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DATA PAPER

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# TetraDENSITY: A database of population density estimates in terrestrial vertebrates

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## Abstract

**Motivation:** Population density is a key demographic parameter influencing many ecological processes, and macroecology has described both intra- and interspecific patterns of variation. Population density data are expensive to collect and contain many forms of noise and potential bias; these factors have impeded investigation of macroecological patterns, and many hypotheses remain largely unexplored. Population density also represents fundamental information for conservation, because it underlies population dynamics and, ultimately, extinction risk. Here we present TetraDENSITY, an extensive dataset with > 18,000 records of density estimates for terrestrial vertebrates, in order to facilitate new research on this topic.

**Main types of variable contained:** The dataset includes taxonomic information on species, population density estimate, year of data collection, season, coordinates of the locality, locality name, habitat, sampling method and sampling area.

**Spatial location and grain:** Global. Spatial accuracy varies across studies; conservatively, it can be considered at 1°, but for many data it is much finer.

**Time period and grain:** From 1926 to 2017. Temporal accuracy is yearly in most cases, but studies with higher temporal resolution (season, month) are also present.

**Major taxa and level of measurement:** Amphibians in terrestrial phase, reptiles, birds and mammals. Estimates derive from multiple methods, reflecting the study taxon, location and techniques available at the time of density estimation.

## KEYWORDS

abundance, amphibians, birds, density, mammals, reptiles

## 1 | INTRODUCTION

Population density has been widely investigated in macroecology and is fundamental to conservation because it is a direct proxy for extinction risk (Brown, Mehlman, & Stevens, 1995; Currie & Fritz, 1993; Sanderson, 2006). Population density varies enormously among species but is also extremely variable within species, both in space and in time (McGill, 2008). Many macroecological studies essentially focus on presence/absence data. Species abundance and density data can be much more informative, but their application is generally limited by the lack of such data. Understanding the temporal, spatial and life-history

drivers of population density in animals is a major challenge of macroecology.

Much research has already focused on these questions, but the noisy and sparse nature of data has led to several unclear findings. For example, it is widely known that body mass scales inversely with population density, presumably because it is the primary determinant of metabolism and resource use (Blackburn et al., 1993; Currie & Fritz, 1993; Damuth, 1981; Silva & Downing, 1995). Although the size-density relationship explains a large part of the variance of population density, a considerable amount of variability in density remains unexplained. In terrestrial mammals, for example, density varies between three

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and four orders of magnitude at any given body mass (Silva, Brimacombe, & Downing, 2001). Confounding factors, such as sampling area (Blackburn & Gaston, 1996), may alter the shape of the density–body size relationship, as may resource partitioning among sympatric species (Pacala & Roughgarden, 1982), biases in the published literature toward high density estimates (Lawton, 1990; White, Ernest, Kerkhoff, & Enquist, 2007), and the spatial extent of studies (Blackburn & Gaston, 1997).

In macroecology, population density has mostly been explored in terms of interspecific variation, yet there is substantial variation in the density of populations within species (McGill, 2008). The environmental context, including climatic conditions, resource availability and partitioning and direct biological competition, certainly plays a fundamental role in determining local population abundance (Currie & Fritz, 1993; Pettoelli, Bro-Jørgensen, Durant, Blackburn, & Carbone, 2009). For an investigation of such patterns, spatial information is required. Yet, these data are generally lacking in global datasets of life-history traits, which are largely based on average estimates (e.g. Jones et al., 2009). Clearly, the more data are available, the better we will be able to explore such questions.

Better data on population density can contribute to conservation biology by identifying conditions and traits that allow species to attain a larger population size within a given area. For example, a common assumption in biogeography and conservation is that abundance is high at the centre of the geographical range and decreases toward the edges (Brown, 1984), but this assumption is controversial and probably does not hold for many, perhaps most, species. Nevertheless, this notion of an 'abundant centre' has proved influential in a variety of areas in conservation biology, such as where reserves should be placed, where extinction risks are high, and around the dynamics of gene flow across broad areas (Sagarin & Gaines, 2002). Improving our understanding of how population density varies across time, space and species will ultimately contribute to more informed conservation decisions. Changes in population density are significant for purposes of biodiversity monitoring (Collen et al., 2009; Santini et al., 2017). Building a large dataset on population density estimates on a wide range of organisms becomes pivotal to building a solid theory that can contribute to conservation efforts.

In this data paper we present TetraDENSITY, a global dataset of population density estimates for terrestrial vertebrates, which can prompt new investigations on this fundamental aspect of animal ecology.

## 2 | DATA COLLECTION

We collected population density estimates from the literature (including peer-reviewed and grey literature) for terrestrial amphibians, reptiles, birds and mammals. For amphibians, a large amount of data exists from breeding aggregations (e.g. counts of breeding individuals/egg clutches per pond). However, these aggregations often last only a few days, whereas the regulation of adult populations is more strongly related to the features of the habitat in which adults spend most of their lifetime (Govindarajulu, Altwegg, & Anholt, 2005; Vonesh & De la Cruz, 2002). Therefore, we excluded short-term breeding aggregations from the dataset.

Data gathering was carried on until August 2017. L.S. searched Google scholar using the following search string: (population density

TABLE 1 Number of density estimates by taxonomic group

Class	Orders	Families	Genera	Species	Records
Amphibia	2	20	43	79	541
Reptilia	3	33	141	284	1,054
Aves	36	141	707	1,174	8,544
Mammalia	17	73	287	564	8,107

OR population abundance OR Mark-recapture OR Distance Sampling OR Census) AND (Amphibian OR Reptiles OR Birds OR Mammals). The first 1,000 returned hits were retained. L.S. and N.J.B.I. complemented this data collection with records from the YouTHERIA (utheria.org). Additionally, L.S. and G.F.F. opportunistically searched for additional articles by searching for cited references in the collected papers, ad hoc search on poorly represented taxonomic groups in the dataset. G. F.F. added unpublished data collected during fieldwork for a few species of amphibians and reptiles. Finally, during the whole duration of the data collection L.S. kept updating and recorded newly published articles by Google notifications using the key word 'population density'. From each paper, we recorded the species name, the density estimate, the year of data collection, the coordinates of the locality, the locality name, the season when applicable, habitat and sampling method (Table 1). In a few instances, data were extracted from figures using WebPlot-Digitizer 3.10 Desktop (<http://arohatgi.info/WebPlotDigitizer/>; Rohatgi, 2016). In some cases, the coordinates were reported in the papers (with no specified precision), whereas in others only the locality name was reported. As a consequence, coordinates can be more or less precise depending on how coordinates were reported, how small the locality was and how large the study area. All coordinates were transformed to latitude–longitude coordinates (in decimal degrees). Most of the references are published in English, and a minority were in Spanish, French, German and Italian.

## 3 | RESULTS

We collected a total of 18,246 population density estimates from 949 references, covering a wide range of orders, families and genera across the four classes of terrestrial vertebrates (Table 1).

These estimates span over several orders of magnitude. Amphibian densities span between 24 and 9,140,000 individuals/km<sup>2</sup>, reptiles between 0.003 and 9,587,000 individuals/km<sup>2</sup>, birds between 0.002 and 9,587 individuals/km<sup>2</sup>, and mammals between 0.00003 and 24,700 individuals/km<sup>2</sup> (Figure 1a,c,e,g). These are not average population densities; therefore, extremely high and low values perhaps reflect transient or boom-and-bust population dynamics. Amphibian estimates are mostly concentrated in America and Europe. Reptile estimates are more widely distributed but lacking from most of Africa, South America and Asia. Estimates of birds and mammals are globally distributed except for most of the Asian continent (virtually no data found for the Middle East and Russia; Figure 1b,d,f,h). Additionally, the spatial distribution of density estimates is largely uneven when considering the number of density estimates available with respect to the number

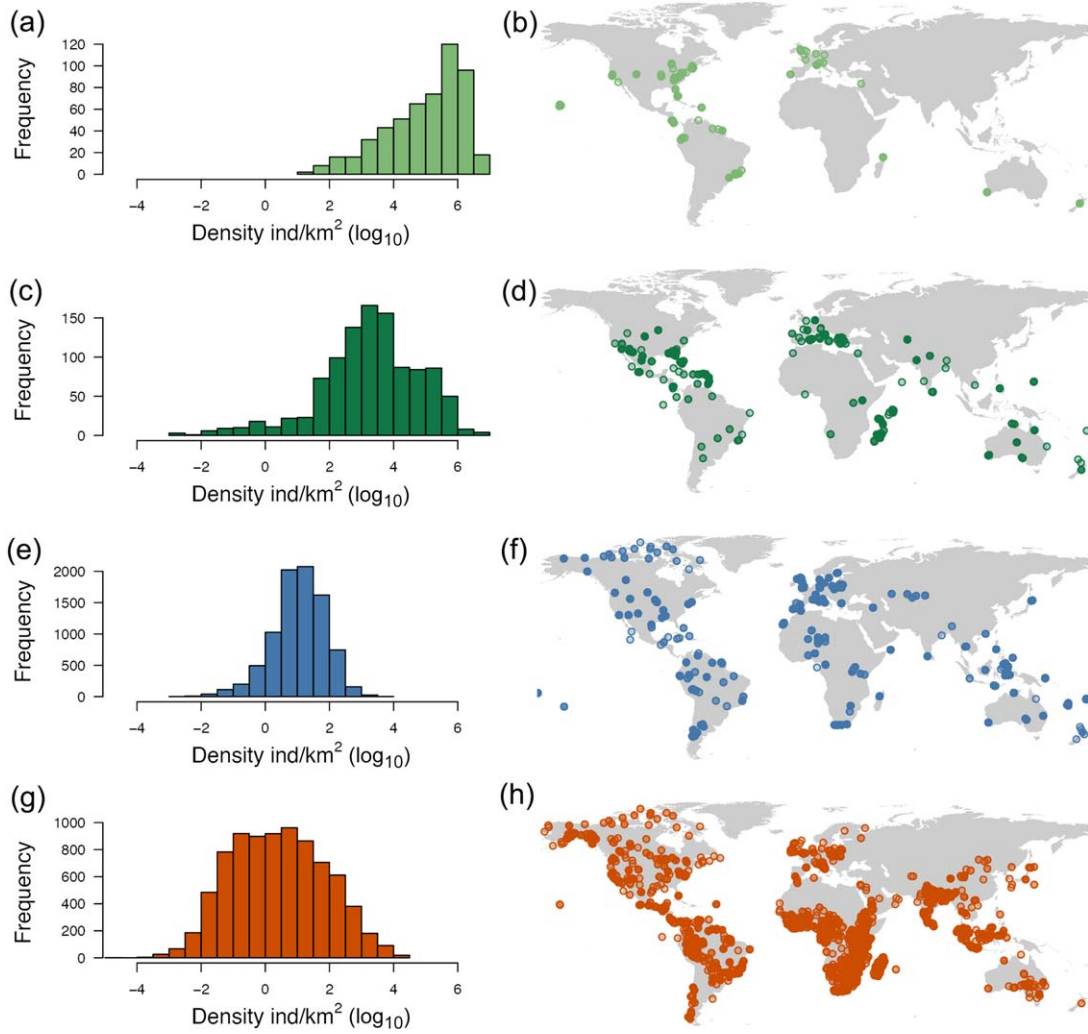


FIGURE 1 Statistical and geographical distribution of the density estimates for amphibians (a, b), reptiles (c, d), birds (e, f) and mammals (g, h)

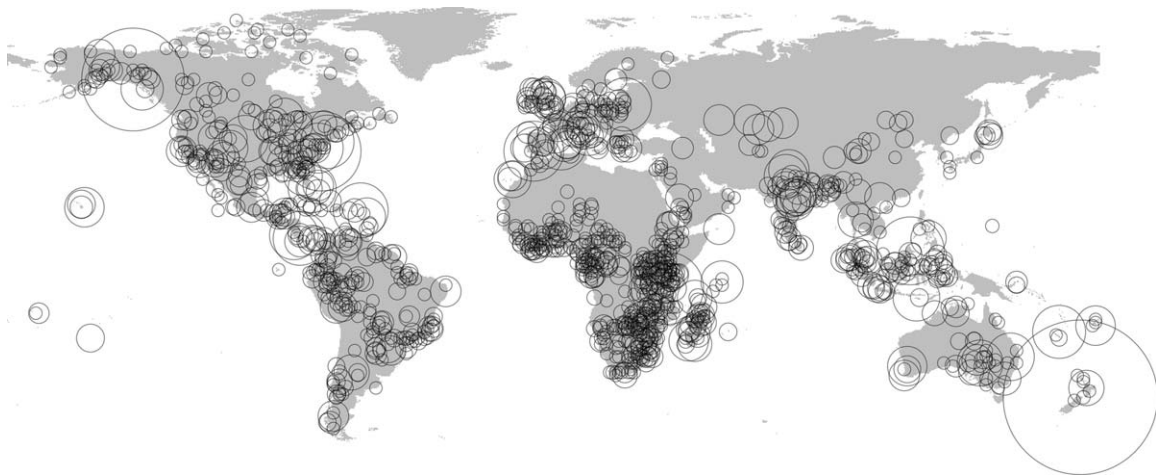


FIGURE 2 Geographic bias in the data collected expressed as number of density estimates divided by number of species with density estimates per 1° cell. Circle size is proportional to the square root of the bias measurement, with large circles indicating areas where a large number of density estimates are available for a small number of species

TABLE 2 Description of the data

Variable	Variable definition	Number of data
Class	Taxonomic class name	18,246
Order	Taxonomic order name	18,246
Family	Taxonomic family name	18,246
Genus	Taxonomic genus name	18,246
Species	Species name	18,246
Subspecies	Subspecies name when applicable	827
Longitude	Longitude in decimal degrees	18,246
Latitude	Latitude in decimal degrees	18,246
Locality	Locality name	15,092
Country	Country name	18,246
Year	Year(s) of data collection	17,129
Season/month	Season(s) or month(s) of data collection. Level of detail dependent on the publication	9,911
Habitat	Qualitative description of habitat type. Level of detail dependent on the publication	8,856
Sampling area	Sampling area size. Depending on the method used, this can refer to the size of the plot, strip transect, grid, trapping area, censused area, etc.	11,085
Sampling area unit	Unit of the sampling area size: ha or km <sup>2</sup>	11,085
Density	Density estimate value	18,246
Density unit	Unit of the density estimate: individuals/km <sup>2</sup> , pairs/km <sup>2</sup> , individuals/ha or males/ha	18,246
Sampling method	Sampling method used to estimate density pooled in broad categories: Incomplete counts (any incomplete count that is extrapolated to a larger area), censuses ('complete' counts, which assume full detection of individuals), distance sampling (including different algorithms and sampling design), home range extrapolation (derived from home range area estimation), mark-recapture (including different algorithms and capture approaches), trapping (removal methods, indicate the minimum number known to be alive)	15,454
Method information	Additional details on the method	9,616
Notes	Opportunistic additional notes on the density estimate or the study	3,521

of species sampled per location (Figure 2). A detailed description of the variables presented in the dataset is provided in Table 2.

## 4 | DISCUSSION

TetraDENSITY is the largest ever assembled dataset of population density estimates in terrestrial vertebrates. It includes site-specific estimates that can vary up to two orders of magnitude within the same species. Amphibians and reptiles, for example, can show extremely high densities, which can refer to highly suitable microhabitats of limited extents, but also reflect the three-dimensional nature of the habitat in arboreal species. Additionally, they can represent temporary fluctuations of the populations. This collation will facilitate exploration of ecological theories such as species abundance distributions (McGill et al., 2007; Xiao, O'Dwyer, & White, 2015) and range size–abundance relationships (Gaston et al., 2000), in addition to large-scale intra- and

interspecific geographical patterns in population density (e.g. Currie & Fritz, 1993; Sagarin & Gaines, 2002).

It is well known that different sampling methods can provide different density estimates. This complicates the comparison of density data gathered using different methods in different areas, and therefore combining densities from a range of sources in the same analysis is non-trivial. However, our dataset includes information on sampling methods, enabling users of our dataset to account for these issues and even perform methodological comparisons.

The population density records are biased toward certain taxa and geographical areas. These biases largely reflect known patterns in ecological research globally. However, our search covered only languages that use Latin script. Including data published in other writing systems would alter the perception of geographical bias, particularly with respect to China and Russia. Additionally, the estimation of population density in animals is not equally applicable to different habitats and

species. The density of populations in more impenetrable habitats and of more rare/cryptic species are less likely to be estimated. Figure 1 provides the clearest view to date of where population density data are lacking.

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## DATA ACCESSIBILITY

The full dataset is accessible at <https://figshare.com/s/e94d0feb494937ce2afa>

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## REFERENCES

- Blackburn, T. M., Brown, V. K. V., Doube, B. B. M., Greenwood, J. J. D., Lawton, J. H., Stork, N. E. N., & Storki, N. E. (1993). The relationship between abundance and body size in natural animal assemblages. *Journal of Animal Ecology*, *62*, 519–528.
- Blackburn, T. M., & Gaston, K. J. (1996). Abundance–body size relationships: The area you census tells you more. *Oikos*, *75*, 303–309.
- Blackburn, T. M., & Gaston, K. J. (1997). A critical assessment of the form of the interspecific relationship between abundance and body size in animals. *Journal of Animal Ecology*, *66*, 233–249.
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, *124*, 255–279.
- Brown, J. H., Mehlman, D. W., & Stevens, G. C. (1995). Spatial variation in abundance. *Ecology*, *76*, 2028–2043.
- Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R., & Baillie, J. E. M. (2009). Monitoring change in vertebrate abundance: The living planet index. *Conservation Biology*, *23*, 317–327.
- Currie, D. J., & Fritz, J. T. (1993). Global patterns of animal abundance and species energy use. *Oikos*, *67*, 56–68.
- Damuth, J. (1981). Population density and body size in mammals. *Nature*, *290*, 699–700.
- Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., & Lawton, J. H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology*, *37*, 39–59.
- Govindarajulu, P., Altwegg, R., & Anholt, B. R. (2005). Matrix model investigation of invasive species control: Bullfrogs on Vancouver Island. *Ecological Applications*, *15*, 2161–2170.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Michener, W. K. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*, 2648.
- Lawton, J. H. (1990). Species richness and population dynamics of animal assemblages. Patterns in body size: Abundance space. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *330*, 283–291.
- McGill, B. J. (2008). Exploring predictions of abundance from body mass using hierarchical comparative approaches. *The American Naturalist*, *172*, 88–101.
- McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., ... White, E. P. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, *10*, 995–1015.
- Pacala, S., & Roughgarden, J. (1982). Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science*, *217*, 444–446.
- Pettorelli, N., Bro-Jørgensen, J., Durant, S. M., Blackburn, T., & Carbone, C. (2009). Energy availability and density estimates in African ungulates. *The American Naturalist*, *173*, 698–704.
- Rohatgi, A. (2016). WebPlotDigitizer 3.10. See <http://arohatgi.info/WebPlotDigitizer>.
- Sagarin, R. D., & Gaines, S. D. (2002). The 'abundant centre' distribution: To what extent is it a biogeographical rule? *Ecology Letters*, *5*, 137–147.
- Sanderson, E. W. (2006). How many animals do we want to save? The many ways of setting population target levels for conservation. *BioScience*, *56*, 911–922.
- Santini, L., Belmaker, J., Costello, M. J., Pereira, H. M., Rossberg, A. G., Schipper, A. M., ... Rondinini, C. (2017). Assessing the suitability of diversity metrics to detect biodiversity change. *Biological Conservation*, *213*, 341–350.
- Silva, M., & Downing, J. A. (1995). The allometric scaling of density and body mass: A non-linear relationship for terrestrial mammals. *The American Naturalist*, *145*, 704–727.
- Silva, M., Brimacombe, M., & Downing, J. A. (2001). Effects of body mass, climate, geography, and census area on population density of terrestrial mammals. *Global Ecology and Biogeography*, *10*, 469–485.
- Vonesh, J. R., & De la Cruz, O. (2002). Complex life cycles and density dependence: Assessing the contribution of egg mortality to amphibian declines. *Oecologia*, *133*, 325–333.
- White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, *22*, 323–330.
- Xiao, X., O'Dwyer, J. P., & White, E. P. (2015). Comparing process-based and constraint-based approaches for modeling macroecological patterns. *Ecology*, *97*, 1228–1238.

## BIOSKETCH

LUCA SANTINI is a postdoctoral research fellow and his research primarily focuses on the link between macroecology and conservation biogeography, with main interests in species biological traits and their covariation, species distribution patterns, and the effect of anthropogenic impact on natural patterns.

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