pitangus sulphuratus*). Furthermore, of the ten alien bird species with population level impacts identified by Baker et al. (2014), six were large-brained (the common myna, crimson rosella (*Platycercus elegans*), Japanese white-eye (*Zosterops japonicus*), red-vented bulbul (*Pycnonotus cafer*), rose-ringed parakeet and shiny cowbird (*Molothrus bonariensis*)), and likewise two of the three most damaging species identified by Martin-Albarracin et al. (2015); the common myna and red-whiskered bulbul (*Pycnonotus jocosus*). Although there has been no formal analysis of the effect of brain size on the magnitude of environmental impacts in birds, as we have more information on species with more severe impacts (Pyšek et al., 2008; Evans et al., 2016), we may know more about the impacts of large-brained species. Therefore, data deficiency may truly reflect low impacts amongst alien birds, and the strong effect of brain size in our analyses may be because it relates to all three factors which positively influence data availability: impact magnitude, availability for study and intrinsic interest.

The size of a species' alien range was also found to be a strong predictor of impact data availability: we have more data on the impacts of widespread alien species (Figure 1, Table 2). A species' impact has been argued to be the product of its abundance, range size and per capita impact (Parker et al., 1999), while range size and abundance are generally positively correlated for birds in both native (Gaston et al., 2000) and alien ranges (Blackburn et al., 2001). Therefore, the positive effect of alien range size on data availability may be because widespread species have more severe environmental impacts, and alien species with more severe impacts have been found to be more frequently studied (Pyšek et al., 2008; Evans et al., 2016). This may also explain some of the exceptions to the trend, relating to the presence of alien birds on islands, where impacts tend to be more severe (Evans et al., 2016). For example, despite their restricted alien ranges (all < 200km^2) we have impact data for green junglefowls (*Gallus varius*) on the Cocos (Keeling) Islands, Australian masked-owls (*Tyto novaehollandiae*) on Lord Howe Island, Chimango caracaras (*Milvago chimango*) on Easter Island, and American crows (*Corvus brachyrhynchos*) on Bermuda. The impacts of these species are classified as Moderate (**MO**), Major (**MR**) or Massive (**MV**) under EICAT, and these species are therefore amongst the most damaging alien birds with impact data (Evans et al., 2016). These effects suggest that species with recorded impacts may genuinely be those with greater impacts, and hence that data deficiency may be indicative of low impact. Lacking information on the impacts of **DD** species, it is impossible to be certain on this point, but we would predict on this basis that future research would find most currently **DD** alien bird species to be classified in low EICAT impact categories (Minimal Concern (**MC**) or Minor (**MN**)).

The size of a species' alien range is also likely to matter due to its influence on the availability of species for study (Figure 1, Table 2). More than one-third (*n* = 81) of the **DD** species in our dataset have alien ranges < 1000km^2 (over 1000 times smaller than the average range size for species with impacts). They include species from orders of birds known for their impacts to biodiversity, such as Sturnidae (starlings, an order including species such as the common myna (*Acridotheres tristis*) which has severe documented impacts; Grarock et al., 2012) and Corvidae (crows and allies, an order including species such as the Indian house crow (*Corvus splendens*), the impacts of which are also well documented; Ryall, 1992). It is therefore possible that the impacts of some species have yet to be noticed due to their relatively small range sizes, and that data deficiency may not guarantee that a species has minor impacts upon biodiversity. The relative importance of range size in our models of data deficiency is likely to arise because it relates both to magnitude of impact and availability of a species for research.

The breadth of habitats occupied by a species in its native range is also positively related to impact data availability (Figure 1, Table 2). This suggests that we may know more about the impacts of generalist species that are able to occupy a broad range of habitats because they are more available for study. Similarly, the number of biogeographic realms occupied by alien birds also influences impact data availability. Some species, such as the house sparrow (*Passer domesticus*), are globally distributed, occupying all eight realms, but > 60% (*n* = 211) occupy one realm alone, including the yellow-vented bulbul (*Pycnonotus goiavier*) and Palawan peacock-pheasant (*Polyplectron napoleonis*) (Dyer et al., 2016). However, both of these relationships were weaker than for the other variables identified during multivariate analysis, most likely because their influence is better captured by alien range size (Table 2). The relatively large joint contributions of alien range size and number of realms occupied identified by hierarchical partitioning (Supplementary Material: Appendix 1, Table A3) may reflect the correlation between these two variables. Nevertheless, we found proportionately more **DD** species amongst those occupying fewer habitats in their native range and fewer biogeographic realms as aliens (Figure 1), even when controlling for alien range size (Table 2). Specialist species are significantly more likely to be threatened with extinction, rare and localised (Sekercioglu, 2011), whereas generalists that occupy more habitats or realms are likely to be more available for study, especially if those habitats or realms are associated with a hotspot of invasion research, such as Australasia.

We find proportionately more **DD** species amongst families considered to be inconspicuous (*Estrildidae*, *Fringillidae* and *Thraupidae*), and proportionately fewer amongst conspicuous families (*Psittacidae*, *Psittaculidae* and *Phasianidae*) (Table 3). This result may be influenced by the presence of parrot species in the dataset, which account for over 25% of species with impact data. Parrots tend to be conspicuous – they often have loud calls and bright plumage. However, as well as possessing large relative brain sizes and high levels of urban tolerance (Maklakov et al., 2011), both traits which we found to be positively associated with the availability of impact data, the alien ranges of all but one of the 28 parrot species for which we have impact data are located in North America, Australasia, Europe or Singapore. These are highly developed regions of the world with capacity for research. Given that human development was found to be a predictor of data availability in univariate analysis (Table 1), it is difficult to determine the influence of conspicuousness alone as a factor driving research into alien birds. Further, we were unable to examine the effect of conspicuousness using the MCMCglmm model because conspicuousness in birds is a combination of several traits (such as their size, shape, colour, and the loudness/distinctiveness of their calls). Therefore the approach used (contingency tables) did not take into account the influence of phylogeny on these results, and neither could it account for covariation with other variables.

Conclusions

Our understanding of the impacts of alien birds remains compromised by the number of species that remain **DD**. This study represents one of the first attempts to identify those factors that influence the availability of impact data amongst alien birds. Whilst some of our results suggest that the impacts of many **DD** alien bird species may be minor (e.g. species with comparatively long residence times as aliens, such as the common waxbill and the Java sparrow), others suggest that data deficiency amongst alien birds may not be related to the severity of their impacts (e.g. species from orders of alien birds known to have damaging impacts but with comparatively small alien ranges, such as the New Caledonian crow (*Corvus moneduloides*)). It is therefore possible that we are overlooking the impacts of some **DD** alien birds. As the severity of impacts generated by alien birds have been found to vary from negligible, to causing declines in populations of native species and in some cases species extinctions, the next step is clearly to examine whether there are certain factors that influence the severity of impacts associated with alien birds for which impact data are available. Studies have looked at traits associated with the impacts of alien birds on a regional scale in Europe (Shirley & Kark, 2009; Kumschick & Nentwig, 2010; Kumschick et al., 2013) and Australia (Evans et al., 2014). However, such work has yet to be undertaken using a global dataset of alien bird impacts or using data from the recently published GAVIA database (Dyer et al., 2016). As such, this remains an area requiring further investigation, as it may help us to identify the types of species that are likely to have more severe impacts when introduced to novel locations, including those that are currently **DD**.

It may also provide further insights as to the factors that influence data availability amongst alien birds.

References

Aagaard, K. & Lockwood, J., 2014. Exotic birds show lags in population growth. *Diversity and Distributions*, 20(5), pp.547–554.

Baker, J., Harvey, K.J. & French, K., 2014. Threats from introduced birds to native birds. *Emu*, 114(1), pp.1–12.

Bellard, C. & Jeschke, J.M., 2015. A spatial mismatch between invader impacts and research publications. *Conservation Biology*, 30(1), pp.230–232.

Bellard, C., Cassey, P. & Blackburn, T.M., 2016a. Alien species as a driver of recent extinctions. *Biology Letters*, 12: 201506.

Bellard, C., Genovesi, P. & Jeschke, J., 2016b. Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences*, 283: 20152.

BirdLife International, 2017. *IUCN Red List for birds.* [Online] Available at: http://www.birdlife.org (accessed 20 February 2017).

Blackburn, T.M., Gaston, K.J. & Duncan, R.P., 2001. Population density and geographic range size in the introduced and native passerine faunas of New Zealand. *Diversity and Distributions*, 7, pp.209-221.

Bland, L.M. et al., 2012. Data uncertainty and the selectivity of extinction risk in freshwater invertebrates. *Diversity and Distributions*, 18(12), pp.1211–1220.

Bland, L.M. et al., 2015. Predicting the conservation status of data-deficient species. *Conservation Biology*, 29(1), pp.250–259.

Briggs, J.C., 2013. Invasion ecology: origin and biodiversity effects. *Environmental Skeptics and Critics*, 2, pp.73–81.

Butler, C.J., 2005. Feral Parrots in the Continental United States and United Kingdom: Past, Present, and Future. *Journal of Avian Medicine and Surgery*, 19(2), pp.142–149.

Capinha, C. et al., 2015. The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348(6240), pp.1248–1251.

Carrascal, L.M. et al., 2008. Explanations for bird species range size: Ecological correlates and phylogenetic effects in the Canary Islands. *Journal of Biogeography*, 35(11), pp.2061–2073.

Chevan, A. & Sutherland, M., 1991. Hierarchical partitioning. *American Statistician*, 45, pp.90–96.

Crooks, J.A., 2005. Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience*, 12(3), pp.316–329.

Duncan, R.P. et al., 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology*, 70, pp.621–632.

Dyer, E.E., Redding D.W. & Blackburn T.M., 2016. *The Global Avian Invasions Atlas – a database of alien bird distributions worldwide.* BIORXIV 090035.

Emery, N.J. & Clayton, N.S., 2004. The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes. *Science*, 306(5703), pp.1903–1907.

Evans, T. et al., 2014. Comparing determinants of alien bird impacts across two continents: Implications for risk assessment and management. *Ecology and Evolution*, 4(14), 2957–2967.

Evans, T., Kumschick, S. & Blackburn, T.M., 2016. Application of the Environmental Impact Classification for Alien Taxa (EICAT) to a global assessment of alien bird impacts. *Diversity and Distributions*, pp.1–13.

Fox, J., & Weisberg, S., 2011. *An {R} Companion to Applied Regression, Second Edition.* Thousand Oaks CA: Sage.

Fritz, S.A. & Purvis, A., 2010. Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24(4), pp.1042–1051.

Gaston, K.J. et al., 2000. Abundance-occupancy relationships. *Journal of Applied Ecology*, 37(S1), pp.39–59.

Grarock, K. et al., 2012. Is it benign or is it a Pariah? Empirical evidence for the impact of the common myna (Acridotheres tristis) on Australian birds. *Plos One*, 7(7), p.e40622.

Guay, P.J. et al., 2014. Hybridization between the mallard and native dabbling ducks: causes, consequences and management. *Pacific Conservation Biology*, 20(1), pp.41–47.

Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33(2), pp.1–22.

Hawkins, C.L. et al., 2015. Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). *Diversity and Distributions*, 21(11), pp.1360–1363.

Hoffmann, B.D. & Courchamp, F., 2016. Biological invasions and natural colonisations: are they that different? *NeoBiota*, 29, pp.1–14.

IUCN, 2016. *The IUCN Red List of Threatened Species.* [Online] Available at: http://www.iucnredlist.org/static/categories_criteria_3_1 (accessed 20 February 2017).

Joseph, L.N., Maloney, R.F. & Possingham, H.P., 2009. Optimal Allocation of Resources among Threatened Species: a Project Prioritization Protocol. *Conservation Biology*, 23(2), pp.328–338.

Kumschick, S. & Nentwig, W., 2010. Some alien birds have as severe an impact as the most effectual alien mammals in Europe. *Biological Conservation*, 143(11), pp.2757–2762.

Kumschick, S., Bacher, S. & Blackburn, T.M., 2013. What determines the impact of alien birds and mammals in Europe? *Biological Invasions*, 15(4).

Kumschick, S. et al., 2015. Ecological Impacts of Alien Species: Quantification, Scope, Caveats, and Recommendations. *BioScience*, 65(1), pp.55–63.

Kumschick, S. et al., 2017. Impact assessment with different scoring tools: How well do alien amphibian assessments match? *NeoBiota*, 33, pp.53–66.

Lefebvre, L., Nicolakakis, N. & Boire, D., 2002. Tools and Brains in Birds. *Behaviour*, 139(7), pp.939–973.

Lefebvre, L., 2013. Brains, innovations, tools and cultural transmission in birds, non-human primates, and fossil hominins. *Frontiers in Human Neuroscience*, 7, p.245.

Mac Nally, R., 1996. Hierarchical partitioning as an interpretative tool in multivariate inference. *Australian Journal of Ecology*, 21, pp.224–228.

Maklakov, A.A. et al., 2011. Brains and the city: big-brained passerine birds succeed in urban environments. *Biology Letters*, 7(5), pp.730–732.

Martin-Albarracin, V.L. et al., 2015. Impact of Non-Native Birds on Native Ecosystems: A Global Analysis. *Plos One*, 10(11), p.e0143070.

McCallum, D., 2005. *A conceptual guide to detection probability for point counts and other count-based survey methods. USDA Forest Service General Technical Report PSW-GTR-191.*

Menchetti, M. & Mori, E., 2014. Worldwide impact of alien parrots (Aves Psittaciformes) on native biodiversity and environment: a review. *Ethology Ecology & Evolution*, 26(2–3), pp.172–194.

Morgan, D., Waas, J.R. & Innes, J., 2006. The relative importance of Australian magpies (Gymnorhina tibicen) as nest predators of rural birds in New Zealand. *New Zealand Journal of Zoology*, 33(1), pp.17–29.

Myhrvold, N.P. et al., 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96(11), p.3109.

Orme et al., 2013. *Caper: Comparative Analyses of Phylogenetics and Evolution in R.*

Pârâu, L.G. et al., 2016. Rose-ringed Parakeet Populations and Numbers in Europe: A Complete Overview. *The Open Ornithology Journal*, 9(1), pp.1–13.

Parker, I., Simberloff, D. & Lonsdale, W., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1, pp.3–19.

Pyšek, P. et al., 2008. Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, 23(5), pp.237–244.

R Core Team, 2016. *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.*

Reif, J. et al., 2016. Linking habitat specialization with species' traits in European birds. *Oikos*, 125(3), pp.405–413.

Russell, J.C. & Blackburn, T.M., 2017. Invasive Alien Species: Denialism, Disagreement, Definitions, and Dialogue. *Trends in Ecology & Evolution*, 32(5), pp.312–314.

Ryall, C., 1992. Predation and harassment of native bird species by the Indian House Crow Corvus splendens, in Mombasa, Kenya. *Scopus*, 16, pp.1–8.

Sax, D.F. & Gaines, S.D., 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, 18(11), pp.561–566.

Sekercioglu, C.H. 2012. Functional extinctions of bird pollinators cause plant declines. *Science*, 331, pp.1019–1020.

Sekercioglu, C.H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology*, 153(Suppl. 1), pp.S153–S161.

Shirley, S.M. & Kark, S., 2009. The role of species traits and taxonomic patterns in alien bird impacts. *Global Ecology and Biogeography*, 18(4), pp.450–459.

Shultz, S. et al., 2005. Brain Size and Resource Specialization Predict Long-Term Population Trends in British Birds. *Proceedings of the Royal Society B*, 272(1578), pp.2305–2311.

Sol, D. et al., 2005. Big brains, enhanced cognition, and response of birds to novel environments. *PNAS*, 102(15), pp.5460–5465.

Sol, D. et al., 2007. Big-brained birds survive better in nature. *Proceedings of the Royal Society B*, 274(1611), pp.763–9.

Sol, D. et al., 2008. Brain Size Predicts the Success of Mammal Species Introduced into Novel Environments. *The American Naturalist*, 172, pp.S63–S71.

Sol, D. et al., 2012. Unraveling the Life History of Successful Invaders. *Science*, 337(6094), pp.580–583.

Walsh, C. & Mac Nally, R., 2013. *Hierarchical Partitioning. R package version 1.0-4.*

Wilson, J.R.U. et al., 2007. Residence time and potential range: crucial considerations in modelling plant invasion. *Diversity and Distributions*, 13, pp.11–12.

Wilson, J.R.U. et al., 2016. Biological invasions and natural colonisations are different – the need for invasion science. *NeoBiota*, 31, pp.87–98.

FIGURE LEGEND

Figure 1: The distribution of alien bird species that are Data Deficient (DD) or have impact data for (A) Alien range size; (B) Relative brain size; (C) Habitat breadth; (D) Human Development Index (HDI); (E) Number of realms occupied; (F) Residence time. DD species: n= 237, species with impact data: n=107. Jitter used to add random noise to data to prevent overplotting.

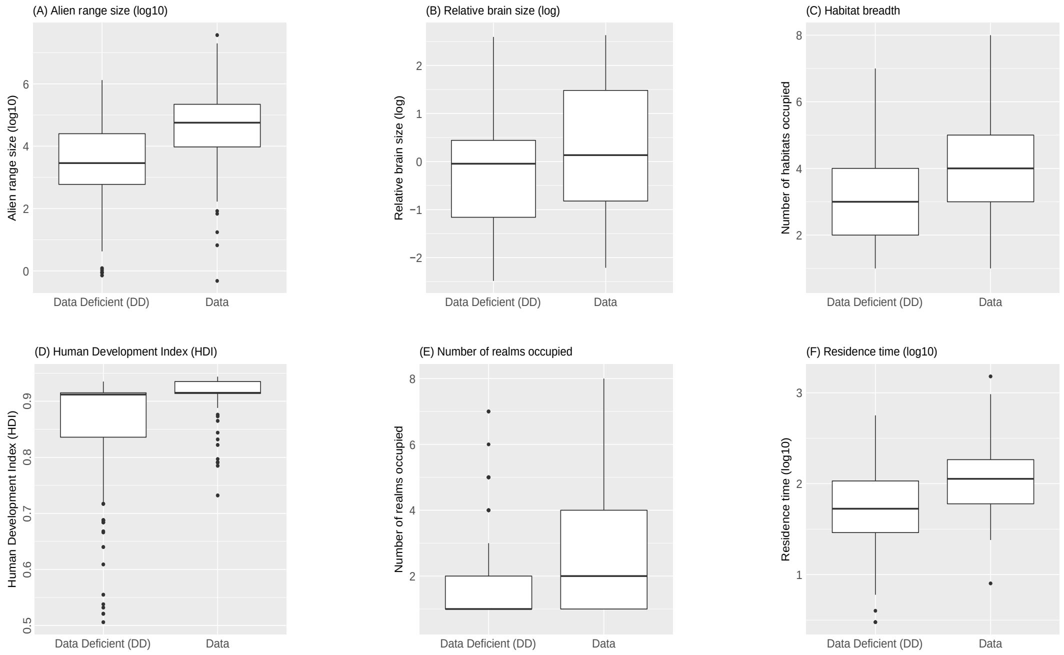

TABLE LEGENDS

Table 1: Univariate analysis undertaken using the MCMCglmm package in R (Hadfield, 2010), showing relationships between the availability of data on the impacts of alien birds and eight predictor variables. Total sample size = 344 species.

	DIC	**Post. mean**	**l-95% CI**	**u-95% CI**	**Eff. samp**	**pMCMC**
Alien range size	308.54	0.79	0.54	1.02	4519	< 0.001 ***
Body mass	375	0.54	0.09	0.10	9975	0.024 *
Brain size	366.3	0.57	0.19	0.95	7504	0.002 **
Diet breadth	370.22	-1.17	-2.39	0.13	9975	0.065
Habitat breadth	349.81	0.42	0.23	0.62	7040	< 0.001 ***
HDI	351.68	1.38	0.64	2.13	6388	< 0.001 ***
Number of realms occupied	303.91	0.73	0.50	0.97	4732	< 0.001 ***
Residence time	314.04	2.36	1.64	3.14	5821	< 0.001 ***

Iterations = 2501: 999901; Thinning interval = 100; Sample size = 9975. DIC = deviance information criterion; Post. mean = mean of posterior samples; l-95% CI and u-95% CI = lower and upper credible intervals; Eff. samp = effective sample size; pMCMC = p-value. Significance codes: '***' P < 0.001 '**' P < 0.01 '*' P < 0.05.

Table 2: Multivariate analysis undertaken using the MCMCglmm package in R (Hadfield, 2010), showing significant relationships (*P* < 0.05) between the availability of data on the impacts of alien birds and predictor variables (following model simplification).

	Post. mean	**l-95% CI**	**u-95% CI**	**Eff. samp**	**pMCMC**
Intercept	-5.92	-8.17	-3.69	3843	< 0.001 ***
Alien range size	0.41	0.12	0.70	7776	0.003 **
Brain size	1.01	0.49	1.59	4150	< 0.001 ***
Habitat breadth	0.24	0.01	0.48	6355	0.035 *
Number of realms occupied	0.33	0.07	0.59	6865	0.011 *
Residence time	1.36	0.53	2.19	6652	< 0.001 ***

Iterations = 2501:999901; Thinning interval = 100; Sample size = 9975; DIC = 268.38. DIC = deviance information criterion; Post. mean = mean of posterior samples; l-95% CI and u-95% CI = lower and upper credible intervals; Eff. samp = effective sample size; pMCMC = p-value. Significance codes: '***' P < 0.001 '**' P < 0.01 '*' P < 0.05.

Table 3: Contingency table (chi-squared test of independence) showing actual and expected numbers of species with and without impact data amongst conspicuous and inconspicuous alien bird families (χ^2 = 18.2, *df* = 1, *P* = 0.00002). Expected values are displayed in italics. Individual χ^2 values are displayed in (parentheses).

	Number of species without impact data (DD)	**Number of species with impact data**	**Total number of species**
Inconspicuous families	50	5	55
(Estrildidae, Fringillidae &	*38.54*	*16.46*	
Thraupidae)	(3.41)	(7.98)	
Conspicuous families	53	39	92
(Psittacidae, Psittaculidae	*64.46*	*27.54*	
& Phasianidae)	(2.04)	(4.77)	
Total	103	44	147