

FEATURE PAPER

Mammal and bird species held in zoos are less endemic and less threatened than their close relatives not held in zoos

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Abstract

Zoos and related institutions make important contributions to the conservation of global biodiversity. However, resource constraints have led to certain faunal groupings being better represented in *ex situ* breeding programmes than others. Some broad patterns of faunal representation in zoos have been identified, although finer-scale differences within taxonomical families remain poorly understood, as do the influence of many geographical and ecological factors. Using a novel paired-species comparison approach, we investigate for the first time how seven of these variables can influence the current representation of mammal and bird species in zoos. Using data from 550 high-quality zoos worldwide, we identified 165 mammal and 228 bird species held in zoos that could be paired with clearly identifiable closest relatives not currently held in zoos. These matched pairs were then compared for threat level, zoogeographical distribution (including global hotspot endemism), spatial range, body mass, island habitat and altitudinal range. Results indicate that mammal and bird species in zoos are, on average, not only larger than their close relatives not held in zoos, but also possess larger spatial ranges, are less likely to be endemic and are distributed in lower-risk geographical regions. Importantly, they also tend to be less, rather than more, threatened with extinction. Multivariate models confirm that many of these correlated predictors act independently. We suggest that key mechanisms which can increase the inherent conservation risk of mammal and bird species can also act as barriers to their representation in zoos, and that this may contribute to a disparity between where *ex situ* resources are spent and where they are most needed.

Introduction

It is widely recognized that anthropogenic activity is driving the rapid and historically unprecedented loss of biodiversity on our planet (Wilson, 1999; Barnosky *et al.*, 2011), with concomitant effort by society to mitigate and manage these losses. While *in situ* conservation strategies are generally considered preferable, being more cost-effective and having more beneficial impacts on an ecosystem scale (Balmford, Leader-Williams & Green, 1996), these face increasing challenges from escalating habitat destruction and fragmentation, and ineffectual management in many protected areas (Balmford *et al.*, 1996; Curran *et al.*, 2004). *Ex situ* conservation breeding programmes may therefore become increasingly important to the long-term survival of many species, especially larger vertebrates (Hutchins, Smith & Allard, 2003; Bowkett, 2009; Conde *et al.*, 2011).

Zoological collections and similar institutions (collectively referred to as 'zoos' henceforth) represent the most powerful agencies of *ex situ* conservation effort. Over 1300 organized zoos have internationally recognized breeding programmes, and the 760 International Species Information System (ISIS)-registered institutions hold more than 2 million organisms of nearly 10 000 species (ISIS, 2011; WAZA, 2011). Zoos have played a pivotal role in the protection (and subsequent recovery) of a number of endangered species, for example Mauritius Kestrel, Golden Lion Tamarin, Père David's Deer (Mallinson, 1995, 2003; Jiang *et al.*, 2000; Kleiman & Rylands, 2002). However, *ex situ* conservation programmes in zoos are limited because restrictions of space and resources only allow for a small percentage of global biodiversity to be afforded a captive breeding 'safety net', and the conflicting priorities of zoos have created a strong bias favouring certain taxonomic

groupings, particularly vertebrates (Rahbek, 1993). Similar disparities within the vertebrate phylum show a much better representation of birds and mammals than other classes (Balmford *et al.*, 1996; Conde *et al.*, 2011).

While these large-scale patterns are well known, little research has been conducted into taxonomic biases at lower taxonomic levels, into what variables affect representation, or the conservation implications of differential representation. A few patterns have been identified, with larger body size, 'charisma' and economic upkeep influencing the chance of a species being subject to a captive breeding programme (Frynta *et al.*, 2010a). However, most existing research has either focused on human preferences for particular species characteristics (Balmford *et al.*, 1996; Maresova & Frynta, 2008; Small, 2012) or has tested a limited range of variables based on small sample sizes (e.g. Born Free Foundation, 2007). Thus a large number of quantitative geographical and ecological variables that may exert an important influence on the likelihood of a species' inclusion in a zoo remain unexplored.

Here, using the well-studied mammals and birds (Sutherland, 2000) as test cases, we investigate how a broader range of geographic and ecological variables can help determine the likelihood of a given species being held in zoos. We take an explicitly comparative approach, pairing species held in zoos with close relatives not held in zoos, and test a set of relevant candidate variables across these pairs. We then discuss the conservation implications of the patterns we uncover by examining the extent to which the current representation of mammals and birds in zoos correlates with those species representing the highest global conservation priority.

Methods

Species pair construction

The core of our comparative approach is the production of phylogenetically independent matched pairs of species (Felsenstein, 1985). We first compiled a list of all mammal and bird species currently held in those zoos adhering to international standards of animal welfare and making a genuine contribution to captive breeding efforts. We defined these 'responsible' institutions as those with membership to the World Association of Zoos and Aquaria (WAZA), the European Association of Zoos and Aquaria (EAZA), the Association of Zoos and Aquaria (AZA) and the Zoo and Aquarium Association (ZAA), giving a sample of 550 institutions. All species held in these institutions were then listed using data from the ISIS (2011). For mammals, we obtained these data directly from the ISIS website. For birds, we obtained the data from the digitized copy of the ISIS holdings provided in Conde *et al.* (2011). Only species with at least one male and one female in at least one collection in our sample were considered.

We then used the most up-to-date mammal (Martyn *et al.*, 2012, based on Fritz, Olaf & Purvis, 2009, and Bininda-Emonds *et al.*, 2007) and bird (Jetz *et al.*, 2012)

supertrees to identify the sister species for each of these species not currently held in zoos. An initial search produced a sample of 647 mammal and 1183 bird 'in-zoos' candidate species and their 'not-in-zoos' closest relatives (these being a combination of true sister-species pairs, and pairs between single species and larger sister clades or between larger sister clades). We then excluded all 'in-zoos' species paired with an entire sister clade (as these clades were often very speciose), and species for which the closest 'not-in-zoos' relative was in a different taxonomic Order. Several 'in-zoos' species also shared the same 'not-in-zoos' closest relative. Here, we averaged the scored values of the 'in-zoos' species sharing the same 'not-in-zoos' species, to produce a single sister pair. We took mean averages of continuous variables and modal averages for categorical variables; where no mode was apparent, we chose randomly. We chose this 'values-averaging' approach as we believed this to produce more representative data than randomly choosing a single species that might be atypical compared with its other shared close relatives. This gave a sample of 165 closely related paired comparisons for mammals and 228 paired comparisons for birds.

We recorded the patristic distance (in millions of years) that separated each of our pairs as a covariate in our analysis, along with seven additional species-specific measures, outlined below.

Selection and scoring of variables

We scored body mass and six poorly studied but potentially important variables associated with being in a zoo. Importantly, we present alternate hypotheses for each variable here based on the projection that zoos may favour species representing the greatest conservation priority.

(1) International Union for the Conservation of Nature (IUCN) threat level: We hypothesize that species represented in zoos are more likely to be threatened than close relatives not kept in zoos (WAZA, 2005, 2011). We scored all species classified by the IUCN as Least Concern and Near-Threatened as '0', and all species classified as Vulnerable, Endangered, Critically Endangered or Extinct in the Wild as '1', based on data obtained from the IUCN website (IUCN, 2011). Analyses were repeated with mammal species classified as Data Deficient, once being scored as Least Concern and once being scored as at risk. No bird species in our dataset were classed as Data Deficient.

(2) Zoogeographical distribution: Species in economically less-developed parts of the world, especially the tropics, often possess higher extinction risk, on average, relative to species in more developed, temperate regions (Vamossi & Vamossi, 2008). We therefore hypothesize that species breeding in 'higher-risk' tropical zoogeographical zones (the South American, African and Oriental regions, scored as 0) will be better represented in zoos than their close relatives breeding in 'lower-risk' zones (Eurasian, North American, Australian and Antarctic, scored as 1). Species with ranges spanning both categories were also scored as 1. Zoogeographical distributions were determined using the IUCN

(2011) and BirdLife International (2012) databases, using boundaries defined by Cox (2001).

(3) Spatial range: We hypothesize that species with smaller spatial ranges will be better represented in zoos than those with wider spatial ranges. Range-restricted species tend to possess an elevated extinction risk, often being adapted to specific habitat niches and possessing narrow ecological tolerances, as well as being more vulnerable to localized habitat destruction and fragmentation (Pimm *et al.*, 1995). Spatial ranges for mammals were obtained from the PanTHERIA database (PanTHERIA, 2009) and from the additional sources in Supporting Information Appendix S1. Breeding extent spatial ranges for birds were obtained from BirdLife International (2012).

(4) Island endemism: We included this category to account for the representation of species endemic to islands, whose small spatial ranges (as described earlier) and associated ecological specialization and vulnerability produce an elevated extinction risk (Fordham & Brook, 2010). We therefore hypothesize that island endemics will be better represented than their continental relatives. Following data on the IUCN (2011) and BirdLife International (2012) databases, we scored all species found on continental landmasses as 0, and all species confined to island ecosystems as 1.

(5) Highland endemism: Highland endemics often display elevated extinction risk for similar reasons as island endemics, that is possessing small ranges and being adapted to narrow ecological niches, which are easily disrupted by habitat disturbance (Jankowski & Rabenold, 2007). Also, highland habitats often face higher rates of habitat degradation and fragmentation, and possess a higher risk from climate change than many lowland ecosystems (Cayuela, Golicher & Rey-Benayas, 2006; La Sorte & Jetz, 2010). We therefore predict that species in zoos are more likely than their close relatives to be highland endemics. We classed all species inhabiting habitats restricted to > 1000 m or above as montane endemics (1) and species with ranges below or spanning this threshold as not montane endemics (0). Altitudinal data were obtained from the IUCN (2011) and BirdLife International (2012) databases, and the additional sources in Supporting Information Appendix S1.

(6) Hotspot endemism: We hypothesize that species that are endemic to one or more of the Biodiversity 'Hotspots' defined by Myers (2003) and Conservation International (2011) to be better represented in zoos than non-hotspot endemics, as again, these species often possess small spatial ranges, high specialization and low ecological tolerance (Pimm *et al.*, 1995). Hotspot endemism was scored from the Conservation International database (2011), with species being classed as hotspot endemics (1) or not hotspot endemics (0).

(7) Body mass: Although this variable has been found to influence representation in zoos (Balmford *et al.*, 1996), it has never been tested as a predictive factor in a matched-pair setting. As in previous studies, we hypothesize larger-bodied species to be better represented than their smaller-bodied relatives, both because large-bodied species are predicted to be more popular exhibits, and because

larger species often possess an elevated extinction risk (Cardillo *et al.*, 2005). Mammal body masses were obtained from the PanTHERIA database (2009) and from additional sources in Supporting Information Appendix S1. Bird body masses were taken from Dunning (2007), with some additions using morphological measurements and genus level averages (W. Jetz, personal communication).

Statistical analysis

We first conducted a series of Z-tests (Zar, 1999) to ensure that scores in our matched-pair sample of 'in zoos' species were representative of all species in zoos for their Order. We compared the mean value of scores for our 165 mammal and 228 bird species samples with the mean values from the respective 647 mammal and 1183 bird candidate species grouped by taxonomic order (as defined by the IUCN, 2011). For each variable, 'in-zoos' species in our matched pairs found to be statistically unrepresentative of the total 'in-zoos' population for their order were excluded from further analysis.

Using our matched pairs, we performed simple sign tests (Zar, 1999) on our categorical variables. For continuous variables, we used randomization techniques to evaluate the average difference in our matched-pair comparisons against the null distribution produced by randomly swapping values within pairs 500 times, standardizing all differences by the square-root patristic distance between the species in a pair (Felsenstein, 1985).

In order to investigate the independent influence of our predictor variables, we first checked for correlations among them, and then used an information theoretic approach (Burnham & Anderson, 2002) to complete a full set of candidate phylogenetic general linear models (PGLS) for zoo presence/absence in the R-package caper (v. 0.5). We used all in-zoo species that we could pair with a unique sister species not in a zoo in these analyses (for a total of $n = 501$ mammal and $n = 612$ bird species). These models use the full phylogeny linking the matched pairs as the predicted error structure term rather than a matched pair design, and we expect that they may exhibit less power.

Results

Z-tests analysis showed that for most of our variables, our sample of 'in-zoos' species were representative of all species within their respective Orders held in zoos (Supporting Information Appendix S2). Only altitude scores for Carnivora ($P = 0.04$) and body mass scores for Insectivora ($P = 0.01$) suggested a non-representative sample in mammals. In birds, body mass scores for Gruiformes and Galliformes ($P \leq 0.05$), hotspot endemism scores for Gruiformes ($P = 0.01$), island endemism scores for Galliformes and Struthioniformes ($P \leq 0.05$), IUCN categories for Coraciiformes ($P \leq 0.05$), and spatial range data for Psittaciformes, Strigiformes, and Coraciiformes were non-representative (all $P \leq 0.05$).

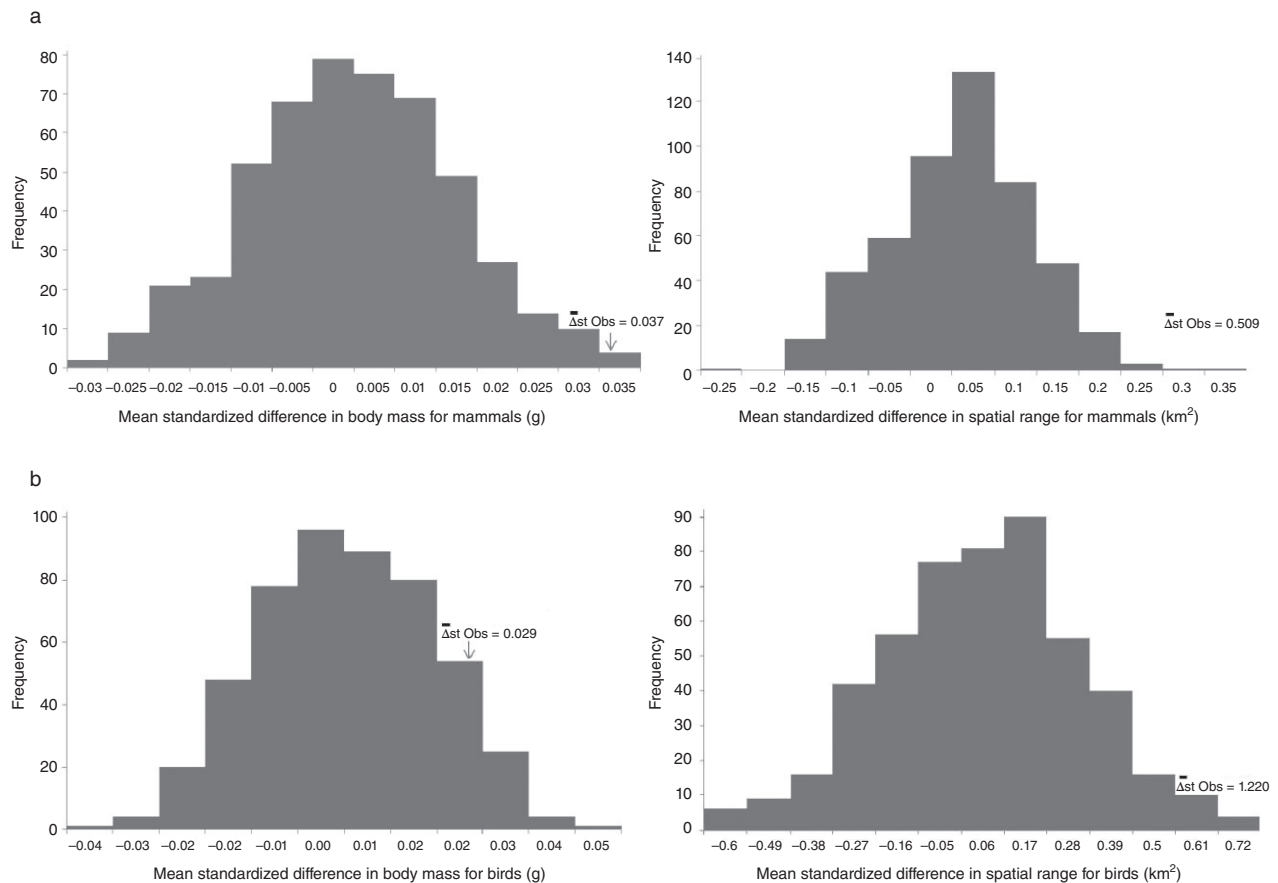


Figure 1 Null distributions based on randomizations of paired tip values of the mean standardized difference between (a) 'in zoo' and 'not in zoo' mammal species for body mass ($P \leq 0.01$) and spatial range ($P \leq 0.01$), and (b) 'in zoo' and 'not in zoo' bird species for body mass ($P = 0.03$) and spatial range ($P \leq 0.01$). Arrows indicate the observed mean standardized difference for each variable.

Table 1 Sign tests comparing differences between zoogeography, hotspot, high altitude and island endemism, and IUCN threat category values between 'in-zoos' and 'not-in-zoos' species pairs for mammals

Variable	n (+ difference)	n (– difference)	n (0 difference)	P -value
Zoogeography	11	1	153	< 0.01
Hotspot endemism	8	35	122	< 0.01
High-altitude endemism	3	15	112	< 0.01
Island endemism	3	18	139	< 0.01
IUCN category – DD as least concern	12	34	119	< 0.01
IUCN category – DD as endangered	12	44	109	< 0.01

Scores were tested using a 95% confidence interval. DD, data deficient; IUCN, International Union for the Conservation of Nature.

Figure 1a,b show comparisons of the observed mean standardized difference in body mass and spatial range between mammals and birds to the expectations based on the randomizations. Mammals and birds in zoos have both significantly larger body masses ($P \leq 0.05$ for both), and significantly larger spatial ranges ($P \leq 0.01$ for both) than their closest relatives not in zoos.

Results for the categorical variables are presented in Tables 1 and 2. Both mammal and bird species 'in zoos' are more likely to be considered not threatened (both $P \leq 0.01$) and to come from more economically developed regions

more often than their closest 'not in zoos' relatives (both $P \leq 0.01$). 'In zoos' species were also less likely to be endemic to high-altitude ecosystems (both $P \leq 0.01$), biogeographic hotspots (both $P \leq 0.01$) and islands (both $P \leq 0.01$) than 'not in zoos' relatives.

Correlations on our data among our predictor variables were low to moderate (all Pearson correlation coefficients < 0.7 , Supporting Information Appendix S3). Our best PGLS model [>3 Akaike information criterion (AICc) units over all others] for mammals included mass, altitude, range size and hotspot endemism. Five other models fell

Table 2 Sign tests comparing differences between zoogeography, hotspot, high altitude and island endemism, and IUCN threat category values between 'in-zoos' and 'not-in-zoos' species pairs for birds

Variable	<i>n</i> (+ difference)	<i>n</i> (– difference)	<i>n</i> (0 difference)	<i>P</i> -value
Zoogeography	29	7	192	< 0.01
Hotspot endemism	9	47	166	< 0.01
High-altitude endemism	4	22	202	< 0.01
Island endemism	6	34	168	< 0.01
IUCN category	4	25	191	< 0.01

Scores were tested using a 95% confidence interval. IUCN, International Union for the Conservation of Nature.

Table 3 Top six multivariate models based on AICc for predicting whether a mammal species is scored as 'in zoos' using phylogenetic general linear models

Mammal model	AICc
In.zoo ~ high altitude + mass + range + hotspot	956.7
In.zoo ~ range + mass + high altitude	960.2
In.zoo ~ island + mass + high altitude + IUCN threat + range + hotspot	960.7
In.zoo ~ island + mass + high altitude + IUCN threat + range + hotspot + zoogeography	962.1
In.zoo ~ island + mass + high altitude + range	962.1
In.zoo ~ island + mass + high altitude + IUCN threat + range	964.1

All these models fall within 10 AICc units of the best model. R^2 for these full models = 0.20; R^2 for the models ignoring phylogenetic covariance = 0.11. AICc, Akaike information criterion corrected; IUCN, International Union for the Conservation of Nature.

Table 4 Top five multivariate models based on AICc for predicting whether a bird species is scored as 'in zoos' using phylogenetic general linear models

Bird model	AICc
In.zoo ~ island + mass + high altitude + IUCN threat + range + hotspot + zoogeography	1465.3
In.zoo ~ island + mass + high altitude + IUCN threat + range	1474.9
In.zoo ~ island + mass + altitude + IUCN threat + range + hotspot	1475.8
In.zoo ~ range + mass + IUCN threat	1487.9
In.zoo ~ mass + hotspot + range + IUCN threat	1488.7

No other model fell within 10 AICc units of the best model. R^2 for the full top model = 0.52; R^2 for this model ignoring phylogenetic covariance = 0.13. Correlation coefficients between predictor variables are displayed in Supporting Information Appendix S3 and parameter fits in Supporting Information Appendix S4. AICc, Akaike information criterion corrected; IUCN, International Union for the Conservation of Nature.

within 10 AICc units of our best model (Table 3). For birds, the best model (>9 AICc units over all others) included mass, island, altitude, range size, threat score, hotspot endemism and zoogeographical zone (Table 4; we also report the top five models here). Supporting Information Appendix S4 includes the model parameters for the best models in Tables 3 and 4.

Discussion

Our results indicate that mammal and bird species in zoos are at once less threatened, have larger spatial ranges, and are less likely to come from high-risk ecosystems than their close relatives – that is, zoos house species of lesser, rather than greater, conservation priority. Factors other than conservation concern seem therefore important in determining which species are selected for *ex situ* conservation programmes and which are not. One key consideration that has been discussed previously is the often-conflicting roles of zoos as both centres of *ex situ* conservation and commercial visitor attractions, and how this bifurcation may influence which species they are most likely to support (Maresova & Frynta, 2008). Other studies have shown that large-bodied species are more likely to be held in zoos than smaller-bodied species as they make more popular exhibits, despite these larger animals being more expensive to keep and displaying lower breeding success than smaller-bodied species (Balmford *et al.*, 1996; Sitas, Baillie & Isaac, 2009; Smith *et al.*, 2012). Our results for mammals and birds support this view, and also suggest that a bias towards larger species not only applies to vertebrates in general, but also operates at small taxonomic scales, that is, between closely related species. A simple presentation of bias for large vertebrates may not fully explain this fine-grained pattern.

Our results also suggest that geographical isolation and ecological specialization might also be important in determining the likelihood of a given species being held in zoos. We found that, even after including body size as a variable, species with smaller spatial ranges and those restricted to biodiversity hotspots, high-altitude ecosystems, and islands were all less likely to be held in zoos than their more cosmopolitan close relatives. While it is unclear what role the geographical barriers that promote high incidences of endemism, such as those inherent in oceanic island and montane ecosystems, have as obstructions to collectors (both for zoos and for the pet trade), our results may suggest that the simple inaccessibility of small islands, high-altitude forests and other remote ecosystems may be predictors of species representation in zoos. Montane and island endemics are also often specialized to narrow ecological niches (Wijesinghe & Brooke, 2004; La Sorte & Jetz, 2010) and recreating their specialist requirements in captivity may prove challenging. Indeed, it is possible that if a zoo faces a choice of obtaining a lowland or continental species with simple requirements and a good breeding record, or a

closely related, superficially similar island or montane endemic that may be hard to obtain, difficult to keep, and with an unknown record of breeding success, the rational choice is to choose the former.

Our research also indicates that the zoogeographical distribution of mammal and bird species can have an influence on their representation in zoos. Species with breeding distributions falling entirely within the more economically developed North American, Eurasian and Australian zones are more likely to be held in zoos than their Oriental, African and South American close relatives. This could be because most 'responsible' zoos are distributed in the wealthier zoogeographical regions. It has been shown that most conservation funds are spent in their country of origin (James, Gaston & Balmford, 2001), which may result in the fauna of these zones being better represented, although the extent to which this applies to *ex situ* conservation rather than conservation as a whole requires further research. The appeal of large-bodied species may also be influential here, as average species mass increases in the higher latitudes, where the more developed zoogeographical regions lie (Ashton, Tracy & de Queiroz, 2000).

Results also show that, importantly, mammal and bird species in zoos tend to possess a lower IUCN threat level than their 'not-in-zoos' close relatives, at least in the matched-pairs test. This may be because of the correlations between body size, island endemism, range size and threat level (Vamossi & Vamossi, 2008; Fordham & Brook, 2010; La Sorte & Jetz, 2010).

Body mass and spatial range sizes are shown to be particularly strong predictors in our models, appearing in all top models for both birds and mammals. Interestingly, although zoogeographical zone was shown to be an important predictor in the matched-pair analysis, it did not appear to be as strong a predictor in the multivariate models. This may result from the large spatial scales of analysis reflected in this variable. Our two zoogeographical zone categories each span several continents and encompass an extremely large variability of habitats and species assemblages. Other variables, especially spatial range and the indicators of endemism, may therefore be heavily nested within these zones. While zoogeography may be strongly correlated with each of these other variables when compared individually, combined they present too great a variation in values and relative statistical weightings to act as powerful predictors of each other.

In conclusion, the results of this study support the view that conservation priority is not a strong variable influencing the inclusion or exclusion of closely related species in zoos, and that other considerations may contribute to a mismatch between where *ex situ* conservation resources are most needed and where they are spent. Our analysis suggests that body size and large (mainland) spatial ranges may be the most important of these driving factors. We suggest that the same geographical and ecological mechanisms that can increase the inherent conservation risk of mammal and bird species may also act as barriers to their representation in zoos, making them harder to obtain, potentially more diffi-

cult to keep in captivity, and less economically and logistically attractive than their more generalist relatives. We recognize though that the variables identified in this study as important influences on the likelihood of the inclusion of a species in zoos may differ from the most important drivers influencing the population sizes of species kept in zoos, or the number of zoos each species is kept in (Frynta *et al.*, 2013).

Our results may have important conservation implications, as they suggest that many of the world's most ecologically vulnerable species, particularly spatially restricted island and high-altitude endemics that often face the highest immediate extinction risk, may be overlooked by *ex situ* conservation planners in favour of their more widespread or easily obtainable relatives.

Our matched-pair study both corroborates and refines the previously reported findings that highly threatened species are often under-represented in zoos (Frynta *et al.*, 2010b; Conde *et al.*, 2011) by showing that this applies even at the level of close relatives. Our matched-pair study also considers for the first time the reasons why threatened species may be under-represented in zoos – as habitat, geographical distribution and endemism all may contribute, alone or in combination. These factors may also act as significant barriers to the inclusion of certain species in zoos. While targeting the threatened and under-represented species groups identified in this study may often be difficult, it should still be recommended that zoo planners carefully consider gaps in the current *ex situ* conservation network, and where possible work to ensure that resources are directed to the species with the most urgent need.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of additional sources used to complete the scoring of body mass, spatial range and montane endemism for species where this information could not be retrieved from the IUCN Redlist (2011) or the PanTHERIA (2009) and BirdLife International (2012) databases.

Appendix S2. Z-tests for representativeness of our subsample of matched-pair 'in zoos' species with all 'in zoos' species in their order for (A) mammals and (B) birds. Taxonomy followed IUCN (2011). Z indicates Z-score and P indicates probability value. We did not conduct Z-tests on Cetaceans for spatial range or island endemism because of lack of data. These gaps are marked 'X' in the table.

Appendix S3. Pearson product-moment correlations among our predictor variables for (A) mammals ($n = 501$) and (B) birds ($n = 612$) kept in zoos.

Appendix S4. Regression coefficient statistics for the best models describing zoo representation for (A) mammals and (B) birds. Positive coefficients mean that larger (or true) values of the predictor are associated with being represented in a zoo.