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ECOGRAPHY

Research article

Differential predation patterns of free-ranging cats among continents

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Co-evolutionary relationships associated with biogeographical context mediate the response of native prey to introduced predators, but this effect has not yet been demonstrated for domestic cats. We investigated the main factors influencing the vulnerability of prey species to domestic cat *Felis catus* predation across Australia, Europe and North America, where domestic cats are introduced. In addition to prey data from empirical records, we used machine-learning models to compensate for unobserved prey in the diet of cats. We found continent-specific patterns of predation: birds were more frequently depredated by cats in Europe and North America, while mammals were favoured in Australia. Bird prey traits were consistent across continents, but those of mammalian prey diverged, notably in Australia. Differences between prey and non-prey species included mass, distribution, and reproductive traits, except in Australian mammals where there was no evidence for a relationship between mass and the probability of being prey. Many Australian mammal prey also have a high extinction risk, emphasizing their vulnerability compared to European and North American counterparts. Our findings highlight the role of eco-evolutionary context in assessing predation impacts and also demonstrate the potential for machine learning to identify at-risk species, thereby aiding global conservation efforts to reduce the negative impacts of introduced predators.

Keywords: cat, co-evolution, machine learning, naivety, predation



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Introduction

Invasive predators have caused the decline and loss of many native species globally, particularly on islands (Medina et al. 2011, Doherty et al. 2019, Bellard et al. 2017). In many cases, native insular species are naïve to such predators and become easy prey for generalist invasive predators (Anton et al. 2020). Such relationships between invasive predators and naïve prey have long been of interest for understanding co-evolutionary processes and for quantifying and managing the impacts of invasive species (Sih et al. 2010, Anton et al. 2020). To understand the responses of naïve prey to invasive predators, several hypotheses and theories have been developed (reviewed by Carthey and Blumstein 2018). For example, relaxed predation theory explores how prey species in Australia respond to invasive predators, considering the marked differences in olfactory (Carthey et al. 2017) and visual cues (Edwards et al. 2021) exhibited by the continent's marsupial predators compared to those of introduced predators from Europe. However, recent research indicates that a predator's origin does not influence the capacity of native species to recognize it as a predator, suggesting that prey naivety might not increase a species' vulnerability to introduced predators (Anton et al. 2020). Moreover, small mammals are wary of mesopredators, regardless of the predator's origin, phylogenetic relatedness, or functional dissimilarities with native mammalian mesopredators (Wallach et al. 2022). Given these conflicting observations, the factors determining the vulnerability and naïvety of native species to introduced predators at broad scales remain unclear, especially on continents.

Originating in North Africa, free-ranging domestic cats *Felis catus* (Driscoll et al. 2007, Kitchener et al. 2017) have been introduced by humans to many regions of the world since the 16th century. They are now found on all continents except Antarctica, and have been introduced to many islands; cats now have the largest geographic range among terrestrial carnivores (Baker et al. 2010). The ecological impacts of *F. catus* are well-documented worldwide, with island fauna especially vulnerable (Medina et al. 2011, Doherty et al. 2019). However, the effects of *F. catus* on continents remain equivocal (Lynn et al. 2019, Woinarski et al. 2019), except in Australia where *F. catus* was introduced more recently (in 1788) (Abbott 2002). While massive killing of birds and mammals by *F. catus* has been documented both in North America (Loss et al. 2013) and Europe (Woods et al. 2003), there is still limited evidence of any ecological impact on populations of the depredated species there. Nonetheless, the prey diversity of *F. catus* has been well-documented in comparison to other species with broad geographic distributions and large diet breadths, like *Vulpes vulpes* or *Herpestes auropunctatus* (Middleton et al. 2021), and therefore provides sufficient resolution to study the impacts of this introduced predator on native fauna across ecological assemblages.

We used cats to explore how different co-evolutionary and biogeographical histories affect the prey–predator relationships of an introduced mammalian predator by identifying

which native fauna are depredated in three continents: Australia, Europe and North America. Considering the naïvety of Australian species (especially mammals) to felines, we hypothesized that cats would prey on a larger proportion of species, and over a greater diversity of traits, than observed in the feline-adapted European and North American prey assemblages.

To test this hypothesis, accurate identification of prey records is essential, but current datasets are incomplete, rendering it impossible to perform unbiased assessments. We addressed these limitations by constructing a comprehensive cat prey database by completing existing records from Europe, North America and Australia using a machine-learning classifier to predict likely (but undocumented) bird and mammal species eaten by cats. These expanded datasets allowed us to: 1) identify species traits associated with a high likelihood of predation by *F. catus* within continents, 2) compare these traits among European, North American and Australian prey assemblages, and 3) identify prey orders experiencing disproportionately high predation. We also assessed the proportion of threatened and non-threatened species in the diet of *F. catus* on each continent, shedding light on the implications of predation for native fauna conservation.

Material and methods

Building original datasets with cat-predation records

Following the methodology of Marino et al. (2021), we constructed a database encompassing all native bird and mammal species in Australia, Europe and North America. To ensure that we included only mainland species, we excluded all insular endemic species based on information from the IUCN database (2022) and BirdLife (2022). To identify species consumed by cats, we used the most comprehensive global diet database currently available for *F. catus* (Lepczyk et al. 2023). While this database might have limitations, such as being unable to distinguish true predation from scavenging, it remains the most complete and accurate resource for inferring predation patterns. Specifically, we focussed on prey records from continental locations, ensuring that they were identified at the species level. In cases where subspecies were involved, we considered only the entries at the species level. When the location was labelled 'continental and island,' we manually cross-referenced with the original articles to confirm continental predation and removed records for which we could not obtain confirmation. We then divided the listed native species of each continent into two categories: 1) prey species, those recorded as being consumed by *F. catus* in Lepczyk et al. (2023) filtered for continental records, and 2) species that were not recorded as prey. To be considered as prey of *F. catus* for a particular continent, a species had to be recorded as prey on that continent. The IUCN red list of threatened species category was reported for each species in the database (IUCN 2022). To focus only on extant species, we removed those categorized as 'Extinct' or 'Extinct

in the Wild.’ Subsequently, we categorized all species classified as ‘Vulnerable,’ ‘Endangered,’ or ‘Critically endangered’ in the Red List as ‘threatened’. We classified ‘Least concern’ and ‘Near threatened’ species as ‘not threatened’. This process resulted in six datasets: 691 birds and 257 mammals in Australia, 466 birds and 166 mammals in Europe, and 738 birds and 368 mammals in North America.

For each species, we collected a set of morphological, physiological and behavioural traits. For birds, we sourced seven traits from two databases: body mass (continuous), tail length (continuous), hand-wing index (continuous; this measure of wing shape is as a proxy for dispersal ability), trophic level (categorical: 0 = scavenger, 1 = herbivore, 2 = omnivore, 3 = carnivore), and primary lifestyle (categorical: insectorial, generalist, terrestrial, aerial, aquatic) from the AVONET database (Tobias et al. 2022); and habitat breadth (categorical: 1, 2, 3, 4, ≥ 5) and average clutch size (numeric) from Marino and Bellard (2023). We selected these traits based on their importance in predicting whether birds were eaten by *F. catus* (e.g. body mass, primary lifestyle; Woinarski et al. 2017), their relevance to anti-predator behaviour (e.g. hand-wing index, tail length, trophic level; Møller et al. 2014, Diaz et al. 2021), their role in influencing vulnerability to invasive species (Marino et al. 2021, Marino and Bellard 2023), and their implications for predicting prey–predator relationships more broadly (Gravel et al. 2013, Desjardins-Proulx et al. 2017, O’Connor et al. 2020, Kopf et al. 2021, Caron et al. 2022).

For mammals, we collected six traits: body mass (continuous), foraging niche (categorical: arboreal, ground, aerial, scansorial, generalist), habitat breadth (categorical: 1, 2, 3, 4, ≥ 5), trophic level (categorical: 1 = herbivore, 2 = omnivore, 3 = carnivore), activity period (categorical: nocturnal, diurnal and other) from Marino et al. (2021), and average litter size (continuous) from Soria et al. (2021). We chose these traits based on the same assumptions as for birds.

For both taxonomic groups, we defined habitat breadth as the number of different habitats where the species is found following the IUCN habitat classification scheme (ver. 3.1) (IUCN 2022). To evaluate the contemporary geographical range size of bird and mammal species across continents, we used spatial distribution data from BirdLife (2022) for birds and IUCN (2022) for mammals. We created a 10×10 km grid in the Mollweide projection to ensure equal-area cells, which avoids distortion across large regions. We overlaid species ranges onto the grid, and counted the number of cells occupied by each species within each continent.

We obtained traits for a total of 675 birds (98% of species) and 251 mammals (98% of species) in Australia, 441 birds (95% of species) and 162 mammals (98% of species) in Europe, and 707 birds (96% of species) and 363 mammals (99% of species) in North America.

Improving prey lists using machine learning

We assessed the sampling coverage of the six prey datasets by calculating rarefaction and extrapolation of species richness

coverage using the Hill number (order $q=0$) and the *estimateD* function in the ‘iNext’ R package (Chao et al. 2014, Hsieh et al. 2016). Coverage was 87% for birds in Australia and Europe, and 74% in North America; mammals had 90% coverage in Australia and Europe, and 85% in North America. To standardize the sampling effort across the datasets, we calculated the expected species richness at 90% coverage (Fig. 1) (*estimateD* from ‘iNext’) (Chao et al. 2014, Hsieh et al. 2016), which corresponded to the highest coverage across the six datasets. This method enabled optimal use of data without excessive extrapolation, which could inaccurately inflate estimates of species richness at high coverage (Roswell et al. 2021). These estimated coverages were similar to values in other studies using the same approach (Maucieri et al. 2023). The difference between the observed richness and the estimated richness at 90% coverage represents the number of species required to be reclassified as prey for each dataset. Next, we applied tree-based machine-learning algorithms for binary classification that are efficient models for predicting predation events using ecological and morphological traits and phylogenetic data (Llewelyn et al. 2023). Specifically, we used a gradient boosting framework implemented in R via the ‘xgboost’ package (Chen et al. 2015).

The traits we selected did not represent all dimensions of what can make a species likely prey for cats. We therefore incorporated phylogenetic information for potential prey species using phylogenetic eigenvectors to account for these

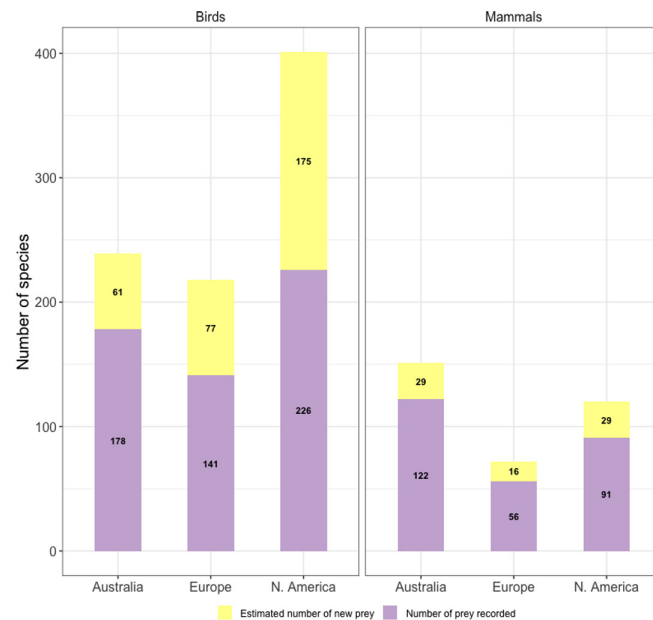


Figure 1. Number of species recorded as *Felis catus* prey and species assigned as prey by gradient boosting. Purple bars represent the number of continental birds and continental non-aquatic mammals recorded as prey in Lepczyk et al. (2023) in Australia, Europe and North America. Yellow bars represent the number of species needed to reach the expected species richness of each dataset at 90% coverage using coverage-based rarefaction and extrapolation curves with the Hill number $q=0$.

missing dimensions (i.e. as latent traits; Guénard et al. 2013). We extracted phylogenies for birds and mammals from www.VertLife.org and we calculated phylogenetic eigenvectors for all species using the 'MPSEM' (Guénard and Legendre 2022), 'ape' (Paradis and Schliep 2019) and 'phytools' (Revell 2012) R packages.

We adopted a bootstrap approach to assign the probability of each species depredated by *F. catus*, running 333 different optimized models for each of the six datasets. We used 333 models because this number offered a good compromise between computation time and the number of predictions of predation probability per species, ensuring that each species was predicted at least 50 times. This bootstrap process involved successively selecting 90% of species from each dataset randomly and splitting these subsets randomly into training (70% of species) and validation datasets (30% of species). We constructed each model using all the traits from the original datasets, ten phylogenetic eigenvectors, and the geographic range of species as predictors. We optimized three hyperparameters (i.e. learning rate, maximum depth of tree, and maximum number of boosting iterations for each model) using grid search, and we selected the model that minimized the log loss function. For each of the 333 models, we derived probabilities of being prey for the species found in the validation dataset, resulting in mean values between 0 and 1. To increase the number of prey species for birds and mammals in the three continents to achieve the estimated 90% coverage, we identified species that had not been recognized as cat prey, but which were considered likely candidates based on the probability attributed by the models (Fig. 1). Rather than adopting a uniform and arbitrary probability threshold (usually set at 0.5) for inclusion, we ranked species according to their probability of cat predation determined by our model (Supporting information). We based the inclusion criteria on this ranking only, without considering specific probabilities. We then added as many species (starting with the species with the highest probability of predation) as necessary to achieve the pre-defined 90% coverage (Fig. 1). As a result, we classified species as prey if they were either (a) found in *F. catus* prey records or (b) shifted to the prey category based on the predicted machine-learning ranking. Species that had not been recorded as prey and were not shifted after the reclassification step remained categorized as non-prey. For each of the 333 optimized models obtained from the bootstrap, we also computed the area under the receiver operating curve (AUC), accuracy, F1 score, Matthews correlation coefficient, sensitivity, and specificity from these models to evaluate goodness of fit.

We evaluated the contribution of each predictor by calculating the mean absolute Shapley importance scores (SHAP) using the 'fastshap' R package (Greenwell et al. 2023), which is model-agnostic. For each bootstrapped dataset, we averaged the mean absolute SHAP of the predictors across 333 models using the *sv_importance* function in the 'shapviz' R package (Mayer 2024). Due to the small sample sizes, the model-agnostic SHAP method included all observations in each dataset (Lundberg and Lee 2017). We chose the SHAP

approach for its unified measure of predictor importance, applicable across different algorithms, enabling comparison of their characteristics. Additionally, we visualized the marginal effect of each variable by plotting the covariate against its corresponding SHAP for each observation, showing how each predictor influences model outputs (Supporting information).

We also compared the species predicted as prey, the goodness of fit, and the importance of predictor variables from the gradient boosting framework to those derived from applying a random forest algorithm using the *randomForest* function in the 'randomForest' R package (Liaw and Wiener 2002).

Comparing prey species within and among continents

Tree-based machine-learning algorithms, despite their higher accuracy compared to generalized linear models (Pichler et al. 2020), can be difficult to interpret because these algorithms does not provide direct relationships between predictors and the probability of a species being prey. To identify the traits with the highest influence on the predictions of our bootstrapped models, we selected the predictors with the highest mean absolute SHAP and checked for collinearity between those selected predictors. We focused on weakly correlated predictors to avoid redundancy between the different analyses. To evaluate collinearity among the selected predictors, we developed a generalized linear model using the *glm* function in R, with prey status (prey versus not prey) as the dependent variable and each predictor as an independent variable. We assessed the variance inflation factor for each predictor using the *check_collinearity* function from the 'performance' R package (Lüdtke et al. 2021). If a predictor in the model exhibited a variance inflation > 2 (indicating collinearity), we removed one of the collinear variables. We repeated this process until we achieved a set of variables that did not exhibit collinearity. We did not include phylogenetic eigenvectors due to the difficulty of linking them to identifiable traits.

To compare geographic ranges among continents, we standardized by dividing the geographic range of each species by the maximum value of the geographic range of a species in the same continent. Additionally, when the distribution of a trait was non-Gaussian, we normalized using a square-root or \log_e transformation for subsequent tests.

To compare trait values between prey and non-prey species across and within continents, we employed different regression analyses according to the nature of each trait. We applied ordinal regression using the *polr* function from the 'MASS' R package (Ripley et al. 2013) for habitat breadth, an ordered integer. We applied beta regression to the square-root transformed geographical range, a continuous variable constrained between 0 and 1, using the *betareg* function from the 'betareg' R package (Cribari-Neto and Zeileis 2010). We used linear regression for all other (continuous) traits with the *lm* function from the 'stats' R package (www.r-project.org). Each model included continent and prey status as interacting independent variables, with the trait value as the dependent variable, modelled as:

trait ~ prey status + continent + prey status × continent (1)

We examined residual diagnostics for all models using Q-Q plots (details in the Supporting information). To identify the top-ranked model, we compared the saturated model (1) to less-complex models using all possible combinations of its independent variables (details in the Supporting information), with evaluations based on their Akaike information criterion weights ($wAIC$) and the proportion of deviance or variance they explained. The proportion of variance explained corresponded to the R^2 for the linear regressions and the proportion of deviance explained corresponded to Mcfadden's pseudo R^2 for other regressions. We used the $wAIC$ (~ model probability) and deviance or variance explained to evaluate the relative likelihood of the interaction effect by indicating support for the saturated versus less-complex models. This analysis tested whether the relationship between species status and a trait varied among continents. Based on the saturated model (1), we then used pairwise comparisons between continents and prey status using the *pairs* function from the 'emmeans' R package (Lenth and Lenth 2018) to quantify the magnitude of the difference in trait values between groups of species. Hereafter, we refer to $\Delta all_{continent}$ when comparing prey and non-prey groups of species in a continent, and $\Delta prey_{continent A - continent B}$ when comparing prey species between two continents, based on pairwise comparisons.

For birds, we assessed the vulnerability of orders among continents by calculating Spearman's ρ , and the number of prey species per order. We focussed on the number of species and not the proportion of prey per order to avoid the extreme sensitivity of results imposed by orders with few species. Due to few common orders between continents, we did not assess the vulnerability of orders between continents for mammals.

Results

Prey species prediction with gradient boosting

The 90% coverage-based rarefaction and extrapolation indicated the need to add putative *F. catus* prey species. For birds, 61, 77 and 175 species needed to be added to the prey lists for Australia, Europe and North America, respectively; for mammals, 22, 16 and 29 species were needed for these regions (Fig. 1). In these standardized datasets that contained prey from empirical records and predicted by supervised machine learning, we observed differences between birds and mammals and among continents in terms of the proportion of species that cats depredate. In Australia, the percentage of species that were putative prey was 59% (151 of 257) for mammals, which was higher than for birds (35%; 239 of 691). In contrast, 43% (72 of 166) of mammal species and 47% (218 of 466) of bird species were prey in Europe; and 33% (120 of 368) of mammal species and 54% of bird species (401 of 738) were prey in North America (Fig. 1).

Bootstrapping revealed good predictive power for both taxa, with a mean AUC > 0.77 for birds and > 0.85 for mammals

in the three continents (standard deviations of AUC scores computed from the 333 optimized models < 0.07). The other metrics of goodness of fit confirmed these results for both taxa and all the continents (Supporting information).

For birds, bootstrapping showed that geographical range size, hand-wing index, body mass, beak length nares, tail length, and clutch size were the most important predictors to classify a species as prey in the three continents, ranging from 0.21 to 0.012 (Supporting information). Phylogenetic eigenvectors had a small effect on the models, with a mean absolute SHAP ranging from 0.026 to 0.0094 (Supporting information).

For mammals, geographical range size, litter size, body mass, and habitat breadth were the most important predictors for classifying a species as prey in the three continents, ranging from 0.24 to 0.020 (Supporting information). Phylogeny had a larger effect than for birds, with a mean absolute SHAP for eigenvectors ranging from 0.047 to 0.010 (Supporting information). The results from the random forest were similar to those from 'xgboost' (Supporting information).

Traits of prey species within and among continents

For birds, the variance inflation analysis indicated collinearity between $\log_e(\text{body mass})$, tail length, and $\log_e(\text{beak length nares})$ ($VIF > 2$); we therefore show results only for $\log_e(\text{body mass})$ (Supporting information). For each analysed trait, models that incorporated the interaction between prey status and continent as independent variables demonstrated superior goodness of fit, indicated by the highest $wAIC$ and percentage of deviance or variance explained (Supporting information). This indicated that the relationship between bird vulnerability and trait values differs across continents. Nonetheless, there were some consistent differences between prey and non-prey bird species across continents. Compared to non-prey species, prey species had greater geographical ranges ($\Delta all_{AUS} = 0.34 \pm 0.019$, $\Delta all_{EUR} = 0.37 \pm 0.022$, $\Delta all_{NAM} = 0.27 \pm 0.017$) and $\log_e(\text{clutch size})$ ($\Delta all_{AUS} = 0.26 \pm 0.042$, $\Delta all_{EUR} = 0.29 \pm 0.050$, $\Delta all_{NAM} = 0.39 \pm 0.040$), and lower hand-wing indices ($\Delta all_{AUS} = -2.75 \pm 1.21$, $\Delta all_{EUR} = -8.71 \pm 1.43$, $\Delta all_{NAM} = -13.87 \pm 1.14$) and $\log_e(\text{body mass})$ ($\Delta all_{AUS} = -0.56 \pm 0.14$, $\Delta all_{EUR} = -1.13 \pm 0.16$, $\Delta all_{NAM} = -1.43 \pm 0.13$) (Fig. 2, Supporting information). For each continent, prey tended to be more similar to each other in terms of their traits than they were to the non-prey species of the same continent ($\Delta prey_{EUR-NAM} = 4.36 \pm 1.28$, $\Delta prey_{EUR-AUS} = 3.39 \pm 1.42$, $\Delta prey_{NAM-AUS} = -0.97 \pm 1.23$ for hand wing index; $\Delta prey_{EUR-NAM} = 0.38 \pm 0.15$, $\Delta prey_{EUR-AUS} = 0.17 \pm 0.16$, $\Delta prey_{NAM-AUS} = -0.22 \pm 0.14$ for $\log_e(\text{body mass})$, and $\Delta prey_{EUR-NAM} = 0.11 \pm 0.044$, $\Delta prey_{EUR-AUS} = 0.41 \pm 0.049$, $\Delta prey_{NAM-AUS} = 0.30 \pm 0.043$ for $\log_e(\text{clutch size})$).

The similarities between bird prey species were confirmed at the phylogenetic level by the similarity of orders' vulnerability (i.e. proportion of species recorded as prey per order) across continents (Fig. 4A). Specifically, there was a strong correlation between Europe and North America in terms of

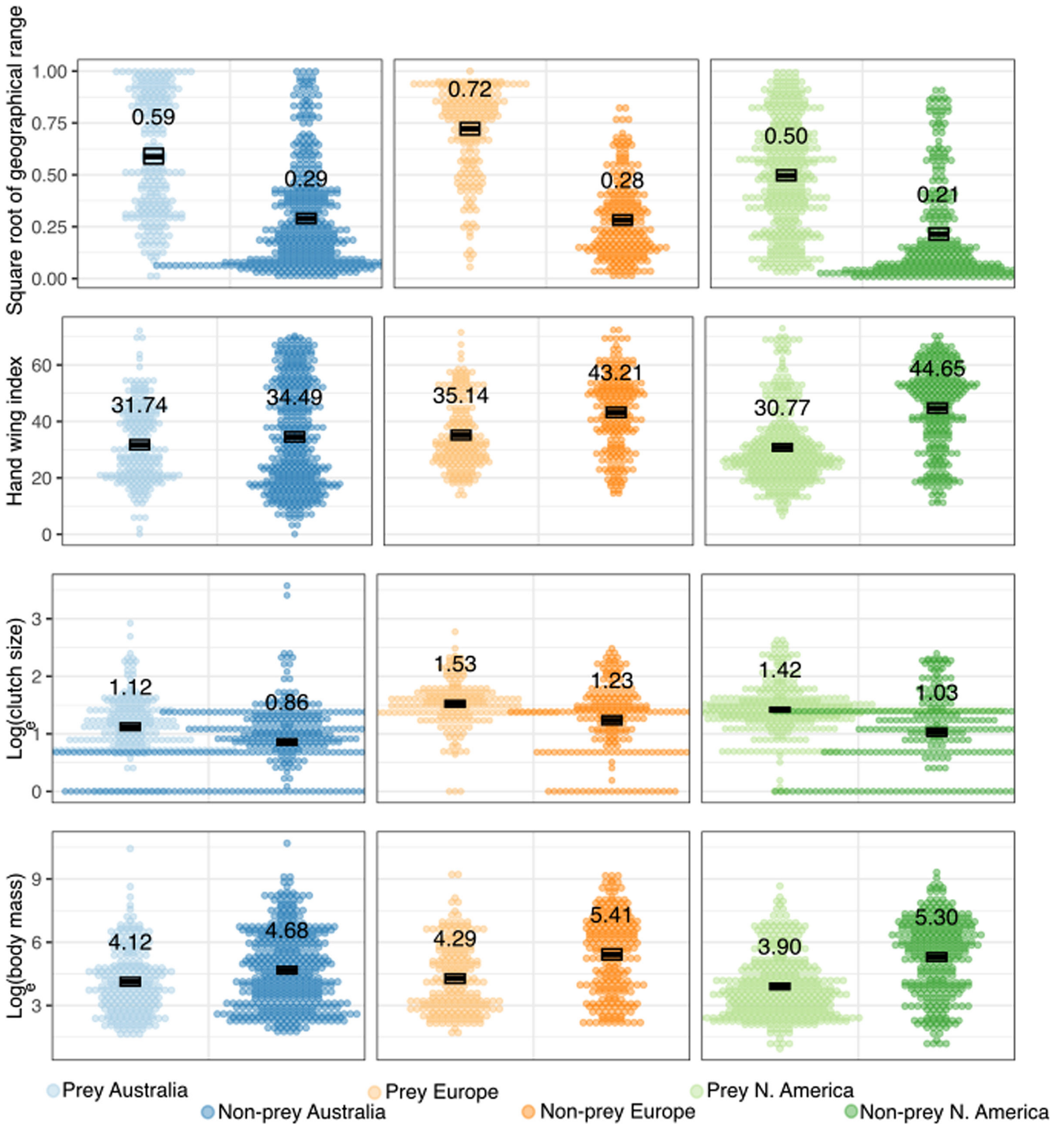


Figure 2. Distributions of bird species traits between prey and non-prey of *Felis catus*. Dots represent Australian (blue), European (orange), and North American (green) species. Darker-coloured dots represent non-prey species (neither found in *F. catus* prey records nor predicted as prey). Light dots represent prey species (either found in *F. catus* prey records or predicted as prey). Boxes illustrate the mean and bootstrapped confidence interval of both non-prey and prey species within each continent. The selection of traits for birds was based on their importance as predictors for classifying prey records using the gradient-boosting algorithm. Numbers represent the mean of each species group.

vulnerability to cat predation ($\rho=0.93$, $p < 0.001$) and a moderate correlation between Australia and North America, and Australia and Europe ($\rho=0.65$, $p=0.003$; and $\rho=0.66$, $p=0.003$, respectively). Among birds, many Passeriformes were prey species, including 128 species in Australia, 113 in

Europe, and 244 in North America. However, vulnerability differed among continents for this order. Passeriformes were more vulnerable in Europe and North America, with > 64% of species predicted as cat prey, compared to < 41% in Australia. In Australia, parrots (Psittaciformes) were highly

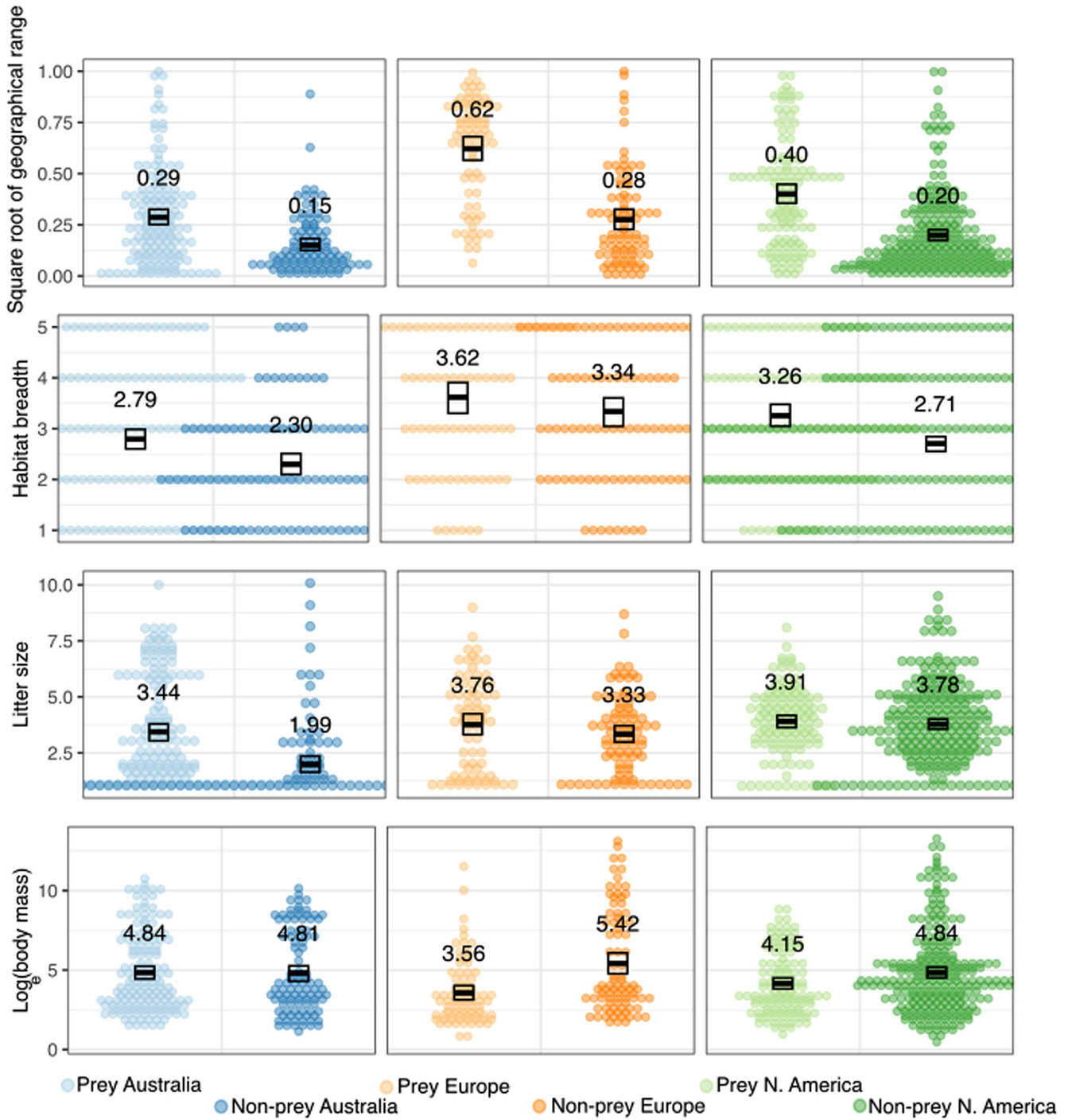


Figure 3. Distributions of mammal species traits between prey and non-prey of *Felis catus*. Dots represent Australian (blue), European (orange), and North American (green) species. Darker-colored dots represent non-prey species (neither found in *F. catus* prey records nor predicted as prey). Light dots represent prey species (either found in *F. catus* prey records or predicted as prey). Boxes show means and their bootstrapped confidence intervals for both non-prey and prey species within each continent. The selection of traits for mammals was based on their importance as predictors for classifying prey records using the gradient-boosting algorithm. Numbers represent means for each species group.

vulnerable to cat predation, with 73% (n = 38) of parrot species predicted as prey.

For mammals, models including interactions between prey status and continent typically demonstrated superior goodness of fit, except for habitat breadth where the model

that did not include an interaction between prey status and continent performed best Fig. 3 (Supporting information). Mammal prey were smaller than, but had similar litter sizes to non-prey in Europe and in North America ($\Delta all_{EUR} = -1.86 \pm 0.40$, $\Delta all_{NAM} = -0.69 \pm 0.28$ for \log_{10} body mass, and

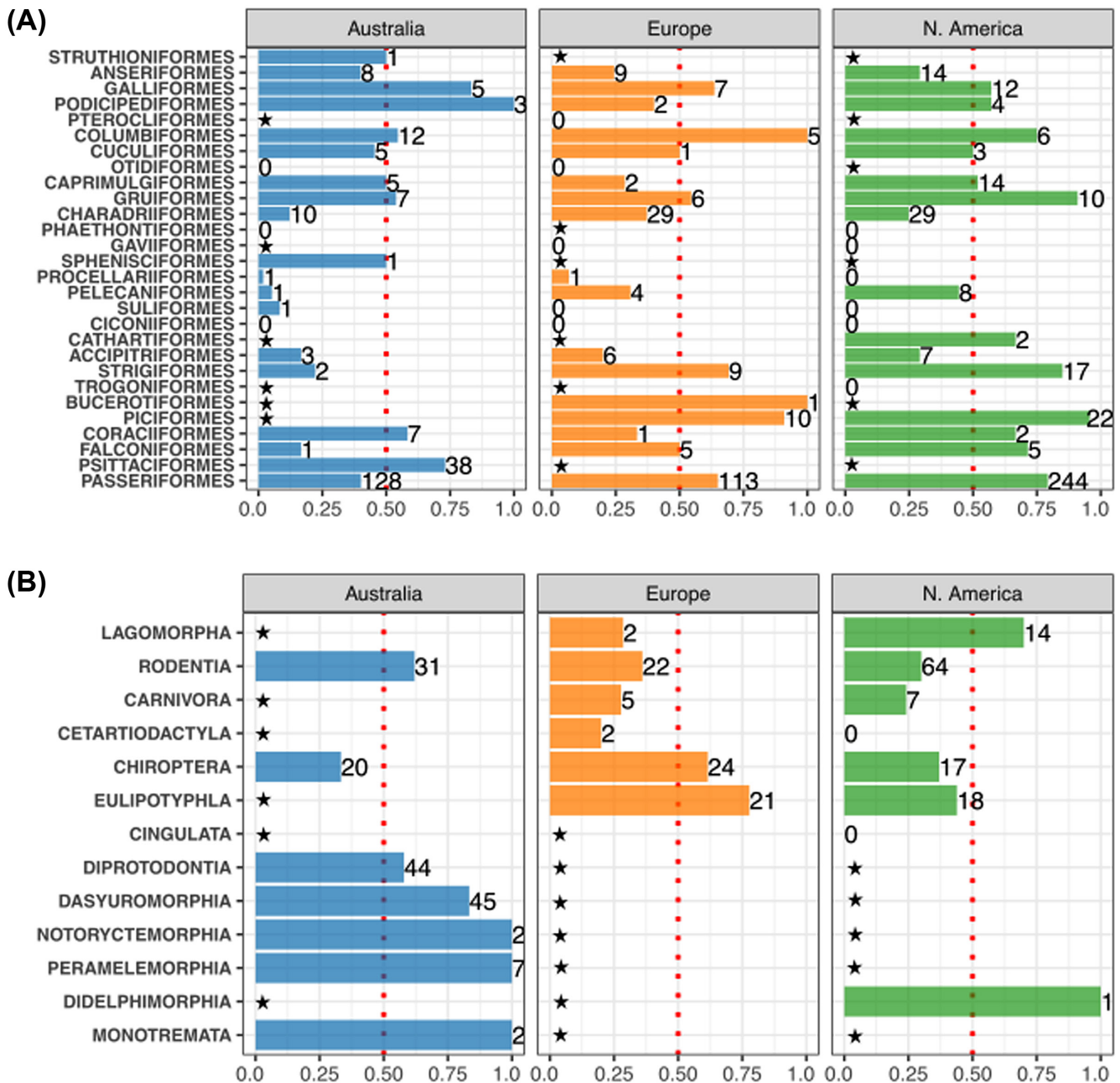


Figure 4. Proportion of species in mammal and bird orders that are *Felis catus* prey in Australia, Europe and North America. (A) Prey proportions across continental bird orders, (B) prey proportions across continental non-aquatic mammal orders. Each bar represents the proportion of species predicted as prey per order based on whether the species were found in *F. catus* prey records or predicted as prey by the machine-learning model. Numbers along bars indicate the count of unique species predicted as prey within that order. The dotted red lines indicate the point at which 50% of species within an order are predicted as prey. Orders that surpass this threshold have more species that are preyed on by *F. catus* than those not preyed on by *F. catus*. Black stars indicate the absence of species from that order on the continent.

$\Delta all_{EUR} = 0.43 \pm 0.30$, $\Delta all_{NAM} = 0.13 \pm 0.21$ for litter size). In Australia, prey and non-prey species had similar mean body mass, but prey had higher litter sizes ($\Delta all_{AUS} = 0.027 \pm 0.33$ for \log_e body mass and $\Delta all_{AUS} = 1.45 \pm 0.25$ for litter size) (Supporting information). For geographical range and habitat breadth, similar differences between prey and non-prey emerged across the continents ($\Delta all_{AUS} = 0.097 \pm 0.026$, $\Delta all_{EUR} = 0.31 \pm 0.037$, $\Delta all_{NAM} = 0.15 \pm 0.026$ for

geographical range, and $\Delta all_{AUS} = 0.70 \pm 0.23$, $\Delta all_{EUR} = 0.45 \pm 0.29$, $\Delta all_{NAM} = 0.78 \pm 0.20$ for habitat breadth). Prey mammals within each continent tended to be more similar to each other than to non-prey species from the same continent ($\Delta prey_{EUR-NAM} = -0.60 \pm 0.37$ for \log_e body mass and $\Delta prey_{EUR-NAM} = -0.14 \pm 0.28$, $\Delta prey_{EUR-AUS} = 0.32 \pm 0.27$, $\Delta prey_{NAM-AUS} = 0.47 \pm 0.23$ for litter size). However, an exception to this pattern was observed in Australia where prey mammal

species were more similar to non-prey species in terms of body mass, compared to the differences observed in their European and North American counterparts ($\Delta\text{prey}_{\text{EUR-AUS}} = -1.28 \pm 0.36$, $\Delta\text{prey}_{\text{NAM-AUS}} = -0.69 \pm 0.31$ for \log_e body mass).

All Australian taxonomic orders were vulnerable to predation. Chiroptera had the lowest proportion of species classified as prey (33%; 20 species). In contrast, marsupials had a high vulnerability, especially Dasyuromorphians (83%; 45 species) and Peramelemorphians (100%; 7 species) (Fig. 4B). All Monotremata and Notoryctemorphia were predicted to be prey (but there are only two species in each of these orders in Australia). In Europe, Eulipotyphla and Chiroptera were the most vulnerable orders, with 21 and 24 prey species corresponding to 77 and 61% of the species in these orders, respectively. In North America, Lagomorpha was the most affected order (70%; 14 species).

Conservation implications of cat predation across continents

For birds, we observed similar partitioning of threatened species in prey species group and non-prey species group across continents, but with a lower proportion of threatened species in the prey group (3.3–3.8% of threatened birds) compared to the non-prey group (10.1–11.7% of threatened birds) (Fig. 5). For mammals, we observed the same pattern, but Australia had a higher proportion of threatened species in the prey group (17.9%; Fig. 5) than in Europe and North America (6.6%). Australia also had a high proportion of threatened mammal species in the non-prey group (26.0%), similarly to Europe (24.4%), but unlike North America (9%) (Fig. 5).

Discussion

We investigated ecological differences among the prey species of *F. catus* across three continents by combining existing literature on global cat prey records with predictions obtained through machine-learning techniques. We found similarities in morphological and ecological traits, geographical range sizes and phylogeny among the prey species across Australia, Europe and North America. For birds, small species with large geographical ranges and large clutch sizes had a higher probability of being recorded as prey of *F. catus* on all continents. For mammals, body masses and litter sizes varied across regions. Among Australian mammals, mean body mass was similar for prey and non-prey species, whereas prey species had larger litter sizes compared to non-prey species. We did not observe this pattern in Europe or North America where prey mammals were smaller than non-prey mammals and had the same litter sizes as non-prey mammals. We also identified patterns of phylogenetic vulnerability in *F. catus* prey across continents. Parrots, which are absent from Europe and North America, were the species most likely to be victim to cat predation among the different orders in Australia. Passeriformes and Piciformes were the most vulnerable bird orders in Europe

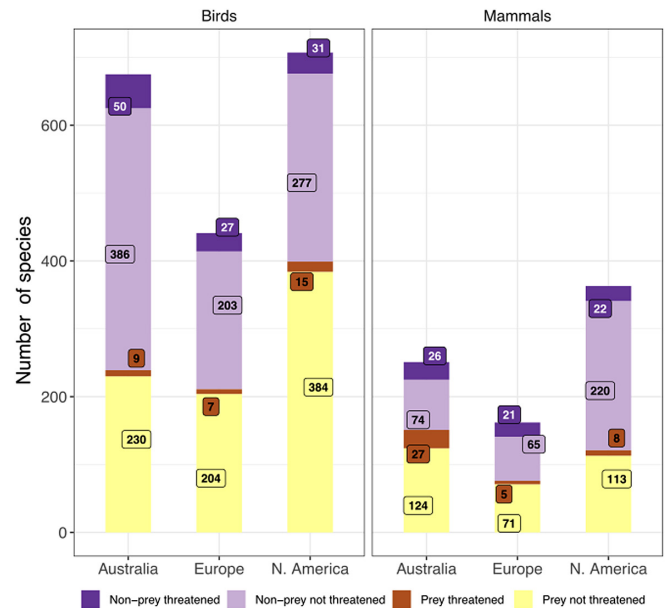


Figure 5. Number of threatened species among prey and non-prey species of *Felis catus*. Yellow and orange bars represent prey species, including species either found in *F. catus* prey records or predicted as prey by the machine-learning model. Purple bars represent non-prey species (neither found in *F. catus* prey records nor predicted as prey). Orange and darker purple indicate species categorized as *threatened* in the IUCN Red List (Vulnerable, Endangered or Critically endangered). Lighter colours represent non-threatened species (Least concern or Near threatened). Numbers show the number of species in each group.

and North America according to the same criteria (Fig. 4a). For mammals, endemic Australian marsupials were highly vulnerable to *F. catus* predation (Fig. 4b), which is consistent with previous findings (Edwards et al. 2021).

Novelty as a hypothesis for different predation patterns

Australia is a continental island with lineages that have evolved in the absence of felid predators. Discounting the dingo *Canis dingo*, a canid predator that was introduced to Australia about 4000 years ago, there is currently only one large (~ 6.1 kg; Bradshaw et al. 2021) endemic mammalian predator in Australia (devil *Sarcophilus harrisii*, now restricted to the island of Tasmania). Thylacines *Thylacinus cynocephalus* – thought to have had similar ecological traits as canids (Rovinsky et al. 2021) – went extinct in mainland Australia about 3200 years ago (White et al. 2018), and with *S. harrisii*, were the only large mammalian predators in Australia that survived the Late Pleistocene pulse of megafauna extinctions (Bradshaw et al. 2021). Native dasyurid quolls *Dasyurus maculatus* share some dietary overlap with *F. catus* (Glen et al. 2011), suggesting quolls are endemic Australian predators potentially exerting similar co-evolutionary pressures on native species. However, their likely use of different visual and olfactory cues, along with distinct hunting methods, suggest that their predation pressure is substantially lower and

different to that of *F. catus*. (Moseby et al. 2022). Although other large mammalian predators have been introduced to Australia, including the dingo and the European red fox *V. vulpes*, recent literature has identified *F. catus* as the most novel mammalian predator ‘archetype’ of Australian invasive species (Banks et al. 2018, Edwards et al. 2021). In contrast, native *Felis* spp. are endemic to Europe and are sympatric with two other feline species (*Lynx lynx* and *L. pardinus*). In North America, while there are no endemic species of *Felis*, there are two genera and three species of endemic felines: *L. canadensis*, *L. rufus* and *Puma concolor*. The unique predation patterns of *F. catus* on Australian mammals compared to Europe or North America are therefore likely attributable to the cat’s higher evolutionary novelty in Australia. According to the ‘relaxed’ predation theory (Edwards et al. 2021), marsupial species (especially those > 2 kg) are particularly vulnerable to new predators larger than quolls due to the absence of coevolution with this type of predator. This could account for the higher average body mass of mammalian prey of cats in Australia and the vulnerability to predation of many species within orders like Diprotodontia. Although global studies (Edwards et al. 2021, Wallach et al. 2022) indicate that mammals generally recognize both native and introduced predators, research has mainly focussed on smaller mammals, and there is a concordant lack of data on the response of larger species (Edwards et al. 2021). Furthermore, cats in Australia might prey upon juveniles of larger species, and our approach did not identify whether predation occurred on juveniles or adults, or even whether a record referred to scavenging only. Thus, juveniles of the largest Australian marsupial would show body mass and other traits compatible with cat predation, whereas this would not be the case in Europe or North America where juveniles of the species with the largest body mass would be too big and/or have other traits not compatible with cat predation. Other factors, such as landscapes more conducive to cat hunting, or a mismatch between anti-predator behaviours of Australian mammals and cat hunting tactics, might also contribute to the observed differences. The general absence of differences between continents in bird prey traits suggests greater stability in prey–predator relationships for that group.

Existing threats on prey species

For mammals and birds, traits can be linked to extinction risk (Purvis et al. 2000, Atwood et al. 2020), the number of threats (Greenville et al. 2021, Capdevila et al. 2022), and the type of threat to which they are exposed (Chichorro et al. 2019, Leclerc et al. 2020). Larger body mass is often associated with a higher extinction risk and more threats, whereas larger geographic ranges and litter sizes reduce extinction risk.

We found the opposite relationship for the bird prey of *F. catus* in Europe, North America and Australia – smaller species with broader geographic ranges and larger clutch sizes were more likely to be recorded as prey. This suggests that predation pressure from cats is not biased toward currently

threatened species. From a conservation perspective, this result is encouraging because species more likely to be eaten by cats are also the least-threatened species on continents, meaning that cat predation does not exacerbate extinction risk in many bird species already deemed vulnerable. Previous works already identified parrots as particularly vulnerable to non-native predators (Marino and Bellard 2023) and at high risk of extinction on islands (Matthews et al. 2022), in contrast to Passeriformes (Evans et al. 2021).

We can also make the same conclusion for mammals in Europe and North America, where the least-impacted species are those most likely to be eaten by cats. However, because body mass was a good predictor of the probability of a mammal being classified as threatened (Supporting information), the consumption of many threatened mammals by *F. catus* in Australia could explain the disproportionately high number of prey already threatened on that continent. The greater vulnerability of Australian marsupials to *F. catus* predation is noteworthy, particularly considering the already precarious status of many Australian species, with some facing extinction due to introduced mammal predators (Woinarski et al. 2015).

Limitations

Our study addressed the incompleteness of the *F. catus* diet record, a known issue highlighted by species accumulation curves and corroborated by Lepczyk et al. (2023). To mitigate this gap, we applied a 90% coverage-based rarefaction and extrapolation to assess the prey richness within each dataset. Despite the utility of these estimates for assessing richness, extrapolation at high coverages might not always be reliable (Roswell et al. 2021) and could overestimate the number of missing prey. Thus, we adopted a conservative strategy to standardize dataset coverage while maximizing data and minimizing extrapolation bias.

In the datasets, 1) we included scavenging, which can be challenging to distinguish from true predation; 2) some studies focussed on rare and threatened species, often limited to single species; and 3) there was a low probability of recording rare or range-restricted species as prey. These potential biases can have diverse effects; for example, scavenging can affect the relationships detected between traits and predation probability if the traits of scavenged species differ from those of species cats depredate. Further, the contrasting effects of species abundance on their inclusion in diet records (i.e. rare species less likely to be detected in diet studies, but single-species studies aimed at identifying predators biased towards rare/vulnerable species) make it difficult to draw definitive conclusions regarding potential over- or under-representation of these species in our database.

Low detectability and the direct derivation of IUCN threat categories from geographical range data suggest that comparing threatened and non-threatened species among prey and non-prey should be interpreted with caution, even

if discriminations are pronounced. The difficulty of quantifying detectability problems in binary databases emphasizes the need for more continuous measures of predation pressure, despite the difficulty of obtaining such data.

By considering species as two groups (depredated or not), we could not detail the relationships between traits and predation probability as did Woinarski et al. (2017) for Australian birds and Woolley et al. (2019) for Australian mammals. Woinarski et al. (2017) identified an optimal body mass with a higher likelihood of predation by *F. catus* (particularly for smaller species), consistent with our findings. Woolley et al. (2019) identified an optimal range of body mass where the likelihood of predation was highest, with both smaller and larger species showing lower probabilities of being prey, but also noted predation across the entire body mass range. Unlike us, they used a body-mass threshold, excluding larger species considered scavenged, which could explain our broader range of accepted prey body mass. Woolley et al. (2019) and Woinarski et al. (2017) assumed that species not observed as cat prey were indeed non-prey species, which appears to be an acceptable assumption for Australia (i.e. where cat diet has been studied in detail; Fig. 1), but might not be elsewhere due to potential missing prey data.

However, when comparing the marginal effects of traits on predicting prey status based on the 333 predation prediction models (trained on observed prey and non-prey species), we found a pattern similar to that detected by Woinarski et al. (2017) and Woolley et al. (2019). In Europe and North America, we found a linear relationship between body mass and the probability of being depredated, with smaller species more likely to be prey (Supporting information).

Conclusion

Our findings emphasize the need for a more ecologically realistic approach when studying and reporting the impacts of *F. catus* at continental scales, particularly in Europe and North America. The existing literature in these regions often provides prey numbers without clearly elucidating the genuine ecological impacts of *F. catus* on native species diversity. Our study demonstrates that *F. catus*, as introduced predators, exhibit selectivity based on specific traits, making some species more likely to be preyed upon than others. This selectivity is particularly stable for birds, with species showing similar traits across various biogeographical contexts. In contrast, Australian mammalian prey had different traits from those in Europe and North America, emphasizing the importance of biogeographical context in shaping prey–predator dynamics for mammals. Understanding the dietary preferences of *F. catus* in different regions could help to elucidate how biogeographical differences influence prey–predator relationships. This knowledge will also improve our ability to identify species most at risk from *F. catus* predation, enabling us to anticipate and mitigate potential negative impacts in both the short and long term.

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Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07169>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hmgqnk9t4> (Philippe-Lesaffre et al. 2024). R scripts are available in the Zenodo digital repository: <https://zenodo.org/records/13920239>.

Supporting information

The Supporting information associated with this article is available with the online version.

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