Mapping Animal Cultures: The Animal Culture Database (ACDB)

Kiran Basava[1,*], Md Nafis Ul Alam[2], Liam Roberts[3], Kristen Martinet[1], Paige Cherry[1], Hector Garcia-Verdugo[1], Cristian Román-Palacios[1]
[1] College of Information Science, University of Arizona, Tucson, AZ, USA
[2] Arizona Genomics Institute, School of Plant Sciences, University of Arizona, Tucson, AZ, USA
[3] Entomology & Insect Science, University of Arizona, Tucson, AZ, USA
*Corresponding author: kcb7@arizona.edu

Abstract
Socially transmitted behaviors are widespread across the animal kingdom, yet comprehensive datasets documenting their distribution and ecological significance remain scarce. Additionally, knowledge of animal behavioral traditions could be essential for understanding many species' responses to anthropogenic disturbances and further enhancing conservation efforts. Here, we introduce the first open-access database that synthesizes data on animal cultural behaviors and traditions. The Animal Culture Database (ACDB) summarizes culture-related features for a total of 56 species. The current release of the database contains descriptions of 112 behaviors including forms of vocal communication, migration, predator defense, foraging practices, habitat alteration, play, mating displays, and other social behaviors for 102 bird and mammal populations across six continents. In addition to offering an open-access resource for researchers, educators, and conservationists, the ACDB represents a critical step toward recognizing the role of social learning in animal populations.
Keywords: *Animal behavior, Conservation, Review, Social learning*

Background and summary

We present the first comparative database of animal culture. This open-access database synthesizes data from studies of behavioral traditions and social learning in wild animal populations collected through a systematic literature review. Our database includes behaviors that have been or could be classified as cultural (i.e., population-specific due to factors other than ecological or genetic differences and transmitted via social learning). These behaviors are described and categorized into domains (e.g., communication, foraging, migration, habitat alteration), and when available, the form of cultural transmission is noted and described (i.e. vertical, horizontal, and/or oblique transmission). We further summarize occurrence data, sampling periods, and taxonomic information on animal populations worldwide. This database, the Animal Culture Database (ACDB), can be used to answer questions related to behavioral flexibility and species' resilience or vulnerability to anthropogenic disturbances. To facilitate the integration between studies of animal culture and conservation measures, the ACDB explicitly documents effects on behaviors and populations from human activity when available from the literature.

Decades of research have documented socially transmitted information forming what have been termed behavioral traditions or cultures in nonhuman animal populations worldwide[1–4]. These traditions include vocal dialects, migration routes, tool-use preferences, and foraging behaviors, which interact with species-typical social structures and behavioral flexibility[5]. Such behavioral diversity is a potentially neglected aspect of current conservation goals, as cognitive and behavioral flexibility have been shown to affect the ability of species to respond to environmental changes, disperse to different habitats, or adapt to human encroachment[6–8]. Despite calls to consider animal cultures when developing conservation strategies (e.g.[9–12]), it is currently unclear how widely cultural behaviors are distributed globally and across the animal tree of life.

Comparative databases have increasingly been used in cultural evolutionary research on human societies to quantitatively test research questions that had previously been explored only qualitatively or in specific cultural settings[13]. While there is extensive literature on behavioral traditions and cultural transmission in a multitude of nonhuman species[1,4,14], there is currently no centralized resource where quantitative data on animal culture can be accessed for analogous research objectives. The Animal Culture Database (ACDB) is an effort to comprehensively catalog socially transmitted behaviors across nonhuman animals. Many species display social learning, but only a proportion of these have recorded sets of behavioral repertoires

in multiple domains[15,16]. Through assembling current scientific knowledge into a consolidated resource, the ACDB could help clarify when this variation is due to research bias and when it constitutes evidence for differences in reliance on cultural behaviors across taxa, highlighting geographic and taxonomic gaps where further primary research is needed. Additionally, the assembled database can be used to test associations between measures of cultural diversity and transmission and responses to anthropogenic disturbances.

A further goal of developing the ACDB is to encourage comparability of research across taxa, in part through integrating data highlighting unifying concepts of socially learned behaviors. For instance, a recent review of research on bird vocal communication discussed the inconsistency in how researchers have historically defined vocalizations as 'songs' versus 'calls' and the need to instead focus on aspects of vocalizations along continuums[17]. The authors argue that this artificial distinction applies not only to the study of vocal communication within birds but across other taxa demonstrating vocal learning, including many mammalian species. Particularities like this may ultimately hinder comparative research on the evolution of vocal communication and social learning. Overall, we suggest that a consolidated resource could promote, when needed, the use of standardized frameworks for behavioral research across taxa.

[Figure 1]

The culture concept

The Animal Culture Database includes published, primary observations of socially transmitted behaviors in wild populations. These observations also encompass work conducted in non-domesticated urban environments or semi-captive research settings. Culturally-relevant behaviors summarized in the database have been present long enough in the relevant groups for the primary researcher(s) to have described them as behavioral traditions or culture. The database at present is agnostic with regards to a definition of animal culture. However, animal behavior researchers have previously discussed the concept of animal culture and its implications in other disciplines. In their paper responding to Brakes et al.'s call[12] for incorporating animal culture into conservation, Carvalho et al.[18] point out the distinction between aiming to preserve behavioral/cultural diversity in a species for its own sake, or evaluating the conservation value of particular cultural behaviors. They caution against the use of the 'culture concept' in conservation in ways that bias towards charismatic groups that are already disproportionately the focus of research and conservation efforts. The same study also highlights the unlikeliness of reaching the evidence standards suggested by Brakes et al.[12] such as demonstrating the effects of particular behaviors on survival and fitness, an attempt at which would slow existing conservation efforts. Although the database at this stage can only emphasize, rather than correct, existing taxonomic biases (see further discussion in Methods and Technical Validation), we tend towards inclusion rather than exclusion of observed behaviors that could be socially learned and transmitted in wild populations to encompass groups that may not have been the focus of significant social learning research.

In addition to compiling the current literature in animal culture, the ACDB further aims to enable researchers to examine the effects of climate change and human disturbances on cross-taxonomic patterns of animal behavior. Specifically, the ACDB currently includes a qualitative variable summarizing anthropogenic effects (discussed further in the Methods section). Similarly, it includes species' IUCN Red List statuses as a proxy for extinction risk and standardized taxonomic data to facilitate interoperability with external datasets on environmental variability and anthropogenic stressors (e.g. [19–22]). Ultimately, as the database expands to include more species and behaviors, data included in the ACDB could be used to explore questions related to environmental heterogeneity and cultural diversity, as well as associations between cultural diversity and conservation status in particular groups.

Methods

We followed four major steps to construct the current release of the ACDB (Figure 1). First, we designed the database following relational database design principles[23]. Second, we conducted a systematic literature search to compile relevant published sources describing animal culture and related topics for particular groups. Third, we conducted a preliminary information extraction from the sources retrieved in the literature for main variables (e.g. culturally transmitted behaviors, behavioral categories, transmission modes, and population locations). Finally, we reviewed the initial coded data and transferred the resulting

information into the relational database structure defined in the first step. Below, we provide additional details.

Database structure

We followed principles of database normalization[24,25] to structure the current release of the ACDB. Specifically, our relational database includes one subject per table with the goal of allowing 1) each species to be linked to multiple groups, 2) each group to be linked to multiple behaviors, and 3) multiple sources to be linked to each of the species, groups, and behaviors tables for different variables. The database includes a total of four tables. First, the species table contains taxonomic data for each species included in the database as well as species-specific information on social structure (Table 1). Second, the groups table contains data pertaining to each group of animals, including location, size, and where it falls in a species' social structure when applicable (Table 2). This last item is particularly important in the case of species with multilevel social structure. One record in the species table can correspond to multiple records in the groups table. Third, the behaviors table contains descriptions for each cultural behavior recorded, including information on social transmission and potential effects from human activity (Table 3). One record in the groups table can correspond to multiple records in the behaviors table. Fourth, the sources table includes details on the relevant primary references for a given entry in the dataset (Table 4). Note that the species, groups, and behaviors table have fields specifying sources for particular variables (e.g. the primary social unit of a species, the size of a group, or the transmission mode of a behavior) linking them to the sources table. A comprehensive description of the database is shown in the diagram in Figure 2.

[Figure 2]

Literature search

We conducted a systematic literature review of published articles examining behavioral traditions and social learning across non-human animals in June 2024. We retrieved relevant papers using the Web of Science search engine based on terms in the title, abstract, and keywords, using the following search terms: (TS=("animal culture" OR "behavio*ral tradition*" OR "cultural evolution" OR "cumulative culture" OR "cultural* transmi*" OR "cultural behavio*r" OR "cultural tradition*" OR "cultural drift" OR "vocal dialect*")) AND TS=("non-human animals" OR "nonhuman animals" OR "bird*" OR "aves" OR "avian" OR "primate*" OR "apes" OR "monkey*" OR "whale*" OR "insect*" OR "spider" OR "arachnid*" OR "arthropod*" OR "chiroptera*" OR "bats" OR "fish" OR "fishes" OR "mammal*" OR "ungulat*" OR "rodent*" OR "amphibia*" OR "reptil*"). These terms were chosen by reviewing papers on social learning and culture in different animal populations and noting frequently used phrases and terms (accounting for different spellings and phrasing), as well as terms for a wide range of taxonomic groups. This initial search resulted in a total of 5,490 papers. Once duplicates were removed using Zotero, the dataset consisted of 5,379 papers. Papers were then imported into Rayyan (rayyan.ai), an online tool for systematic reviews[26] for an initial screening. Rayyan allows users to create lists of keywords for inclusion and exclusion that highlight terms and facilitate filtering of papers. Using Rayyan, we removed the most clearly irrelevant papers, including those on human behaviors, diseases, medical studies, and papers where animal culture referred to cell cultures. This first cleaning step in Rayyan reduced the original number of unique papers identified by the initial search from 5,379 to 2,364. We then manually curated the resulting dataset of articles through excluding conference abstracts, theses, reviews, and methodological papers and studies focused on non-animal groups. We restricted inclusion to papers containing original data on behavior in wild animal populations. This manual filtering resulted in a total of 1,058 papers, which formed the basis for the sources table in the relational database described above.

Qualitative coding of animal culture

The initial coding of the database was focused on extracting qualitative descriptions of relevant behaviors from each paper using a modified schema from the final relational database structure. Papers with original data on animal behavior were tagged with a unique key in Zotero (generated by Rayyan) to link with the working dataset, and following data extraction tagged 'read'. Papers which appeared to be relevant but not available were tagged 'unavailable', and those which appeared relevant but were not in English were tagged with the language to flag for later review; however, for the current release they were excluded. Papers which were not relevant (review papers or those not relating to animal behavior) were tagged

'irrelevant'. For the relevant papers, we extracted taxonomic information, location, dates, and descriptions of possible culturally-transmitted behavior.

Transfer to relational database

After the initial qualitative data extraction, the dataset was reviewed to determine variables for a standardized coding system. The dataset was then converted from CSV files to a relational database structure. This version of the database is stored as a SQLite database. The structure of the database was initialized using SQLiteStudio[27] and was built in R using the packages DBI[28] and RSQLite[29]. The relational structure of the database is shown in Figure 2. The variables for the species, groups, behaviors, and sources tables are defined in Tables 1-4 respectively and in the GitHub repository associated with this publication.

[Tables 1-4]

Data Records

The SQLite database and CSV files for the individual tables which form the database are available on the GitHub repository (https://github.com/datadiversitylab/ACDB_datarelease). These are the files ACDB_v1.sqlite, and species.csv, groups.csv, behaviors.csv, and sources.csv. The R script used to construct the SQLite database from the CSV files is included as ACDB_RSQLite.R. To view and interact with the database in R, the script example_queries.R is included in the repository with the required libraries and some example queries of the tables. Variables for each table are described in Tables 1-4 with the primary and foreign keys linking tables indicated.

Technical Validation

For the construction of the initial qualitative dataset, papers were divided and screened by seven coders (KB, MD, LR, KM, PC, HGV, CRP). To facilitate standardization among coders, we held an initial collaborative training session where the lead author presented the coding approach and we discussed potential challenges and answered questions about the information extraction process. This session was also used to code an initial set of articles. We held weekly meetings for approximately five months to code papers and discuss potential problems in data extraction or solve general questions from coders. During transfer to the relational database, the leading author reviewed this dataset to assess data quality and fix potentially inaccurate codes by referring to the original papers.

The Animal Culture Database V1

The current release of the database contains data from a total of 96 papers on 29 mammal and 28 bird species. 24 of the birds are Passeriformes and the remainder are one each of Accipitriformes, Apodiformes, Charadriiformes, and Otidiformes. Of the mammals, 12 are primates, nine are cetaceans, four are bats, two are rodents, and there are one each of Artiodactyla and Proboscidea. Most of the records in the database are from groups in the tropics (i.e. temperate=40%, tropical=60%). Behaviors can be classified under one or more domains. 64 behaviors were nonexclusively tagged as vocal communication, 38 as foraging, 37 as mating, 32 as social, four each as migration, architecture, and antipredation, one as play, and one as other (not fitting under any of the categories). As many of the behaviors were vocal displays used to attract mates (primarily song in birds and in some whales), 35 of the behaviors tagged as mating were also tagged as vocal communication. A distribution of the domains for which behaviors were tagged, with the counts for each domain corresponding to behavioral records for either Mammalia or Aves, is shown in the Figure 3. Of the species sampled in the database, 34 have an IUCN status of Least Concern, four are Near Threatened, three are Vulnerable, eight are Endangered, four are Critically Endangered, and two are Data Deficient.

[Figure 3]

Limitations

There are clear biases to the data in the current version of the database. In particular, although the literature search used terms to encompass as broad a range of animal taxa as possible, sufficient research was only found on wild populations of mammal and bird species. Although there is evidence for social learning in other taxa, including invertebrate groups such as bees[30] , our search only retrieved

experimental studies on these groups (e.g. [31]). The sample of taxa in the database broadly reflects overall research effort in animal behavior[32,33]. Analyzing the interaction between animal cultural behaviors and responses to anthropogenic disturbances while considering such discrepancies in research effort in conjunction with previously observed biases in conservation research[34] will be an ongoing challenge. Addressing this can include ongoing testing of taxonomic and geographic bias as the database expands and variables from more literature is included.

The coding of the first version of the database was not conducted by taxonomic experts on the relevant groups. While the variables defined so far are relatively straightforward, this is a potential limitation on accuracy and depth of coverage. We have adapted guidelines for best practices from the construction of comparative cultural databases in the social sciences[13] such as making the data open access and inviting feedback/corrections, and including qualitative evidence and references for each code. As the database expands, we hope to develop a pipeline for integration of external contributions from animal behavior researchers.

Usage Notes

Taxonomic names were matched to their records in the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy to ensure consistency and interoperability with other datasets. The GBIF usageKey is included as a column in the species table containing taxonomic information as variable 'GBIF'. We acknowledge that the current release of the database includes a limited sample of potential populations and behaviors. We invite commentary on the structure, variables, and data to alter and improve future versions as the database grows to include more studies, groups, and behaviors. The database will also be deployed as a website, and we plan to add functionality for other researchers to submit primary observations from field research to broaden coverage and refine existing records of socially learned behaviors and cultural groups. Soliciting these contributions will ideally encourage knowledge sharing by researchers of a diverse range of taxa and with expertise in different methodologies.

Code Availability

R version 4.3.2 and SQLiteStudio[27] were used to build the relational database and populate tables with data from the CSV files. The R script and CSV files are available in the GitHub repository at https://github.com/datadiversitylab/ACDB_datarelease.

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Author contributions

K.B. conceived of the database. K.B. and C.R.P. wrote the draft. K.B., M.D., L.R., K.M., P.C., H.G.V., and C.R.P. coded the initial data from the literature search. K.B. curated the data for the linked tables and coded the relational database with supervision from C.R.P. All authors reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

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TABLES

Table 1. Definitions for species-level variables

species	
species_id [primary key]	Scientific name of the organism(s) in the format Genus_species. If the population/behavior was attributed to a subspecies, formatted as Genus_species_epithet. If the source(s) describing the group or behavior used an older version of the species name, the accepted form of the species name in GBIF was used.
common_name	Common name of the species in English
GBIF	GBIF usageKey for the species following gbif.org/species/
canonicalName	Canonical name from GBIF API
Genus …Phylum	Taxonomic names from GBIF backbone
primary_social_unit unit_evidence unit_source	The largest social unit for this species in which individuals maintain stable membership, adapted from Prox & Farine 2020 and Groot et al. 2023. Individual (no stable association with conspecifics); pair (two individuals, presumably mating pair); family (unit is composed of related individuals); group (unit includes unrelated individuals, may display fission-fusion behavior)
IUCN	Current IUCN Red List status

Table 2. Definitions for variables on social groups within species

groups	
group_id [primary key]	Unique ID for each group. Integer starting with 700000
species_id	Foreign key linking to species table
group_name	Name of the group or population, e.g. Northern Resident killer whales or Gombe chimpanzees. Was assigned based on location if none appears to be commonly used.
group_level	The group level, relative to the species primary unit, to which cultural behaviors are attributed. 0+ with primary unit as 0; e.g. for killer whales 0 = matriline, 1 = pod, 2 = clan, 3 = community/population, 4 = ecotype, 5 = species
group_above	In the case of species with nested social structure, name of group directly above or encompassing the coded group; e.g. if focal group is Southern Resident killer whales, the group above this is the R-type or resident killer whale ecotype
size size_evidence - size_date - size_source -	Approximate group size in number of individuals
location_evidence	As specific information possible on location, including research site, city, country, etc.
lat	Approximate latitude for location of population
long	Approximate longitude for location of population

Table 3. Definitions of variables describing behaviors for groups

behaviors	
group_id	Foreign key linking to groups table
behavior_id [primary key]	Unique ID for each behavior. Integer starting with 2.
behavior	Short name describing behavior, e.g. vocal dialect, termite fishing, lobtail feeding
behavior_description	Description of the behavior, placed in context of the species and the focal population(s)
behavior_source	Primary source used to describe the behavior
start_date	First observed date of behavior in the literature
end_date	Most recent observed date of behavior in the literature
vertical vertical_evidence - vertical_source -	Behavior is transmitted from parents to offspring
horizontal horizontal_evidence - horizontal_source -	Behavior is transmitted among peers in the same generation
oblique oblique_evidence - oblique_source	Behavior is transmitted from unrelated adults to juveniles
domains domains_evidence - domains_source	One of more of migration (knowledge of migration routes or sites); foraging (methods or tools of hunting or obtaining food, knowledge of food or resource patches, etc.); vocal communication (vocal transmission of information to others, e.g. songs and vocal dialects); antipredation (predator knowledge and avoidance); play (nonfunctional behavior that appears to be ‘for fun’); mating (mating displays, breeding sites, mate selection); architecture (modifications to the physical environment- nest building, burrows, etc.); social (non-mating social behaviors, such as those that reinforce group identity)
anth_effects anth_source -	Any effects of human activity on the behavior

Table 4. Metadata for variable sources and references

sources	
source_id [primary key]	Unique ID for each source in format firstauthoryear, e.g. baker2004
title - year - authors - doi -	

Caption: Descriptions of variables in each table. For Tables 1-4, all variables named _evidence indicate free text descriptions or evidence for the above coded variable. All variables named _source indicate source for the above variable code and evidence, in the source_id format to link with the sources table.

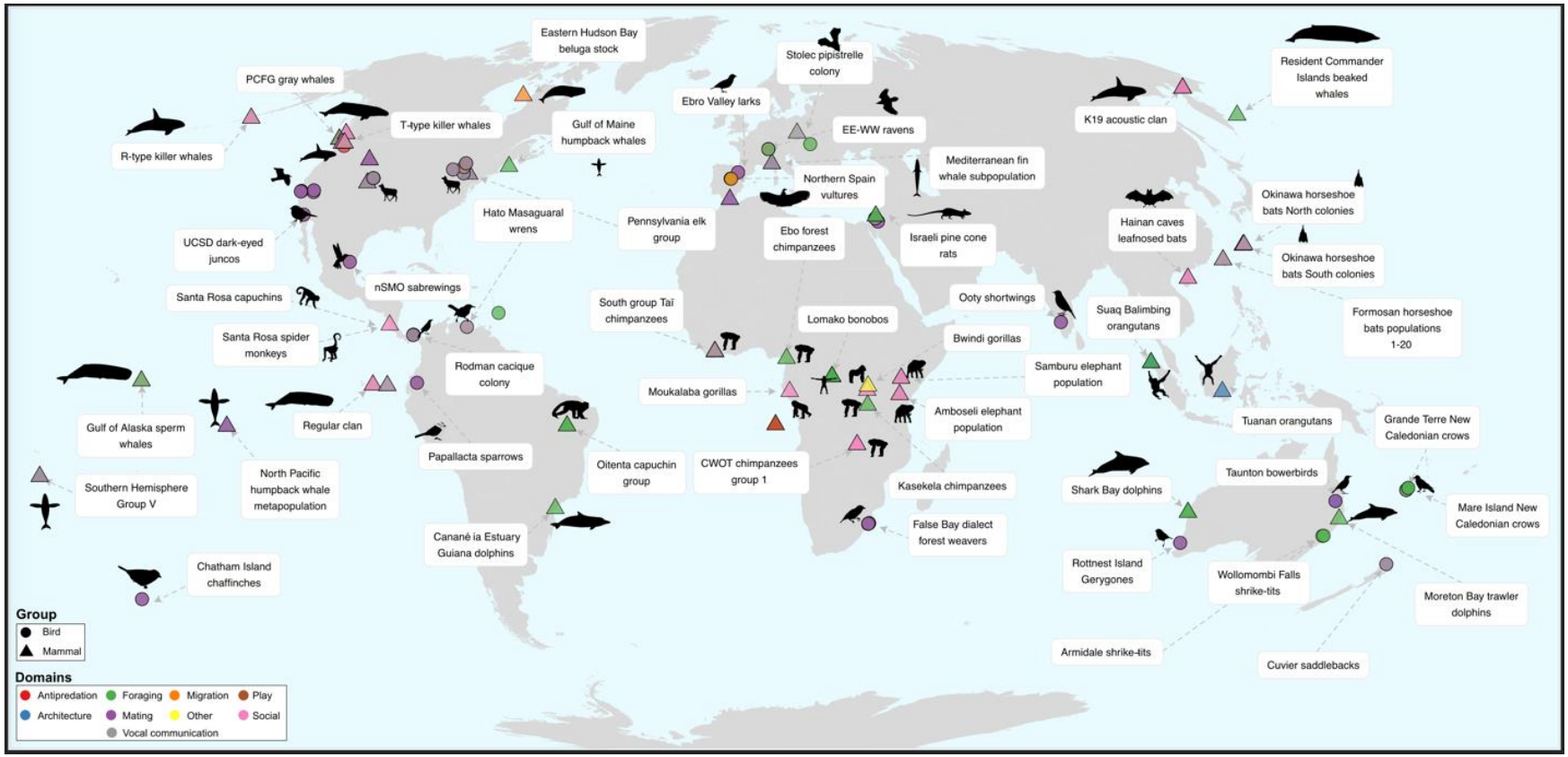

Figure 1. World map showing the geographic distribution of behavior records included in the current release of the Animal Culture Database. Colors indicate domains under which behaviors are classified. Shapes indicate taxonomic class (bird or mammal). A selected number of groups to which the behaviors are attributed are labeled. Images from phylopic.org[35].

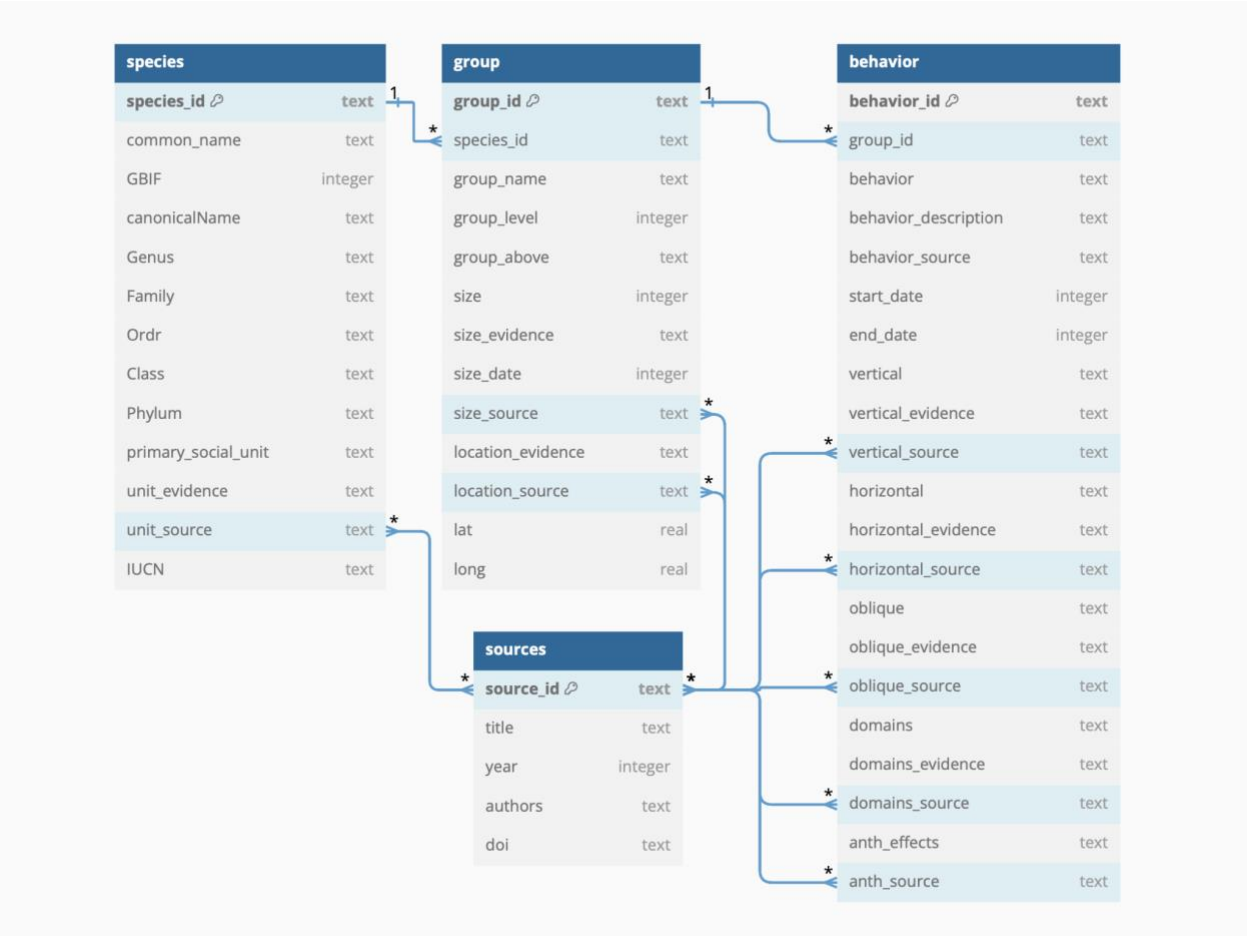

Figure 2. Structure of the relational database used to construct the Animal Culture Database. The four linked tables are shown with blue lines indicating one-to-many or many-to-many relationships. Key symbols indicate primary keys for each table. We define each of the tables and features in them in Tables 1–4.

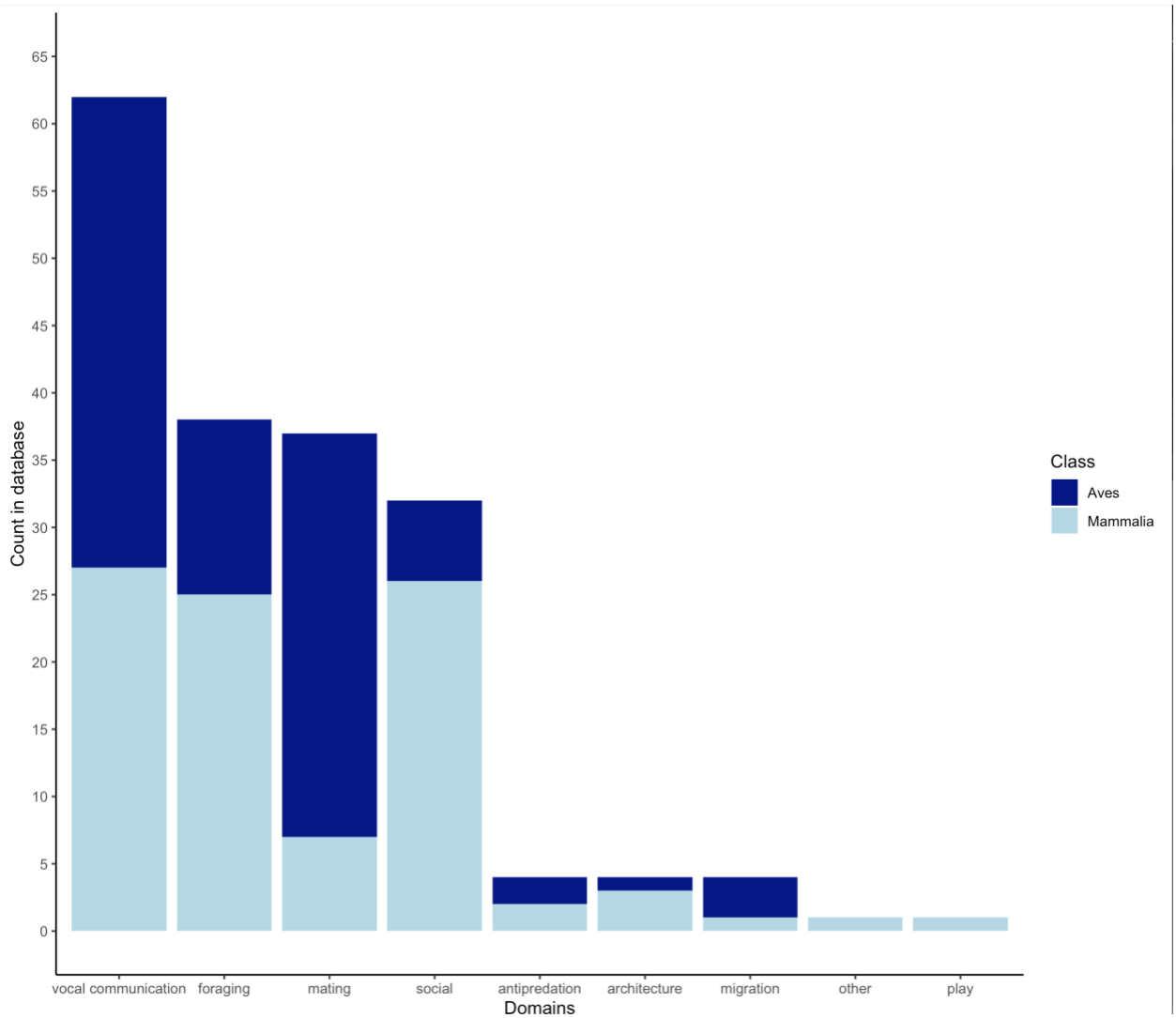

Figure 3. Count of domains under which behaviors are classified in the behaviors table, indicating counts for Aves or Mammalia.