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Short Communication

Biased assessment of thermal properties of birds from estimated body density

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A R T I C L E I N F O

Original content: Raw Mass Data from RVertnet and Calculated Densities (Original data)

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A B S T R A C T

Parameter approximation is often necessary when calculating species thermal properties, and researchers historically have assumed animals are spherical when estimating volume and density. We hypothesized that a spherical model would result in significantly biased measures of density for birds, which are generally longer than they are tall or wide, and that these inaccuracies would significantly alter the outputs of thermal models. We calculated the densities of 154 bird species using sphere and ellipsoid volume equations and compared these estimates to one another and to published bird densities measured using more exact volume displacement methods. We also calculated evaporative water loss as a percentage of body mass per hour, a variable known to be critical for bird survival, twice for each species, once with the sphere-based density and once with the ellipsoid-based density. We found that volume and density estimates were statistically similar between published densities and those estimated using the ellipsoid volume equation, suggesting that this method is suitable for approximating bird volume and calculating density. In contrast, the spherical model overestimated body volume and therefore underestimated body densities. This resulted in the spherical approach consistently overestimating evaporative water loss as a percent of mass lost per hour than the ellipsoid approach. This outcome would result in mischaracterizing thermal conditions as lethal for a given species, including overestimating vulnerability to increased temperatures due to climate change.

1. Introduction

Body density (mass per unit volume) is a critical parameter for calculating the fundamental thermal constraints on an animal (Kearney et al., 2021). This parameter, however, is not often available for a given species. Both mass and volume are needed to calculate density, and although mass is relatively easy to measure and is available for many species (e.g., Chamberlain, 2021; Dunning, 2008; Silva and Downing, 1995), finding the volume of an animal is more difficult. Exact volumes of birds, for example, have sometimes been calculated using water displacement (Hazlehurst and Rayner, 1992) or by making casts (Dubach, 1981), but this can be tricky (or not allowed) if working with museum specimens that may not be damaged.

There are published equations for estimating volume from body length for frogs (Tracy, 1972) and lizards (Norris, 1967). Generally, however, when we calculate a bird's volume we assume that the creature is a sphere (Buckley et al., 2021; Mitchell, 1976); this is likely a historical artifact because the equation for a sphere is relatively simple $\left(V = \frac{4}{3}\pi r^3\right)$ and museums often record a specimen's body length (2r) before archiving it in a collection, or the length can be acquired readily. Every point on the outside of a sphere is at the same distance *r* from the center of the sphere; birds, however, are distinctly non-spherical, typically being significantly longer than they are tall or wide. These are characteristics of an ellipsoid rather than a sphere, and is likely why well-used thermal programs such as NicheMapR assume an endotherm is represented by an ellipsoid by default (Kearney et al., 2021). Although the distinction may seem pedantic, the greater the difference between length and radius of a bird's body, the more volume will be overestimated by use the sphere equation. This would result in significantly smaller estimations of density and inaccurate conclusions regarding thermal constraints. Here we estimate the degree to which sphere-based volume calculations of birds underestimate body density, and whether ellipsoid measurements of volume result in sufficient approximations of body density for quantifying thermal properties of birds in a mechanistic model.

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2. Methods

We obtained 5 specimens each (3 males and 2 females) for 154 species of birds at the Harvard Museum of Comparative Zoology (MCZ). Specimens were selected as part of a separate project on birds in the Mojave Desert. Species were included in the study if they appeared in the Mojave Desert surveys conducted by Iknayan and Beissinger (2018), or if their ranges as calculated by Fink et al. (2020) cross into the Mojave Desert. Waterbirds were excluded from these measurements unless the species was specifically surveyed for by Iknayan and Beissinger (2018).

For each specimen, we measured the length, width, and height to 0.1 mm using digital calipers. If the bird was too large for the calipers, as with some of the bigger raptors, we used a steel ruler to measure to the nearest millimeter. Length was measured from the base of the mandible to the base of the cloaca; as bird feathers are not part of the metabolic process, we did not include measurements of tail feathers as part of the body length. Width was measured at the widest part of the bird near the midpoint of the breast, not including the wings. Height was measured from back to the greatest distance of the breast.

These specimens usually did not have their masses recorded at the time of collection. We obtained mass data for each species from VertNet, a database that contains data for specimens from hundreds of museum collections around the world. For each species, we used the rvertnet package (Chamberlain, 2021) to search for specimens that had their masses and sexes recorded prior to their preparation for a museum collection, and we downloaded all data associated with these specimens. Through proofing, we discovered that apparent typographical errors existed in this dataset, usually in instances where the original data transcriber forgot to place a decimal point and inflated a single data value by a factor of 10 or 100. We removed outliers from each species using the outlier R package (Komsta, 2022) to ensure that mean mass was not influenced by what were likely typographical errors.

Sexual dimorphism in body size is common in birds (Owens and Hartley, 1998), which would result in different volumes and masses depending on sex, though there is no reason it should affect density. To ensure we were calculating density as accurately as possible, we assumed intraspecific males and females had different average masses. We calculated the volume for each specimen individually using the equations for both an ellipsoid and a sphere, assumed males of the same species had the same mass as the average of all the males of that species from VertNet, and assumed females of the same species had the same mass as the average of all the females of that species from VertNet. We then calculated the density of each specimen twice, once by dividing the mass by the ellipsoid-estimated volume and once by dividing the mass by the spherical-estimated volume. We then averaged these values to calculate a single average ellipsoid-based density and a single average sphere-based density per species.

After comparing volume and density estimates from ellipsoid and spherical estimates, we compared their densities estimates to known values from 15 of the species published by Seamans et al. (1995) and Dubach (1981). Due to unbalanced sample size and unequal variance (as revealed by a Levene's Test), we used a one-way ANOVA with a Welch's correction and a post hoc Bonferroni test to determine whether there is a significant difference between the pre-measured densities and the densities calculated using the sphere or ellipsoid volume equations.

Our next step was to see whether differences in densities as calculated by the ellipse and sphere equations resulted in significant differences in estimates of the birds' thermoregulatory processes and constraints. We used the endotherm function mechanistic thermal modeling R program NicheMapR (Kearney et al., 2021; Kearney and Porter, 2017) to generate thermal properties to test these predictions. For each species, we left all parameters in the function at their default settings except for mass and density, and we ran the mechanistic models twice for each species: once with the density calculated from the sphere equation, and once with the density calculated from the ellipse equation. The average species' mass was kept the same for each run so that density was the only variable to change. NicheMapR calculates many output variables, but we selected evaporative water loss as a percentage of body mass per hour as a characteristic variable. This variable is known to be critical for bird survival, particularly those living in desert regions (Albright et al., 2017). We used a paired *t*-test to compare estimated evaporative water loss as a percentage of body mass per hour as calculated with the ellipsoid and spherical methods to determine whether the two approaches for estimating bird densities result in consistent differences in thermal properties.

3. Results

Body volume estimated from spherical estimates of birds (770 specimens of 154 species) was consistently higher than when using the ellipsoid method, resulting in an average difference of 663.6 ± 173.2 kg/m^3 in densities between the two methods (Fig. 1). This apparent bias increased with birds that were of higher body densities (Fig. 1). There were statistically significant differences found in the categories of known densities, ellipsoid-based estimates, and sphere-based estimates (ANOVA, $F = 1219.4$, corrected $df = 34.1$, $p < 0.001$), A post-hoc Bonferroni test revealed that there was no statistically significant difference between published empirical densities and those calculated using the ellipsoid volume equation (Bonferroni test, corrected $df = 26.6$, mean = 769.1, sd = 190.4, $p = 0.82$) (Fig. 2); densities calculated using the sphere volume equation were significantly lower (Bonferroni test, corrected $df = 13.9$, mean = 104.2, sd = 55.2, $p < 0.001$) (Fig. 2). Furthermore, the spherical approach gave consistently lower estimates of estimated evaporative water loss as a percent of mass lost per hour than the ellipsoid approach (paired *t*-test, $t = -22.5$, $df = 153$, p-value <0.001) (Fig. 3).

4. Discussion

We predicted that volume, and therefore density, of birds would be statistically systematically different based on whether we used the sphere or ellipsoid equation. We also expected that these differences would cause densities as predicted by the sphere equation to be less accurate, and that these differences would also influence conclusions about a species' thermal constraints. Indeed, we found that body volume from spherical estimates of birds was consistently higher than when using the ellipsoid method. This, in turn, resulted in a consistent bias in predicted body densities, with the spherical method underestimating densities compared to the ellipsoid method. When compared to empirical measures of body densities (Dubach, 1981; Seamans et al., 1995), the estimates based on the ellipsoid equation was not significantly different. Average body densities estimated by calculating volume with the sphere equation were on average 150.6% lower than those reported from empirical studies. Furthermore, we found that if data from the spherical equations were used to calculate thermal models, they would result in significantly higher estimations of evaporative water loss as a percentage of body mass per hour than from the ellipsoid equation.

This overestimation would lead to inaccurate depictions of an animal's response to its environment at current and predicted increases in temperature due to climate change (see Arnell et al., 2019). Desert birds, such as those measured in this study, are known to live at the edge of their thermal tolerance (Smith et al., 2015, 2017; Talbot et al., 2017), routinely withstanding evaporative water loss of at least 5% of body mass per hour despite a lethal level of 15% per hour (Albright et al., 2017). Overestimations of this variable would inevitably result in mischaracterizing certain thermal conditions as lethal for a given species when in fact the species is still able to survive. Accurate estimations of a bird's response to its thermal environment is critical for researchers aiming to predict how these species will fare under climate change conditions (e.g., Albright et al., 2017; Riddell et al., 2021; Riddell et al., 2019); therefore, scientists should avoid approximating an animal as a sphere when calculating volume or density for thermal equations.

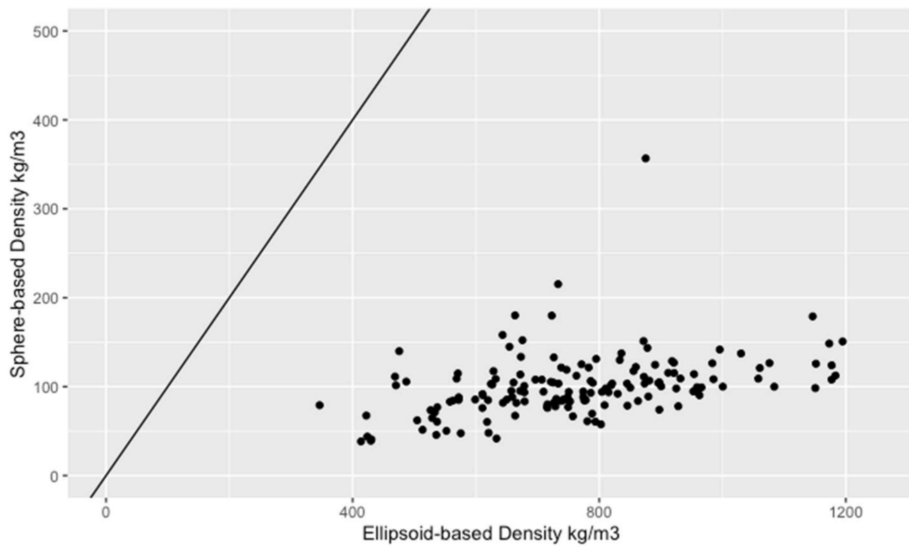

Fig. 1. Densities of each measured species using the ellipsoid volume equation (x axis) and the sphere volume equation (y axis). The solid black line represents a hypothetical 1:1 relationship between the two variables.

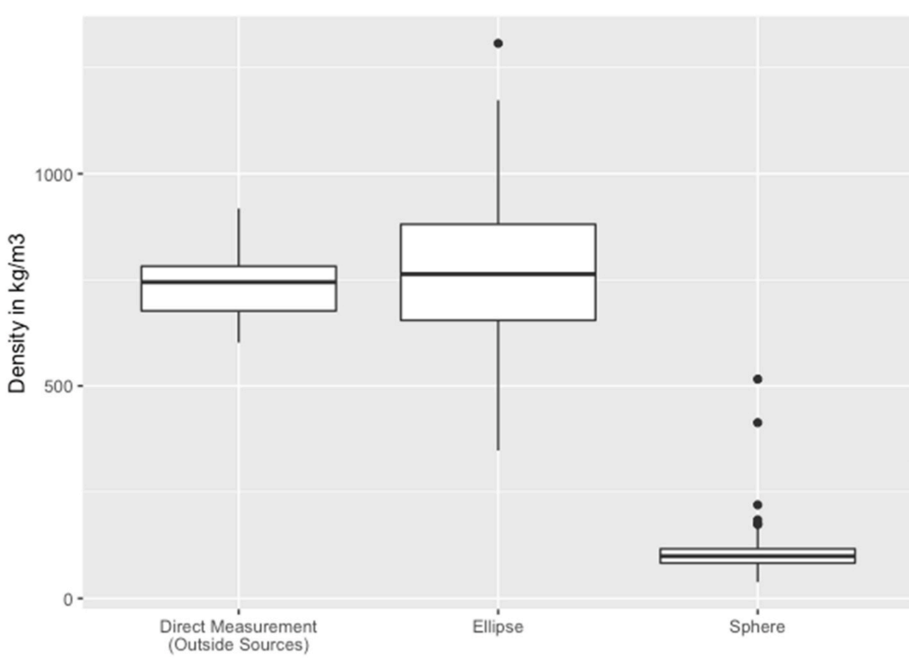

Fig. 2. Body densities calculated for each species measured in this study using the ellipsoid equation (middle) and the sphere equation (right) (n = 154 species). Densities calculated from direct measurement (left) were gathered from published studies (n = 15 species; a subset of the species we assessed). There was no significant difference between the pre-measured densities and the densities calculated using the ellipsoid volume equation (Welch Two Sample *t*-test, t = −1.37, df = 25.95, Bonferroni-corrected p = 0.35). Densities calculated using the sphere volume equation were significantly smaller than the pre-measured densities (Welch Two Sample *t*-test, t = 27.58, df = 13.88, Bonferroni-corrected p < 0.001).

We note that although our ellipsoid estimates of density were not different from empirical measures, some error in our approach could occur because of variation in the degree to which a bird is stuffed compared to its living volume. We anticipate, however, that this would have little effect on our conclusion about ellipsoid vs. spherical assessments. We also found that for some species, we estimated densities over 1000 kg/m^3. We find this unlikely, as water itself has a density of approximately 1000 kg/m^3. At face value, our calculations would suggest that those few species are denser than water. Instead, it is probable that these species do have higher densities than do others in the real world, but the specimens we measured in the MCZ had different masses when they were alive than the average calculated from VertNet. This could result in inflated body densities.

5. Conclusions

These results demonstrate that scientists aiming to create mechanistic thermal models of birds – and likely other endotherms – should not rely on sphere-based equations for calculating volume to estimate density. Instead, it is better to calculate density using volume obtained from the ellipsoid equation, which will require more data but will significantly improve accuracy of results and predictive capacity.

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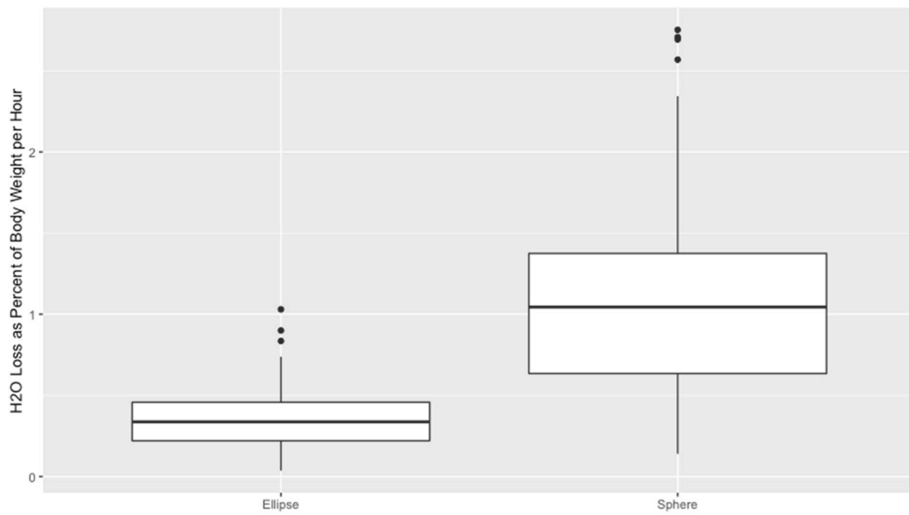

Fig. 3. Estimated evaporative water loss for 154 bird species where body densities were calculated using two different models for estimating body volume (paired *t*-test, $t = -22.5$, $p < 0.001$).

CRediT author statement

Adam J. Eichenwald: Conceptualization, Methodology, Investigation, Funding Acquisition, Visualization, Software, Data curation, Formal Analysis, Writing- Original draft preparation.

J. Michael Reed: Investigation, Formal Analysis, Writing- Reviewing and Editing, Supervision.

Declaration of competing interest

We declare that we have no known competing interests that could have appeared to influence the work reported in this paper.

Data availability

Raw Mass Data from RVertnet and Calculated Densities (Original data) (Dryad)

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