

Bee brain size is positively associated with urban lifestyles but not with positive population trends

Miguel Á. Collado¹  Jose B. Lanuza²  and Ignasi Bartomeus² 

Departamento de Ciencias de la Computación e Inteligencia Artificial, Universidad de Sevilla, Seville, Spain

Estación Biológica de Doñana (EBD-CSIC), E-41092 Seville, Spain

Author for correspondence:

Abstract

The rapid conversion of natural habitats to anthropogenic landscapes is threatening insect pollinators worldwide, raising concern on the consequences for their fundamental role in ecosystems for fruit and seed production. However, not all pollinators are negatively affected by habitat conversion, but some find in anthropogenic landscapes appropriate resources to survive and reproduce. Why some animals can thrive in anthropogenic environments that most species cannot tolerate remains insufficiently understood, but it might in part reflect enhanced behavioural plasticity to exploit new resource opportunities. While this hypothesis has received ample support in studies of vertebrates, it is less obvious whether the small brain of insects can offer enough behavioural plasticity to cope with the many challenges of anthropogenic habitats. To address this issue, we measured brains for 145 individuals from 44 species of bees —the most important group of pollinators— from North America and Europe, and compared them with detailed information on habitat preferences and population trends. Our analyses revealed that bees that prefer forest habitats had smaller brains relative to their body size, but those who prefer urban habitats tended to have larger brains compared to forest dwellers. However, we found no evidence that either larger brains or a preference for urban habitats are associated with positive population trends. These results suggest that a large brain can help maintaining bee urban populations, but also highlight that being tolerant to urbanisation is not enough to compensate for the worldwide decline of their populations.

Keywords: encephalisation, brain-body mass ratio, habitat preference, Apoidea, GBIF

Introduction

Relevant refs:

<https://onlinelibrary.wiley.com/doi/10.1111/ele.14133?af=R>

This may be also relevant:

Although recent studies challenge the use of absolute brain size as an estimator for behavioral complexity and computational power (Chittka and Niven, 2009, and references therein), many studies have shown correlations between brain size and performance (Deaner et al., 2007; Gronenberg and Couvillon, 2010; Lefebvre and Sol, 2008).

Pollination is a fundamental ecosystem service that connects the earth's vegetation and human economy. Pollination services are performed by both managed and wild pollinators, mostly bees (James, James, and Pitts-Singer 2008; Winfree et al. 2011), both of which might be affected by a range of current and projected human-related environmental changes. There are indeed clear shreds of evidence of recent declines in pollinator populations (Bartomeus et al. 2019), and parallel declines in the plants that rely upon them (Potts et al. 2010; Scheper et al. 2014). For example, in the UK, the third part of wild pollinator species has decreased from 1980 to 2013 (Powney et al. 2019), including six of all 16 non-parasitic bumblebees (Williams and Osborne 2009). The decline of pollinators currently observed is projected to increase in the future (Dormann et al. 2008). Because most wild plant species (80%) and crop species (75%) are directly dependent on insect pollination for fruit and seed production (Klein et al. 2007; Ollerton, Winfree, and Tarrant 2011), there is an increasing concern that the loss of pollinators from both natural communities and agricultural areas will have severe negative consequences for ecosystem functions and services (Ashman et al. 2004; Klein et al. 2007).

Although the reason why many pollinator are declining is insufficiently understood, a factor that is considered central is the loss and alteration of their habitats (Brown and Paxton 2009). The destruction and fragmentation of natural habitats and their replacement by anthropogenic landscapes present new challenges for survival and reproduction of organisms, increasing the risk of extinction by negative population growth (Brown and Paxton 2009). However, not all pollinators species are equally affected by habitat loss and alteration. In bees, for example, there are also “winners” —like *Bombus terrestris* (Rasmont et al. 2008)— that are able to thrive in human-altered environments, and there are also other species that although do not proliferate in such environments can at least maintain self-sustaining populations [Biesmeijer et al. (2006); Bartomeus et al. (2013); Reemer et al., 2012????; Collado, Sol, and Bartomeus (2019)].

Human-dominated habitats —notably cities— offer unique ecological opportunities in the form of new nesting spots, reduced predation pressure and high food availability associated with non-indigenous plants (Cane et al. 2006; Winfree et al. 2011; Collado, Sol, and Bartomeus 2019). Although variation across species in tolerance to habitat loss and alteration is likely to have important demographic consequences, whether this is the reason why some pollinators are declining while others are increasing is currently unknown. Hence, the ability to adapt to human-dominated new habitats and to exploit new opportunities have become important

for species to thrive (Manenti, Denoël, and Ficetola 2013). For species that tolerate human-related disturbances, human-dominated habitats—notably cities—offer unique ecological opportunities in the form of new nesting spots, reduced predation pressure and high food availability associated with non-indigenous plants (Cane et al. 2006; Winfree et al. 2011; Collado, Sol, and Bartomeus 2019). The question is then why only some species are able to enjoy the benefits of an urban life. In a novel environment, the chances to successfully survive and reproduce largely depends on cognition, that is, the processes involved in gathering, storing and reacting to environmental information. Cognitive limitations have thus help explaining the low success of many species in novel environments in general, and urban areas in particular. For example, reptiles, amphibians and birds that flourished after being introduced to new regions outside their native ranges tend to have larger brains (relative to their body size) than unsuccessful invaders (Sol et al. 2008, 2005; Amiel, Tingley, and Shine 2011). In vertebrates, relative brain size is a good proxy of problem-solving and learning (e.g. see chapter 2 of this thesis for its relationship with learning), which can help individuals to cope with the many challenges on novel environments. However, similar evidence is lacking for insects, in part because advanced cognitive abilities were not considered possible with their tiny brains. More important, there was no unequivocal evidence that brain size was related to cognitive performance. However, we now know that bees and other insects have advanced cognition, being able for instance to use tools to resolve new problems and learn socially how to do so (Alem et al. 2016). There is in addition evidence that cognitive differences in the brain are reflected in differences in their brain size (Chapter 2). We used previously published data on bee forest and urban preference (Collado, Sol, and Bartomeus 2019) as opposite points of habitat complexity, expecting to find bigger brain sizes for urban dwellers because a wider array of cognitive abilities are needed to inhabit these habitats. Species population trends were extracted from Bartomeus et al. (2013) and both datasets were crossed with a newly collected brain weight database. We wanted to explore if there is a relationship between brain size, habitat preference, and population trends. Hence, our questions were the following: Are brain sizes, as a proxy of behavioural plasticity, related to habitat preferences? Is population stability related to brain size as it has been seen in other taxa? Are habitat preferences related to population stability? Or alternatively, are urban dwellers populations increasing?

Methods

Overview

Our study explores the long standing idea that species with higher encephalisation (i.e., large brain mass relative to their body) are more likely to thrive in urbanised areas. To evaluate this hypothesis, we have used a dataset of bee species captured in North America and Europe with measurements of brain mass and body size. For all these species, we downloaded the occurrence records from the Global Biodiversity Information Facility (GBIF) and selected as study area the states or countries with highest density of records. After filtering the data to avoid possible biases, we extracted the land use classification of the different georeferenced records and summarised them into 3 different categories when possible: (1) natural, (2) agricultural and (3) urban. To evaluate if the different bee species occur more in some habitats than others, we calculated their habitat preference by comparing the observed occurrences with the ones of null models. Finally, for the species that showed low and high statistical preference for the different habitats, we investigated how the association between habitat preference and encephalisation changed by habitat type.

All analyses were undertaken in R version 4.0.5 ([R Core Team 2021](#)) and the manuscript was written in rmarkdown version 2.17 ([Allaire et al. 2022](#)).

(a) Bee species dataset

Our dataset contains measurements of brain and body size for bee specimens captured by hand netting in different areas of the East Coast of United States and Europe (i.e., Spain and Netherlands). In total, the dataset includes 433 female individuals from 113 species that represent 6 different families and 30 genera. We only considered female specimens because: (i) females are involved in a larger number of tasks than males and are likely to experience greater selective pressures from the environment; and (ii), there are evident behavioral and morphological differences between sexes that are associated with the size and structure of the brain ([Streinzer et al. 2013](#); [Roselino et al. 2015](#)). In addition, because brain size can change with age and experience of the different individuals within a species ([Durst, Eichmüller, and Menzel 1994](#); [Withers et al. 2008](#)), we limited our sampling to specimens foraging on flowers. Note that 93 of the species used in our study were previously published with their respective trait measurements in Sayol et al. ([2020](#)).

(b) Brain and body size measurements

Brain size was measured as the weight of fixed brain for each specimen. First, all collected individuals were kept in cold and sent them to the laboratory where they were identified by expert taxonomists and anesthetise in cold ([Crook 2013](#)). Then, heads were removed with a scalpel and placed in a fixative solution (4% paraformaldehyde in 0.1 M phosphate-buffered saline -PBS- pH = 7.4) to avoid degradation. Subsequently, brains were extracted from the head capsule and placed on a petri dish after removing the retina from the optic lobes and cleaning the entire brain of all tracheae and fat bodies. By doing this, we ensured that our brain measurements mainly accounted for neural tissue. We then placed the brains on a

small piece of Parafilm® and dried the exceeding fixative solution with Kimwipes® tissues. Finally, within 4 seconds of the liquid removal, we weighted the brains with the help of a microbalance Sartorius Cubis® and calculated the average weight for the species with more than one specimen.

We considered as a proxy of body size the average intertegular span (ITS) per species. ITS represents the distance between the base of the wings (tegulae) on the bee thorax and has been shown to accurately predict body size as it is highly correlated with dry body weight (Cane 1987; Kendall et al. 2019). All ITS measurements were conducted with a stereomicroscope (magnification 16x or 80x) with a calibrated ocular micrometre (resolution down to 0.02 mm).

(c) Occurrence data

We downloaded occurrence information for all species from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) for North America and Europe. The data was downloaded through R programming language with the help of the function *occ_download* from the package *rgbif* version 3.7.3 (Chamberlain et al. 2017). Because the records were biased towards some areas that were associated with political boundaries, we selected the states or countries with highest density of records for our set of species. We selected the boundaries from the maps packages *spData* version 2.2.0 (Bivand, Nowosad, and Lovelace 2022) and *giscoR* version 0.3.2 (Hernangómez 2022), and extracted the occurrences with the help of the function *st_intersection* from the package *sf* version 1.0-7 (Pebesma et al. 2018). For North America, we selected states located on the East Coast of United States (Figure 1A) that covered an approximate area of 136,937 km². These states were: Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York metropolitan area, New Jersey, Delaware and Maryland. Similarly, we selected countries located on the north and center of Europe (Figure 1B) that represented a total area of 600,497 km². These countries were: England, Belgium, Netherlands, Germany and Denmark. All occurrence data used in this study can be downloaded from <https://doi.org/10.15468/dl.nenuem> where just the countries of interest were retrieved. To avoid biases in our analysis, we filtered the occurrence records according the following criteria: (i) we only included species with a widespread distribution of occurrences along our study area; (ii) all species had a minimum number of 50 records; (iii) all duplicated records were excluded (i.e., records of specimens with the same date and location); (iv) we only included georeferenced records with a minimum of two decimals of latitude/longitude coordinates; and (v), we only included records between the time interval 1990 and 2022 in order to avoid large differences with the extracted land cover classifications from 2006. After pruning the data, our final dataset comprised 93 species with 20,782 occurrence records for United States (37 species; median occurrences = 348) and 309,729 records for Europe (56 species; median occurrences = 1077).

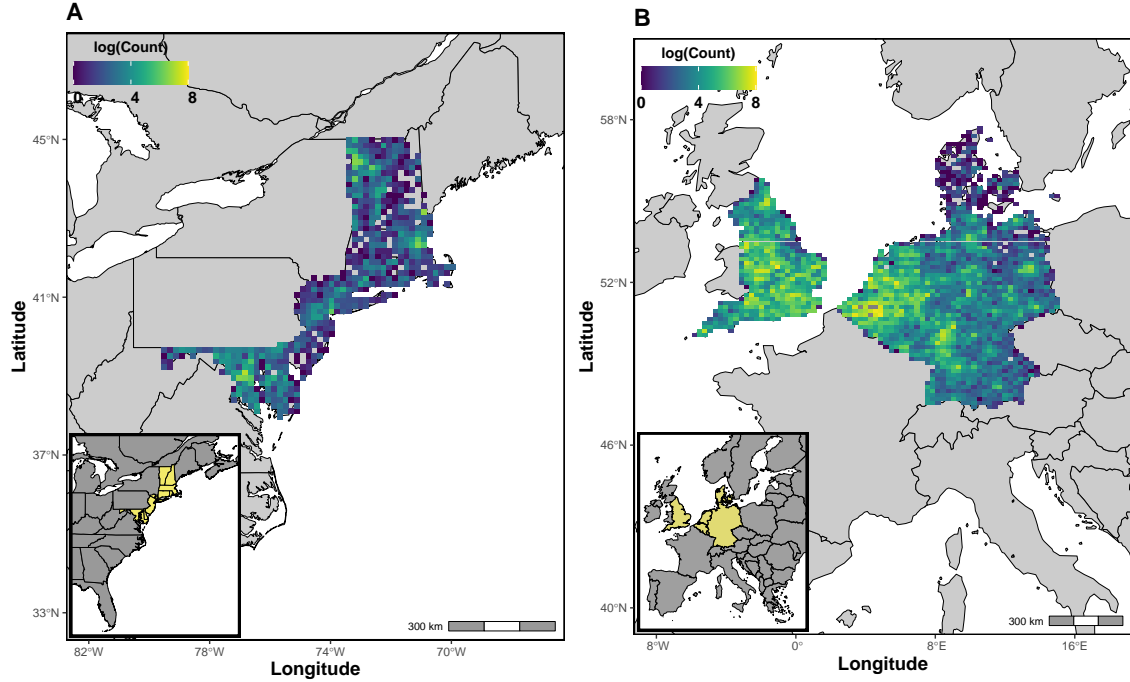


Figure 1. Maps showing the study areas and the number of GBIF occurrences in logarithmic scale for the selected bee species. A) East Coast of United States with records for Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York metropolitan area, New Jersey, Delaware and Maryland. B) European continent with records downloaded for England, Belgium, Netherlands, Germany and Denmark.

(d) Land cover classification

We assigned a habitat type for all GBIF occurrences by merging land cover information with the different georeferenced records. The land cover classification was obtained from the 2006 online inventories of the National Land Cover Database (NLCD) for United States and the Corine Land Cover (CLC) for Europe. After downloading these as raster files, we used the functions *rast* and *extract* from the *Terra* package version 1.6-41 (Hijmans et al. 2022) to read and obtain the cover classification of the different georeferenced records, respectively. Then, to simplify the interpretation and conduct a joint analysis for both occurrence datasets, we divided the resulting cover classes into three single categories: (i) natural, (ii) agricultural and (iii) urban. The original extracted cover classes and our classification into these three different categories are shown in Table S1 for United States and Table S2 for Europe.

(e) Construction of the phylogenetic tree

We constructed a phylogeny with all studied species by using a previously published genus-level bee phylogeny (Hedtke, Patiny, and Danforth 2013). For this, we first read the backbone phylogeny with the function *read.tree* and drop the missing genera with function *drop.tip* from the package *ape* version 5.6-2 (Paradis et al. 2019). Then, we selected as an outgroup a wasp genera (*Tachysphex*) and recalculated distances to the root with the function *chronos*

from *ape*. Species tips were added to genera nodes as polytomies of equal branch length relative to the genera branch length using the *phytools* package version 1.2-0 (Revell 2012). From the resulting tree, we created a scaled phylogenetic covariance matrix with the function *inverseA* from the package *MCMCglmm* version 2.33 (Hadfield 2010).

(f) Analysis

We estimated brain size relative to the body (i.e., encephalisation) by modeling the log-transformed association between brain weight and intertegular span. For this, we specified a simple Bayesian regression with the function *brm* from the package *brms* version 2.18 (Bürkner 2017) where brain weight was the response variable and intertegular span the predictor. To correct for the non-independent evolutionary histories among species, we included the phylogenetic covariance matrix as random factor. Note that this matrix contained all species of our dataset ($N = 113$) because we expect better predictive power with a larger sample size than the one with the filtered dataset ($N = 93$). Lastly, we extracted the differences between the observed and predicted values (i.e., residuals) that represent the degree of encephalisation. High values indicate larger brains than expected for their body size and low values denote smaller brains than expected.

Habitat preference was estimated by comparing species occurrences per habitat with the ones that we would expect if they occur at random. For this, we generated from our occurrence matrix 10,000 randomised matrices with help of the function *nullmodel* from the package *bipartite* version 2.16 (Dormann et al. 2008). We implemented this function with the method ‘r2dtable’ which maintains row and column sums constant by using Patefield’s algorithm (Patefield 1981). In other words, it maintains the proportional dominance of the species and habitats constant but reshuffles their associations. We then estimated the percentage of simulated occurrences per species and habitat that were under the observed ones. Finally, we considered that a bee species exhibited statistical preference when the observed occurrences per species and habitat were under the 5th percentile (low preference) or above the 95th percentile (high preference) in comparison with the simulated ones.

To evaluate if the degree of encephalisation changes by habitat type, we modeled with Bayesian generalised linear models their association. For this, we first joined the resulting habitat preference and encephalisation datasets by species and extracted those with statistical habitat avoidance or preference on any of these three habitats. Because we assessed habitat preference as binary (low or high), we specified a Bernoulli distribution where habitat preference was the response variable and encephalisation the predictor. Again, we included the phylogenetic covariance matrix as random factor. Moreover, we also explored how habitat preference changed by brain weight and intertegular span independently. For this, we conducted two analogous models with these two different predictors. Finally, we also investigated the different trends for United States and Europe separately.

All our models were run with 4,000 iterations with previous 1,000 warm up iterations and with non or very weakly informative priors from the *brm* function so the priors had negligible influence on the results (Bürkner 2017). Finally, the different posterior predictive checks were conducted with the function *pp_check* also from the *brms* package.

Results

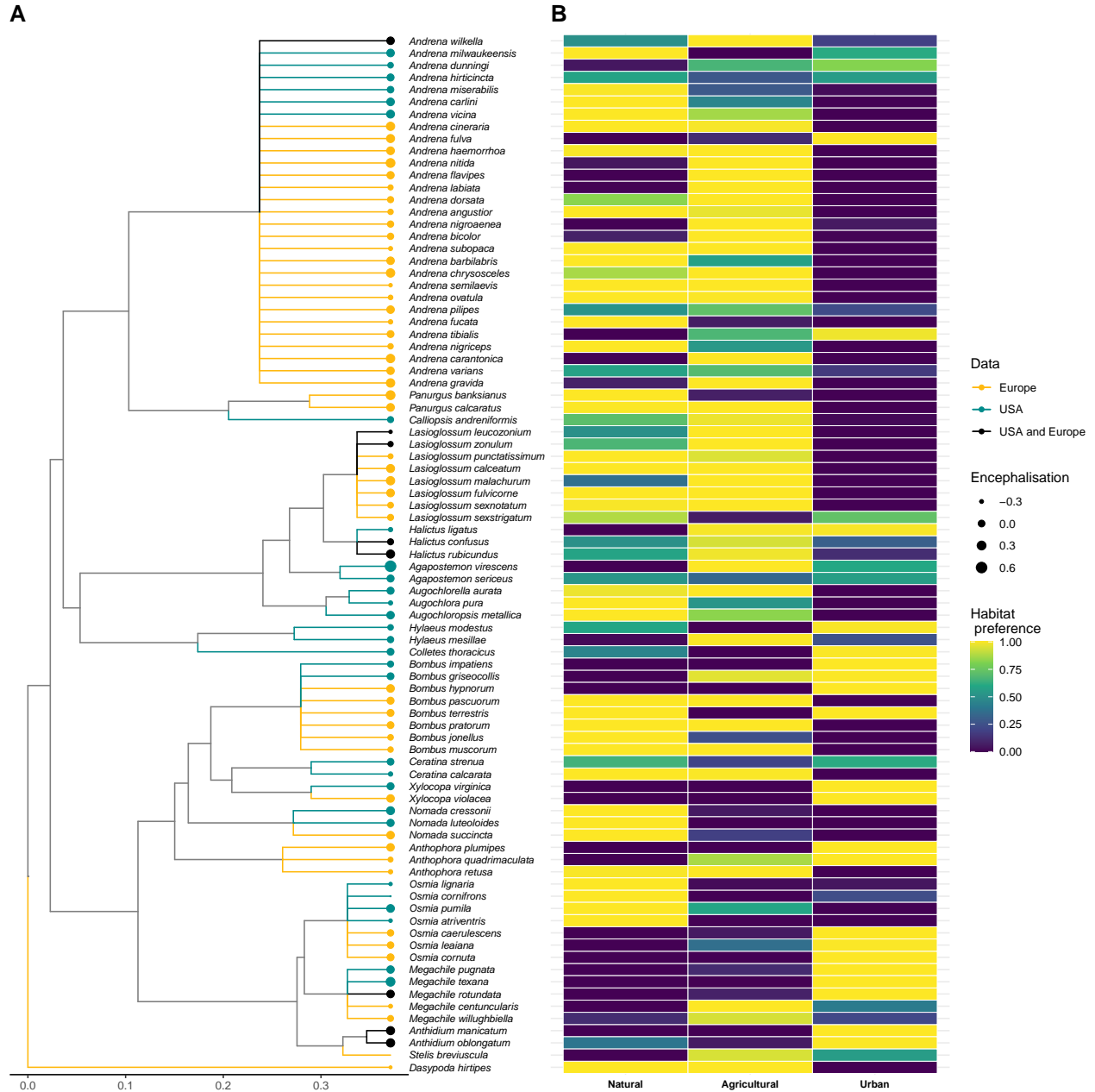


Figure 2. Phylogenetic relationship and habitat preferences for the selected bee species with brain weight and intertegular distance information (N=100). A) Phylogenetic tree at the genera level. Tree branches are coloured based on the geographical location of the different bee species (North of Europe, East Coast of United States or from both regions). The deviation of the brain size in relation to the body (i.e., residuals) is indicated with weighted points at the end of the tip branches. Larger points indicate larger brains in proportion to their body size and vice versa. B) Heatmap showing the habitat preference for each bee species. The columns delimit the habitat type (i.e., natural, agricultural, semideveloped and urban) and the rows the different bee species.

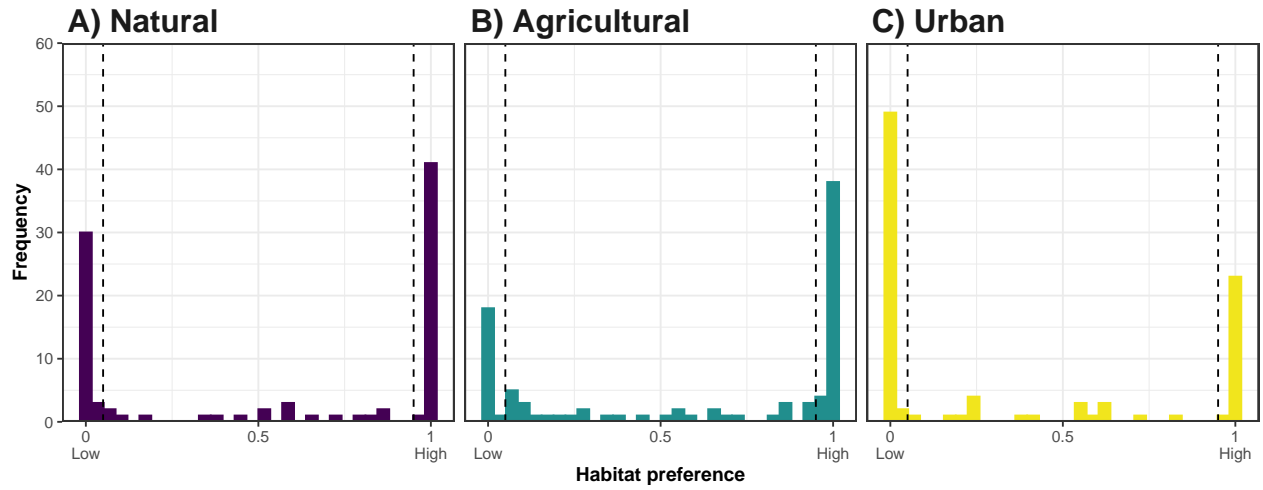


Figure 3. Frequency distribution of the bee preferences for each habitat type (i.e., natural, agricultural and urban). The different habitats are reclassifications from the 2006 land use categories of the Corine Land Cover (CLC) inventory for Europe and the National Land Cover (NLC) database for Unites States.

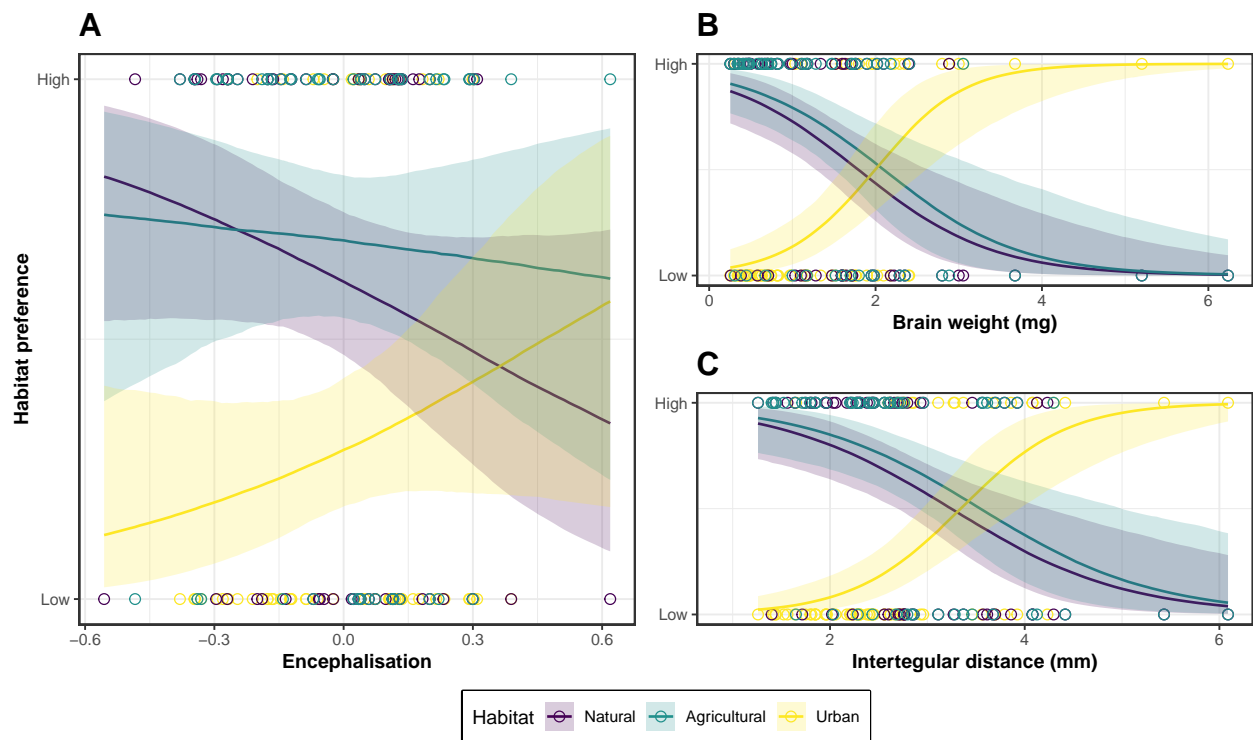


Figure 4.

Discussion

Bees with urban habitat preferences tended to have bigger brains related to their body sizes, and those with forest preferences had relatively smaller brains. Surprisingly, neither brain sizes nor habitat preference explained population trends, against what we expected. Therefore, species with bigger brains appearing on urban habitat can be indicating that while only bees with large cognitive capacities are surviving in these modified environments, they do not have experienced notorious increases in their populations. We hypothesized that bees with bigger brains related to body size should be more flexible in their behaviour because a large brain may confer better cognitive abilities, as it has been observed in some species (Lefebvre et al., 2004) and as we show specifically for bees in relation to learning (Chapter 2 of this thesis). Therefore, to exploit complex urban environments, we expect bigger brains to be required. Urban habitats are typically harsher, with less and/or new resources to explore, also containing new unknown threats and a highly changing environment (Wheater, 1999). Hence, urban dwellers may need to have better cognitive abilities and flexibility in their behavior than the forest dwellers counterpart. Some examples of behaviours needed to survive in urban environments (see Table S2 for a full set of examples) are the use of human-made materials to nest (Allasino et al., 2019) or being able to collect pollen and nectar from exotic flowers from gardens (Lowenstein et al., 2014). We should not expect forested habitats to require such a plastic behaviour because the resources found in these habitats are homogeneous, stable, and bees are already pre-adapted to use them (Smith et al., 2019). In accordance, we found smaller brain sizes than expected by their body sizes in bees that preferred forests indicating that an investment in bigger relative brain sizes is not required. In addition, other traits have already been described to be filtered in anthropogenic land uses, like early spring or brood parasitism (Harrison et al., 2017), which are present in the forest dwellers. We could not explain population trends with brain size as it happens in other taxa. For example, in birds, brain size is a good predictor of how a population does in the long-term (Shultz, 2005). However, this is not always the case as bigger brains increase the risk of extinction in mammals (González-Voyer et al., 2016). Despite brain weight is relatively easy to measure and standardize with the used protocol, we lack information on certain neuropils size, like mushroom bodies (the suspected centers of cognitive processes in bees), which can be variable even within species (Barth & Heisenberg, 1997; Withers et al., 1995; Fahrbachand & Robinson 1995). Differences in more subtle brain structures could explain differences in behaviours, and in consequence, shed extra light on species population trends. Therefore the isolation and measurement of these neuropils could be interesting because we could get more accurate information. On the other hand, also note that population trends data is hard to find or measure, especially for invertebrate taxa. Long term data is often lacking and we count only with data indirectly taken from museums. This data is also scarce and hard to standardize (Bartomeus et al., 2018), therefore not being optimal for comparative studies of declining or increasing populations (Shultz, 2005). Species body size is generally related to population trends. In mammals, it is known that bigger body sizes decreases population density and increases the risk of extinction (Damuth, 1981; González-Voyer et al., 2016). This relation has also been seen in bees (Scheper et al., 2014). Although body size is directly related to absolute brain size, we did not find a strong correlation between body size and population trends in our subset of North American bees as it was found for the complete

set in Bartomeus et al., 2013. Our subset may be biased towards the most common genera and contain fewer species per genus. If the body size-decline relationship occurs mainly within genus, and not across genus, as indicated by the strong phylogenetic signal of body size (Pagel's $\lambda > 0.9$), we may lack the power to detect this variation within genus in our restricted analysis. Population trends or habitat preferences could be explained by the availability of the resources consumed, for example, in the Netherlands, population trends of some bee species are related to the availability of their preferred plants (Scheper et al., 2014). A polylectic diet could help species to adapt to new environments, and we know that species able to forage on crop plant families tend to have stable or increasing populations (Scheper et al., 2014, Bartomeus et al. 2013). If we consider habitats being conditioned by their availability of the preferred resources, then we may be able to explain our link between brain size and preference for certain habitats. For example, differences in bee community composition and abundance are found for oligolectic (i.e. diet specialist bees) associated to their preferred resources along forested gradients (Grundel et al., 2010). Dietary data should be an interesting next step to see if broader (polylectic) or narrower (oligolectic) diet are generally related to habitat preferences and brain sizes. In fact, it has been already described for other taxa a relationship between brain size and diet (DeCasien et al., 2017). Finally, the absence of relationship between urban preferences and increasing population trends is interesting. Despite these bees have found new niches to occupy, they are not increasing its populations but just persisting. The transformation from natural to urban habitats is filtering which species can survive, and hence, biodiversity in urban habitats is usually lower (Collado et al., 2019, Chapter 3 of this thesis). However, survivors are not thriving either in this new conditions. Some negative effects of urbanization have already been studied in bees, like for example, biased sex ratio, with increasing males in urban areas (Fitch et al., 2019) with unknown future population consequences. It should be interesting to fully assess the costs and benefits of living in urban environments, including brain investment and other selected strategies to adapt to the new conditions.

References

- Alem, Sylvain, Clint J Perry, Xingfu Zhu, Olli J Loukola, Thomas Ingraham, Eirik Søvik, and Lars Chittka. 2016. “Associative Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect.” *PLoS Biology* 14 (10): e1002564.
- Allaire, JJ, Yihui Xie, Jonathan McPherson, Javier Luraschi, Kevin Ushey, Aron Atkins, Hadley Wickham, Joe Cheng, Winston Chang, and Richard Iannone. 2022. *Rmarkdown: Dynamic Documents for r*. <https://github.com/rstudio/rmarkdown>.
- Amiel, Joshua J, Reid Tingley, and Richard Shine. 2011. “Smart Moves: Effects of Relative Brain Size on Establishment Success of Invasive Amphibians and Reptiles.” *PLoS One* 6 (4): e18277.
- Ashman, Tia-Lynn, Tiffany M Knight, Janette A Steets, Priyanga Amarasekare, Martin Burd, Diane R Campbell, Michele R Dudash, et al. 2004. “Pollen Limitation of Plant Reproduction: Ecological and Evolutionary Causes and Consequences.” *Ecology* 85 (9): 2408–21.
- Bartomeus, Ignasi, John S Ascher, Jason Gibbs, Bryan N Danforth, David L Wagner, Shannon M Hedtke, and Rachael Winfree. 2013. “Historical Changes in Northeastern US Bee Pollinators Related to Shared Ecological Traits.” *Proceedings of the National Academy of Sciences* 110 (12): 4656–60.
- Bartomeus, Ignasi, JR Stavert, Darren Ward, and Oscar Aguado. 2019. “Historical Collections as a Tool for Assessing the Global Pollination Crisis.” *Philosophical Transactions of the Royal Society B* 374 (1763): 20170389.
- Biesmeijer, Jacobus C, Stuart PM Roberts, Menno Reemer, R Ohlemuller, Mike Edwards, Tom Peeters, AP Schaffers, et al. 2006. “Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands.” *Science* 313 (5785): 351–54.
- Bivand, Roger, Jakub Nowosad, and Robin Lovelace. 2022. *spData: Datasets for Spatial Analysis*. <https://jakubnowosad.com/spData/>.
- Brown, Mark JF, and Robert J Paxton. 2009. “The Conservation of Bees: A Global Perspective.” *Apidologie* 40 (3): 410–16.
- Bürkner, Paul-Christian. 2017. “Brms: An r Package for Bayesian Multilevel Models Using Stan.” *Journal of Statistical Software* 80: 1–28.
- Cane, James H. 1987. “Estimation of Bee Size Using Intertegular Span (Apoidea).” *Journal of the Kansas Entomological Society*, 145–47.
- Cane, James H, Robert L Minckley, Linda J Kervin, T’ai H Roulston, and Neal M Williams. 2006. “Complex Responses Within a Desert Bee Guild (Hymenoptera: Apiformes) to Urban Habitat Fragmentation.” *Ecological Applications* 16 (2): 632–44.
- Chamberlain, Scott, Karthik Ram, Vijay Barve, Dan Mcglinn, and Maintainer Scott Chamberlain. 2017. “Package ‘Rgbif.’” *Interface to the Global Biodiversity Information Facility ‘API’* 5: 0–9.
- Collado, Miguel Á, Daniel Sol, and Ignasi Bartomeus. 2019. “Bees Use Anthropogenic Habitats Despite Strong Natural Habitat Preferences.” *Diversity and Distributions* 25 (6): 924–35.
- Crook, RA. 2013. “The Welfare of Invertebrate Animals in Research: Can Science’s Next Generation Improve Their Lot.” *Journal of Postdoctoral Research* 1 (2): 1–20.
- Dormann, Carsten F, Oliver Schweiger, Paul Arens, Isabel Augenstein, ST Aviron, Debra

- Bailey, Jacques Baudry, et al. 2008. "Prediction Uncertainty of Environmental Change Effects on Temperate European Biodiversity." *Ecology Letters* 11 (3): 235–44.
- Durst, Cordula, Stefan Eichmüller, and Randolph Menzel. 1994. "Development and Experience Lead to Increased Volume of Subcompartments of the Honeybee Mushroom Body." *Behavioral and Neural Biology* 62 (3): 259–63.
- Hadfield, Jarrod D. 2010. "MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package." *Journal of Statistical Software* 33: 1–22.
- Hedtke, Shannon M, Sébastien Patiny, and Bryan N Danforth. 2013. "The Bee Tree of Life: A Supermatrix Approach to Apoid Phylogeny and Biogeography." *BMC Evolutionary Biology* 13 (1): 1–13.
- Hernangómez, Diego. 2022. *giscoR: Download Map Data from GISCO API - Eurostat* (version 0.3.2). <https://doi.org/10.5281/zenodo.4317946>.
- Hijmans, Robert J, Roger Bivand, Karl Forner, Jeroen Ooms, Edzer Pebesma, and Michael D Sumner. 2022. "Package 'Terra'."
- James, Rosalind, Rosalind R James, and Theresa L Pitts-Singer. 2008. *Bee Pollination in Agricultural Ecosystems*. Oxford University Press on Demand.
- Kendall, Liam K, Romina Rader, Vesna Gagic, Daniel P Cariveau, Matthias Albrecht, Katherine CR Baldock, Breno M Freitas, et al. 2019. "Pollinator Size and Its Consequences: Robust Estimates of Body Size in Pollinating Insects." *Ecology and Evolution* 9 (4): 1702–14.
- Klein, Alexandra-Maria, Bernard E Vaissière, James H Cane, Ingolf Steffan-Dewenter, Saul A Cunningham, Claire Kremen, and Teja Tscharntke. 2007. "Importance of Pollinators in Changing Landscapes for World Crops." *Proceedings of the Royal Society B: Biological Sciences* 274 (1608): 303–13.
- Manenti, Raoul, Mathieu Denoël, and Gentile Francesco Ficetola. 2013. "Foraging Plasticity Favours Adaptation to New Habitats in Fire Salamanders." *Animal Behaviour* 86 (2): 375–82.
- Ollerton, Jeff, Rachael Winfree, and Sam Tarrant. 2011. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120 (3): 321–26.
- Paradis, Emmanuel, Simon Blomberg, Ben Bolker, Joseph Brown, Julien Claude, Hoa Sien Cuong, Richard Desper, and Gilles Didier. 2019. "Package 'Ape'." *Analyses of Phylogenetics and Evolution* 2 (4): 47.
- Patefield, WM. 1981. "Algorithm AS 159: An Efficient Method of Generating Random $r \times c$ Tables with Given Row and Column Totals." *Journal of the Royal Statistical Society. Series C (Applied Statistics)* 30 (1): 91–97.
- Pebesma, Edzer J et al. 2018. "Simple Features for R: Standardized Support for Spatial Vector Data." *R J.* 10 (1): 439.
- Potts, Simon G, Jacobus C Biesmeijer, Claire Kremen, Peter Neumann, Oliver Schweiger, and William E Kunin. 2010. "Global Pollinator Declines: Trends, Impacts and Drivers." *Trends in Ecology & Evolution* 25 (6): 345–53.
- Powney, Gary D, Claire Carvell, Mike Edwards, Roger KA Morris, Helen E Roy, Ben A Woodcock, and Nick JB Isaac. 2019. "Widespread Losses of Pollinating Insects in Britain." *Nature Communications* 10 (1): 1–6.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.

- Rasmont, Pierre, Audrey Coppée, Denis Michez, and Thibaut De Meulemeester. 2008. “An Overview of the *Bombus Terrestris* (l. 1758) Subspecies (Hymenoptera: Apidae).” In *Annales de La Société Entomologique de France*, 44:243–50. 2. Taylor & Francis.
- Revell, Liam J. 2012. “Phytools: An r Package for Phylogenetic Comparative Biology (and Other Things).” *Methods in Ecology and Evolution*, no. 2: 217–23.
- Roselino, Ana Carolina, Michael Hrnčíř, Carminda da Cruz Landim, Martin Giurfa, and Jean-Christophe Sandoz. 2015. “Sexual Dimorphism and Phenotypic Plasticity in the Antennal Lobe of a Stingless Bee, *Melipona Scutellaris*.” *Journal of Comparative Neurology* 523 (10): 1461–73.
- Sayol, Ferran, Miguel Á Collado, Joan Garcia-Porta, Marc A Seid, Jason Gibbs, Ainhoa Agorreta, Diego San Mauro, Ivo Raemakers, Daniel Sol, and Ignasi Bartomeus. 2020. “Feeding Specialization and Longer Generation Time Are Associated with Relatively Larger Brains in Bees.” *Proceedings of the Royal Society B* 287 (1935): 20200762.
- Scheper, Jeroen, Menno Reemer, Ruud van Kats, Wim A Ozinga, Giel TJ van der Linden, Joop HJ Schaminée, Henk Siepel, and David Kleijn. 2014. “Museum Specimens Reveal Loss of Pollen Host Plants as Key Factor Driving Wild Bee Decline in the Netherlands.” *Proceedings of the National Academy of Sciences* 111 (49): 17552–57.
- Sol, Daniel, Sven Bacher, Simon M Reader, and Louis Lefebvre. 2008. “Brain Size Predicts the Success of Mammal Species Introduced into Novel Environments.” *The American Naturalist* 172 (S1): S63–71.
- Sol, Daniel, Richard P Duncan, Tim M Blackburn, Phillip Cassey, and Louis Lefebvre. 2005. “Big Brains, Enhanced Cognition, and Response of Birds to Novel Environments.” *Proceedings of the National Academy of Sciences* 102 (15): 5460–65.
- Streinzer, Martin, Christina Kelber, Sarah Pfabigan, Christoph J Kleineidam, and Johannes Spaethe. 2013. “Sexual Dimorphism in the Olfactory System of a Solitary and a Eusocial Bee Species.” *Journal of Comparative Neurology* 521 (12): 2742–55.
- Williams, Paul H, and Juliet L Osborne. 2009. “Bumblebee Vulnerability and Conservation World-Wide.” *Apidologie* 40 (3): 367–87.
- Winfree, Rachael, Ignasi Bartomeus, Daniel P Cariveau, et al. 2011. “Native Pollinators in Anthropogenic Habitats.” *Annual Review of Ecology, Evolution and Systematics* 42: 1–22.
- Withers, Ginger S, Nancy F Day, Emily F Talbot, Heidi EM Dobson, and Christopher S Wallace. 2008. “Experience-Dependent Plasticity in the Mushroom Bodies of the Solitary Bee *Osmia lignaria* (Megachilidae).” *Developmental Neurobiology* 68 (1): 73–82.

Supplementary material

Table S1.

Original NLCD Cover class	Occurrences	Assigned cover class
Hay/Pasture	3763	Agricultural
Developed, Open Space	3397	Urban
Developed, Low Intensity	2773	Urban
Deciduous Forest	2687	Natural
Developed, Medium Intensity	2306	Urban
Cultivated Crops	1075	Agricultural
Mixed Forest	1005	Natural
Developed, High Intensity	943	Urban
Woody Wetlands	940	Natural
Shrub/Scrub	478	Natural
Evergreen Forest	390	Natural
Herbaceous	335	Natural
Open Water	275	Discarded
Emergent Herbaceous Wetlands	269	Natural
Barren Land	146	Discarded

Table S2.

Original CLC Cover class	Occurrences	Assigned cover class
Discontinuous urban fabric	100801	Urban
Non-irrigated arable land	55692	Agricultural
Pastures	47477	Agricultural
Complex cultivation patterns	19643	Agricultural
Broad-leaved forest	14021	Natural
Land principally occupied by agriculture	9704	Agricultural
Sport and leisure facilities	8767	Urban
Industrial or commercial units	8615	Urban
Mixed forest	7690	Natural
Coniferous forest	6783	Natural
Green urban areas	5580	Urban
Natural grasslands	2711	Agricultural
Moors and heathland	2571	Natural
Water bodies	2374	Discarded
Vineyards	2146	Agricultural
Water courses	1737	Discarded
Inland marshes	1725	Natural
Continuous urban fabric	1681	Urban
Road and rail networks and associated land	1625	Discarded
Mineral extraction sites	1183	Discarded
Fruit trees and berry plantations	1140	Agricultural
Transitional woodland-shrub	1008	Natural
Peat bogs	991	Natural
Construction sites	979	Urban
Beaches, dunes, sands	601	Natural
Intertidal flats	506	Natural
Estuaries	411	Discarded
Sea and ocean	387	Discarded
Airports	347	Urban
Port areas	343	Urban
Dump sites	264	Discarded
Salt marshes	165	Natural
Sparsely vegetated areas	31	Natural
Coastal lagoons	22	Natural
Bare rocks	8	Discarded

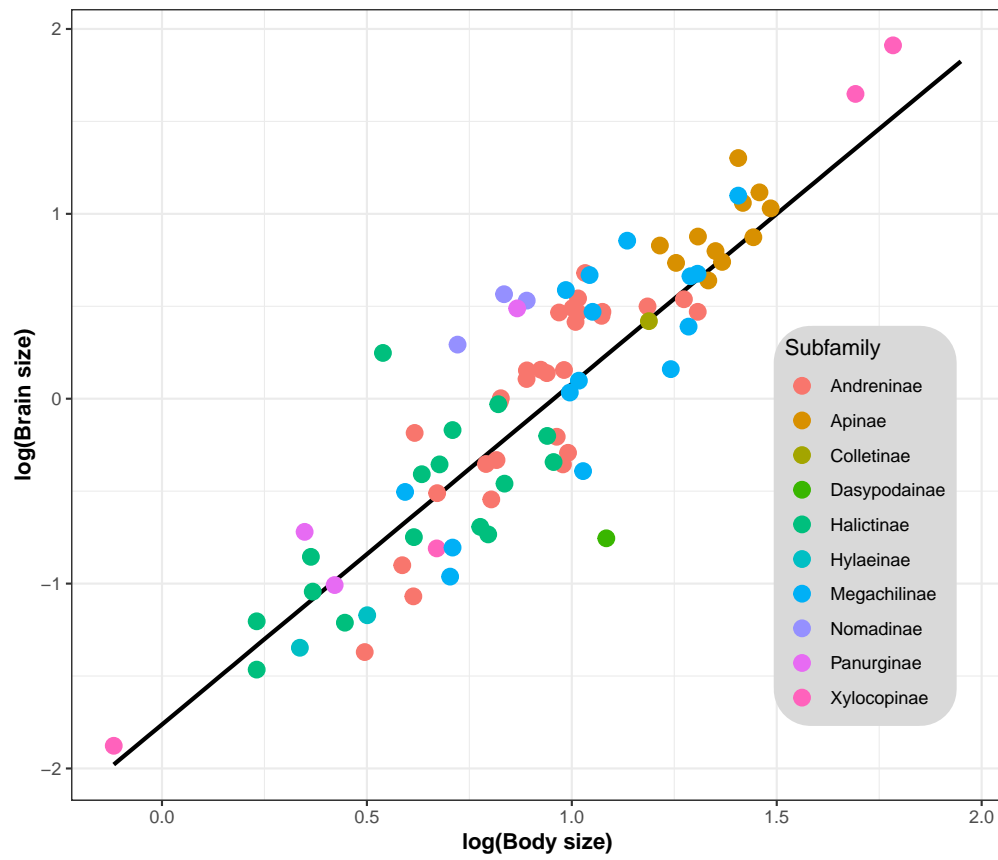
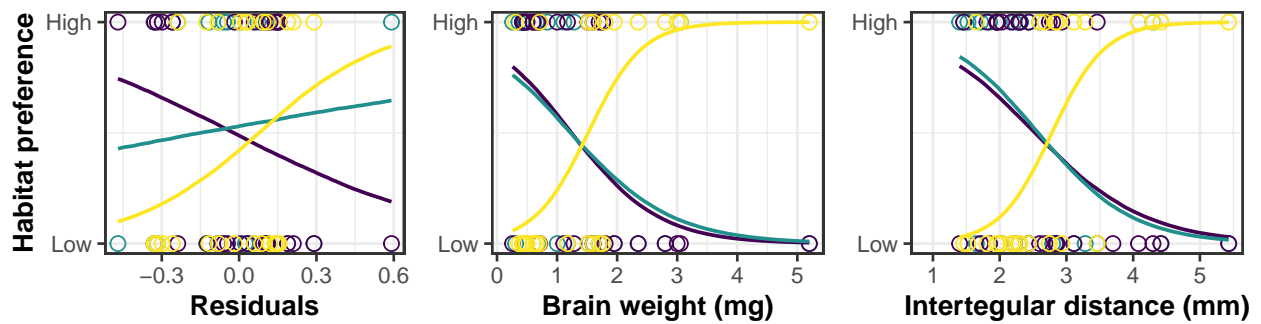
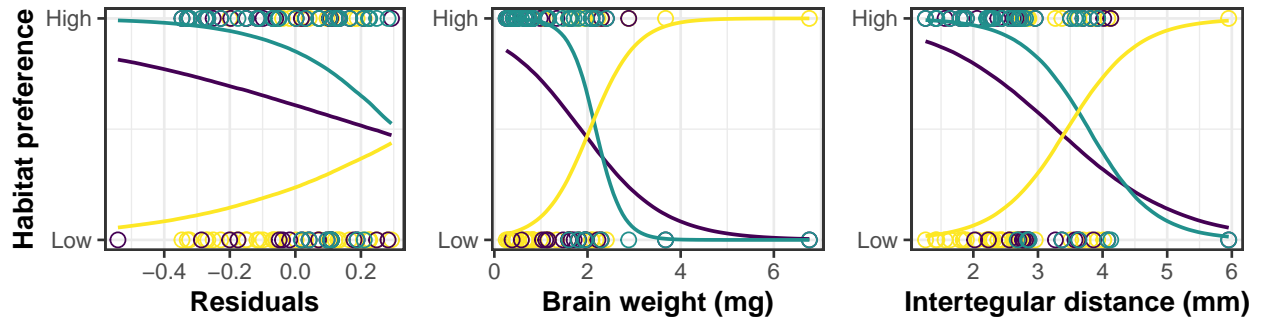


Figure S1.

United States occurrences (N = 20,782)



Europe occurrences (N = 309,729)



Habitat — Natural — Agricultural — Urban

Figure S2.