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Practical implications of temporal body mass variation for biologging and comparative studies

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Body mass is an important factor in studying animal behaviour and helps determine the permissible mass of animal-borne devices. However, body mass varies over time, and ignoring temporal variation may risk (i) overestimating the permissible mass to be deployed on animals and (ii) biasing comparative research. Here, we quantify how daily and annual variation in body mass may result in these biases using data from wild populations of birds (Arabian babbler (*Argya squamiceps*), $n = 2281$ body-mass measurements, 145 individuals) and mammals (dwarf mongoose (*Helogale parvula*), $n = 10602$ body-mass measurements, 170 individuals). First, for both species, we demonstrate that when a 5% body mass threshold is calculated when the animals are usually heavier (e.g. evening), the deployed device may be equivalent to 5.4%–6% of body mass when the animals are lighter (e.g. on the following morning). Second, we simulate our data to quantify the relationship between imbalanced weighing times and type-I and type-II error rates. For example, a true sex difference may be missed, if Arabian babbler females tend to be weighed in the evenings but males in the mornings. We conclude with practical recommendations for how to avoid these issues, thereby improving both data reliability and animal welfare.

1. Introduction

Body mass is a fundamental measurement that can help answer diverse questions about animal life history [1,2], behaviour [3,4], physiology [5,6] and health [7,8]. Furthermore, it is a vital consideration when deploying animal-borne research devices, such as

audio recorders, geolocators and identification tags on wild animals [9,10]. Animal-borne devices can provide various pieces of valuable information for animal research [11,12] and facilitate conservation [13,14], but, to do so, they must not considerably affect the animal's behaviour, welfare and survival [15,16]. Accurate evaluation of body mass is therefore critical for safe biologging and reliable research on wild animals [17,18].

While body mass is often treated as a fixed characteristic, it is known to exhibit considerable within-day and within-year variation in a range of birds (e.g. kestrel (*Falco tinnunculus*), southern yellow-billed hornbills (*Tockus leucomelas*) [19,20]) and mammals (e.g. cotton rats (*Sigmodon hispidus*), prairie voles (*Microtus ochrogaster*) and meerkats (*Suricata suricatta*) [21,22]). Neglecting this temporal variation may compromise research in two important ways. First, it may lead to overestimation of the permissible mass of animal-borne devices. Common recommendations for birds and mammals forbid animal-borne devices that, in total, exceed 1%, 3% or 5% of the animal's body mass [23–25], although accumulating studies warn against using these fixed thresholds and emphasize the need to set a biologically relevant threshold for each study (e.g. according to the animal's 'lifestyle' [25–28]). Each individual animal should therefore be weighed before the deployment of research devices to ensure limits, however chosen, are not exceeded. However, if the animal is weighed at a time of day or season when it has relatively high mass, such as before entering the night roost [20,29], the mass of the research device will exceed the target threshold during study periods in which the animal has a relatively lower mass, such as the following morning. Consequently, the burden of carrying extra mass may negatively affect physiology and/or behaviour, which in turn compromises data reliability, animal welfare and even survival [26,27,30–34].

A second issue with ignoring temporal variation in body mass is that if weighing times in comparative studies are not standardized (e.g. if the compared animal groups are more likely to be weighed at different day times), body mass estimates will potentially generate type-I or type-II error rates. A type-I error would be if natural temporal variation in individual body mass is mistakenly interpreted as between-groups differences. For example, diurnal species usually exhibit lower body mass in the morning and higher body mass in the evening [29,35]. Hence, if one population is often weighed in the mornings but another population later in the day (e.g. because researchers always drive a transect in the same direction and start time), within-day mass variation may mistakenly be interpreted as population differences. A type-II error would be if true body mass differences between groups are overlooked. For instance, a true sex difference (e.g. males are heavier than females) may be missed if males are more likely to be weighed when individuals are lighter, and females are often weighed when individuals are heavier. This could occur if, for example, automatic scales are placed at the nest and there are temporal sex differences in nest attendance; females of many species, including Eurasian coots (*Fulica atra*) and house sparrows (*Passer domesticus*), incubate at night while males incubate during the day [36,37].

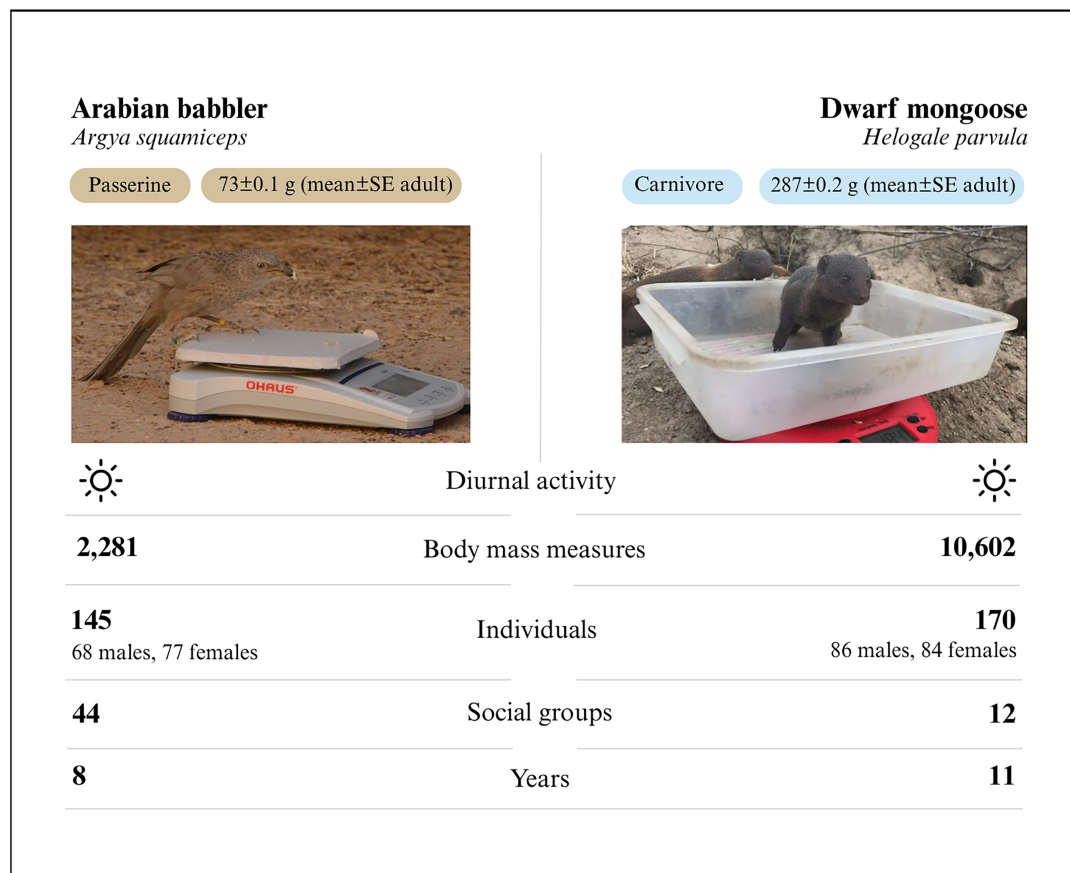
Despite broad interest in patterns of body mass change in animals [38–40] and continued attention to the ethics involving animal-borne research devices [27,34], the two are rarely synthesized. We are also aware of only limited efforts to quantify the extent to which temporal variation in body mass may bias comparative research [22]. One reason for this research paucity may be the difficulty in collecting repeated mass measurements from the same wild animals while they maintain natural behaviour (see, for example, [22]). To address these methodological concerns, we here quantify the extent to which temporal variation in body mass may bias research using extensive repeated-measures datasets from individually identifiable wild birds (Arabian babbler, *Argya squamiceps*) and mammals (dwarf mongooses, *Helogale parvula*) (figure 1). The specific goals of the study are twofold. First, we examined whether mass thresholds for animal-borne devices may be violated when individuals are weighed at specific times of day or year. Second, we tested whether temporal sampling bias could produce type-I and type-II errors when attempting to answer comparative questions. To this end, we used the example of sex differences, quantifying how much weighing times need to be balanced between females and males to avoid type-I and type-II errors.

2. Methods

2.1. Arabian babblers

2.1.1. Study species.

Arabian babblers are songbirds inhabiting the hyper-arid deserts of the Arabian and Sinai Peninsulas, Palestine and Israel [41]. They live in cooperatively breeding social groups of 2–20 individuals [42]. They



body mass measurements (5–9 h after waking up) were taken on an opportunistic basis, with most measurements taken during 2025–2026. Evening observations started by following the group 1–2 h before dusk until it reached its roosting site. During these observations, we took a body mass measurement approximately 30 min before the group entered their night roost. We could reliably anticipate this timing since we observed the group approaching one of its permanent roosting sites shortly before the usual time of roosting (i.e. evening civil twilight [53]).

Weighing was performed using an electronic top-pan balance (accuracy 0.1 g) placed on flat ground and near vegetation into which the birds could flee if feeling unsafe. Each bird was lured with small breadcrumbs into standing on the scale one at a time (figure 1). Mass was recorded only after the bird stood still on the balance, and the reading was stable for approximately 2 s. While individuals varied in their readiness to stand on the scale long enough, all individuals in the study population could be weighed after an initial period of habituation [49] and could potentially be weighed during each observation. The timing of onset and termination of daily activity [53], the timing of each mass measurement and the corresponding body mass were recorded on a smartphone using CyberTracker software [54]. During data preparation, the total mass of one aluminium ring (0.186 g) and 0–3 plastic rings (0.05 g each) was subtracted from the measured mass according to the bird's ring composition at the time.

2.2. Dwarf mongooses

2.2.1. Study species.

Dwarf mongooses are mammals found throughout sub-Saharan Africa, predominantly living in semi-arid savanna habitats [55,56]. They live in cooperatively breeding social groups of 3–20 individuals [55,57] and feed primarily on invertebrates but opportunistically eat snakes, lizards, smaller mammals and eggs [58]. Young reach adult mass around the age of 2 years (Dwarf Mongoose Research Project, unpublished data) at which age breeding positions can be obtained [57], and there is no sexual dimorphism in adult body mass [55].

2.2.2. Study site.

All dwarf mongoose data were collected on the 4 km² Sorabi Rock Lodge Reserve, Limpopo Province, South Africa (24°11'S, 30°46'E) between 2013 and 2023 as part of the Dwarf Mongoose Research Project's long-term data collection protocol. The study site is part of the savanna biome characterized by warm, wet summers and cool, dry winters [55,59]; all groups live in a largely wild habitat free from human modification with the exception of access roads. Study mongooses were habituated to the close presence of human observers, and individuals were uniquely identifiable by small blond hair-dye marks that were routinely applied to their fur.

2.2.3. Weighing procedure.

Mongooses were trained to climb onto an electronic balance in exchange for a few crumbs of hard-boiled egg that formed a negligible proportion of daily food intake. Body masses were recorded after the scale had settled on a fixed value, or a mean value was taken if the scale was oscillating between values within a small range. Three weighing sessions were conducted per observation day. The first weighing session occurred once the majority of the group had emerged from the overnight sleeping burrow (counted in this study as the onset of daily activity), but before they had commenced daily foraging, as groups usually spend some time sunning themselves and grooming before commencing daily foraging [29]. Groups were then weighed approximately 3 h after morning foraging had begun (i.e. after 50% of group members had left the area of the sleeping refuge). The third weighing was conducted once at least 50% of the group had ceased foraging activity at the burrow in which they would go on to sleep that evening. The time when 50% of group members went into the evening sleeping burrow was considered the time at which daily activity ceased. All body mass measurements were collected voluntarily, most individuals in the study population could be regularly weighed, and all group members could potentially be weighed in each session.

2.3. Study species

In sum, both study species are diurnal [29,49] and live in arid/semi-arid environments [53,58]. These similarities allow for investigating variation in body mass during similar daily time frames and annual seasonality. In addition, the absence of sex differences in dwarf mongoose body mass enables simulating the type-I error rate (i.e. detecting a false sex difference), while natural sex differences in Arabian babbler body mass enable simulating type-II error rates (i.e. missing a true sex difference). Finally, the habituation of individuals from both species to the weighing procedure allowed recording of body mass multiple times per day from unstressed wild animals that maintain natural behaviour between measurements [29,49], thereby avoiding a reduction in body mass from repeated trapping [22].

2.4. Data preparation and statistical analyses

Data preparation and statistical analyses were conducted in R (version 4.2.2 [60]). To avoid variance caused by early-life growth [17], only Arabian babblers more than 12 months old [45] and dwarf mongooses more than 24 months old were used (Dwarf Mongoose Research Project, unpublished data). Animals of unknown sex and pregnant dwarf mongoose females were excluded to avoid obscuring differences related to sex *per se*. Weighing time was standardized to represent the number of minutes from the onset of daily activity.

The exact time of activity onset was not known for 64% of the 2281 Arabian babbler body mass measurements. Arabian babblers were shown to initiate daily activity within a short time window around civil twilight [53]. Hence, when the exact activity onset time was not known, we used the time of activity onset from the closest date within 2 weeks of the focal date. If these data were not available, we used the average time of activity onset as a proxy (4 min post morning civil twilight [53]). Similar proxies were used for 5% of evening mass measurements (less than or equal to 45 min before termination of daily activity) for which the exact termination time of daily activity was not known (total $n = 192$ evening body masses; i.e. 4 min before evening civil twilight [53]). Time of morning and evening civil twilight were extracted using the 'suncalc' package (version: 0.5.1, keep: 'dawn' for morning and 'dusk' for evening civil twilight [61]). All local times were converted to UTC times (Coordinated Universal Time).

Linear mixed-effect models (LMMs) were used to account for repeated measurements (lme4 package: version 1.1-35.1 [62]). Model assumptions were assessed using the performance package (version 0.17.0 [63]), which provides diagnostic checks for residual normality, homoscedasticity, multicollinearity and overall model fit. Collinearity between fixed effects was examined by their variance inflation factor, and all were less than 1.1; R^2 was calculated using the part R2 package and 1000 boots (version 0.9.2 [64]).

2.4.1. Temporal variation in body mass

To examine factors affecting body mass, we constructed an LMM with body mass as the response variable. For both study species, we modelled the effect of the following factors, previously shown to affect body mass in birds and mammals: (i) sex [5], (ii) season [5] and (iii) time of day (number of minutes since onset of daily activity [17,65]). For Arabian babblers, we additionally tested the effect of habitat type (wild/human-modified). Following the criteria of Alamán *et al.* [66], habitats were classified as human-modified if the group's territory at least partly overlapped with human settlement or agricultural fields. Seasonal effects were modelled using sine and cosine transformations of Julian date, which capture cyclical annual patterns without imposing abrupt boundaries between calendar years. A nonlinear effect of time of day was tested using a natural spline ('splines' package: version 4.2.2 [60]), with three knots (i.e. the number of points along the predictor where the spline curve may bend and adapt to changes in the data). The models included the animal ID, its social group ID and date (as a factor to account for the non-independence of multiple records per date) as random intercepts. Having year (as a factor) as an additional random intercept did not improve the model. See tables 1 and 2 for sample sizes. The statistical significance of each term was evaluated by comparing the full model with its reduced version without that fixed effect via a likelihood ratio test using the drop1 function with the test argument 'Chisq' [67]. The significance of the seasonal term was compared manually because it consisted of two terms that are only meaningful together (sine_date + cosine_date, see supplementary material code).

Table 1. Results of a linear mixed model testing determinants of body mass in adult dwarf mongoose.

response variable: body mass (gram). random effects: animal ID, group ID and date of observation. n = 10 602 body masses, 1337 dates, 170 animals, 12 groups. Significant terms are in bold.						
term	estimate	SE	χ^2	df	p	R ² estimate (lower–upper CI)
intercept	272.40	6.394				
sex (male)	4.38	3.33	1.72	1	0.19	0.21 (0–2.7)
season			184.49	2	<0.001	3.44 (2.4–6.0)
season (sine_date)	8.51	0.60				
season (cosine_date)	1.2	0.66				
time of day			1756.67	3	<0.001	2.71 (1.7–5.2)
Knot 1	13.78	0.93				
Knot 2	14.14	0.76				
Knot 3	11.17	0.60				

Table 2. Results of a linear mixed model testing determinants of body mass in adult Arabian babblers.

response variable: body mass (gram). random effects: animal ID, group ID and date of observation. n = 2281 body masses, 488 dates, 145 birds, 44 groups. Significant terms are in bold.						
term	estimate	SE	χ^2	df	p	R ² estimate (lower–upper CI)
intercept	68.74	0.67				
sex (male)	4.97	0.61	53.11	1	<0.001	21.70 (13.5–31.1)
season			72.21	2	<0.001	2.90 (0–14.1)
season (sine_date)	0.89	0.14				
season (cosine_date)	0.91	0.13				
time of day			674.36	3	<0.001	6.54 (0–17.3)
Knot 1	3.36	0.39				
Knot 2	5.54	0.25				
Knot 3	2.83	0.25				
habitat (natural desert)	–1.98	0.74	6.80	1	0.009	2.84 (0–14.1)

2.4.2. Temporal body mass change

Relative body mass change between two time points was calculated as a percentage from the mass taken during the earlier time point (i.e. $[(2\text{nd mass} - 1\text{st mass})/1\text{st mass}] \times 100$). This formula was used to calculate mass change: (i) during the day, (ii) during the night and (iii) between seasons. To calculate body mass gain during the day, we compared morning mass (i.e. less than 30 min after activity onset) to evening mass (i.e. less than 45 min before the termination of daily activity) taken from the same individual on the same day. To calculate body mass loss during the night, we compared evening mass to the following morning mass taken from the same individual. To calculate seasonal change, we first identified annual periods with relatively high and low mass for each species. To this end, we extracted the predicted values for the seasonal terms in each model (while holding the other fixed effects in the model at reference or mean values). The distribution of predicted daily body mass values was then divided into three categories based on quantiles. Days with predicted mass values of 33rd percentile or below were classified as the low-mass season, and days with predicted mass values of 67th percentile or more were classified as the high-mass season. Days with predicted mass values between these thresholds were classified as a transition season. We then compared the mean of body mass measurements taken from the same individual during the high-mass season to the mean of body mass measurements taken during the following low-mass season.

2.4.3. Temporal body mass variation and animal-borne devices

To estimate the potential to exceed the permissible body mass for animal-borne devices, we first calculated 5% of the body mass recorded at a time when the animals are usually heavier (e.g. evening). We then calculated how much this absolute mass will be equivalent to at a future time point when the animals are normally lighter (e.g. morning), using the formula $(5\% \times \text{mass at heavier time point} / \text{mass at lighter time point})$. For the daily analysis, we considered all evening body mass measurements as time points with heavier mass and morning measurements from the same individual during the following morning as time points with lighter body mass.

2.4.4. Within-day body mass variation and type-I and type-II error rates

The rate of type-I error was quantified based on the dwarf mongoose data because this species does not exhibit sexual dimorphism in body mass (table 1 [55]). The rate of type-II error was quantified using the Arabian babbler data since this species exhibits sexual dimorphism in body mass (table 2 [5]). We constructed a separate simulation for each species. Both simulations started with initial samples that are maximally biased. The dwarf mongoose simulation started with a random sample of 60 male evening body mass measurements (when both sexes are usually heavier) that were compared to a random sample of 60 female morning body mass measurements (when both sexes are usually lighter). The Arabian babbler simulation started with a random sample of 60 female body mass evening measurements (when both sexes are usually heavier) that were compared to a random sample of 60 male morning body mass measurements (when both sexes are usually lighter). At the first round, we ran 100 LMMs (each with a different random sample), with body mass as the response variable and individual ID as a random effect. The fixed effects were those specified in tables 1 and 2 for each species, in addition to time of day. To test the effect of sex, each model was compared to its 'null' version that was only missing the sex fixed effect via a Likelihood Ratio Test. The proportion of these full-null model comparisons with p -values < 0.05 was considered as the proportion of models detecting a statistically significant sex difference. In the next five rounds, the proportion of sex-wise balanced measurements was increased by 20% per round (figure 2). For instance, in each round (of 100 LMMs each) of the dwarf mongoose simulation, an additional 10% of the male evening body mass measurements were replaced with morning measurements and 10% of the female morning body mass measurements were replaced with evening measurements. At the sixth and final round, the sample was fully balanced (i.e. 50% of male and female measurements were morning body masses and 50% evening body masses).

3. Results

3.1. Temporal variation in body mass

In both species, body mass was lowest at the onset of daily activity and increased significantly across the day (figure 3, tables 1 and 2). In Arabian babblers, body mass rose relatively sharply until around midday,

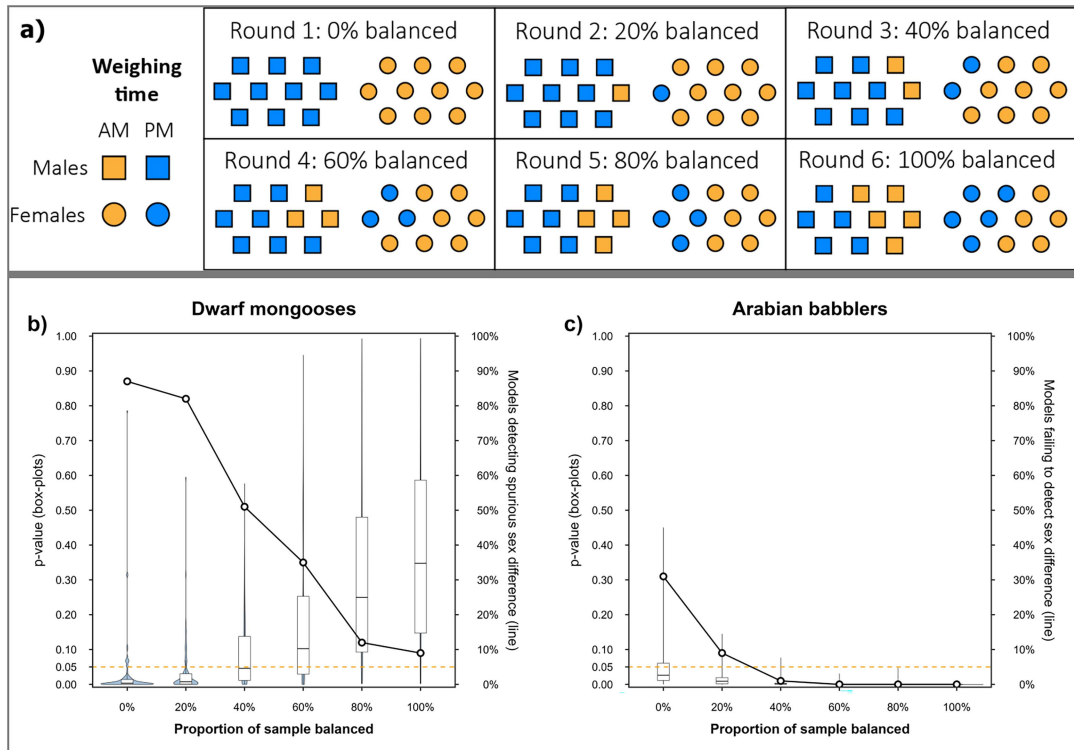


Figure 2. The effect of sampling balance on type-I and type-II error rates. (a) Schematic representation of the simulation design of the dwarf mongoose analysis. Each shape represents six sampled body masses from either males (squares) or females (circles) in either the morning (orange) or evening (blue) that were modelled against the body mass of the opposite sex. Across the six rounds, balance was increased as individuals were more evenly sampled from the two time points. Each simulation was repeated 100 times, resulting in 600 total simulations. The Arabian babbler simulation had a similar structure, but started with all females sampled in the evenings. The distribution of p -values (box-plots) and proportion of models (black solid line and points) detecting (b) a false sex difference in dwarf mongoose body mass (i.e. rate of type-I error) and (c) failing to detect the true sex difference in Arabian babbler body mass (i.e. rate of type-II error).

and then increased more moderately until the birds retreated to their night roost. In dwarf mongooses, body mass increased slowly throughout the day, reaching a plateau in the afternoon. Both species lost body mass overnight and were lighter during a specific annual season (figure 4, tables 1 and 2).

3.2. Temporal body mass variation and animal-borne devices

Devices deployed on animals will often exceed their permissible mass (less than or equal to 5% of the animal's body mass) if it is calculated when diurnal animals are typically heavier (supplementary material, table S2). That is, after midday and in a certain annual season (figure 5).

3.3. Within-day mass variation and type-I

Adult dwarf mongooses did not exhibit a significant sex difference in body mass (figure 3 and table 1). However, bias in weighing time between the sexes will often result in finding a statistically significant sexual dimorphism in body mass (i.e. type-I error, figure 2b).

3.4. Within-day mass variation and type-II error

Adult Arabian babbler males were $7.8\% \pm 0.6\%$ heavier (mean $\pm$ SE) than females ($N = 220/152$ morning, not-summer measurements of 45/42 males/females, respectively; figure 3 and table 2). The proportion of statistical models detecting this true sexual dimorphism depended on the proportion of measurements taken at the same time of the day per sex (figure 2c). For example, if weighing is completely imbalanced between the sexes (i.e. 100% of males are weighed in mornings and 100% of females are weighed in

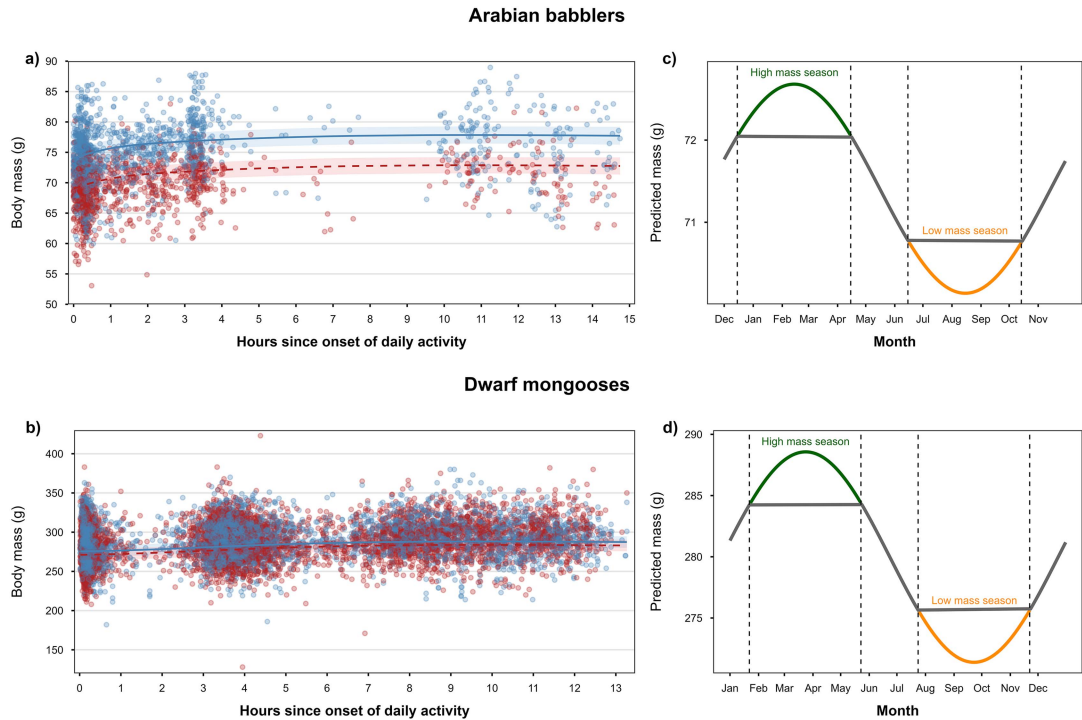


Figure 3. Within-day body mass change in wild adult (a) Arabian babblers and (b) dwarf mongooses. Blue (and solid lines) and red (and dashed lines) represent males and females, respectively. Lines are the predicted curves from the models for time of day per sex. The shaded areas represent the predicted 95% confidence intervals. Predicted body mass by date in (c) Arabian babblers and (d) dwarf mongooses. Low/high mass seasons were defined as dates with predicted body mass less than 33rd percentile/more than 67th percentile, respectively. Dates with predicted body mass between these thresholds were classified as a transition season (grey line).

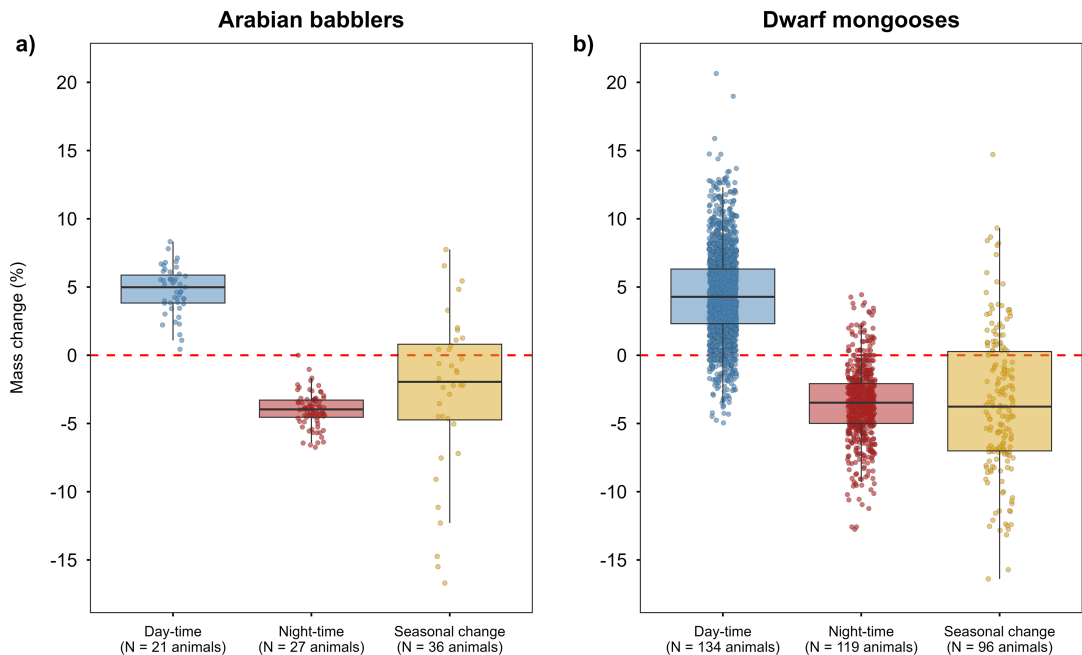


Figure 4. Within-day, overnight and seasonal changes in body mass from consecutive measurements of wild adult (a) Arabian babblers and (b) dwarf mongooses. The horizontal bars represent the median, boxes represent the 25% and 75% quartiles and points beyond the vertical lines (whiskers) are considered outliers. See table S1 in the supplementary material for a summary of the information in this figure.

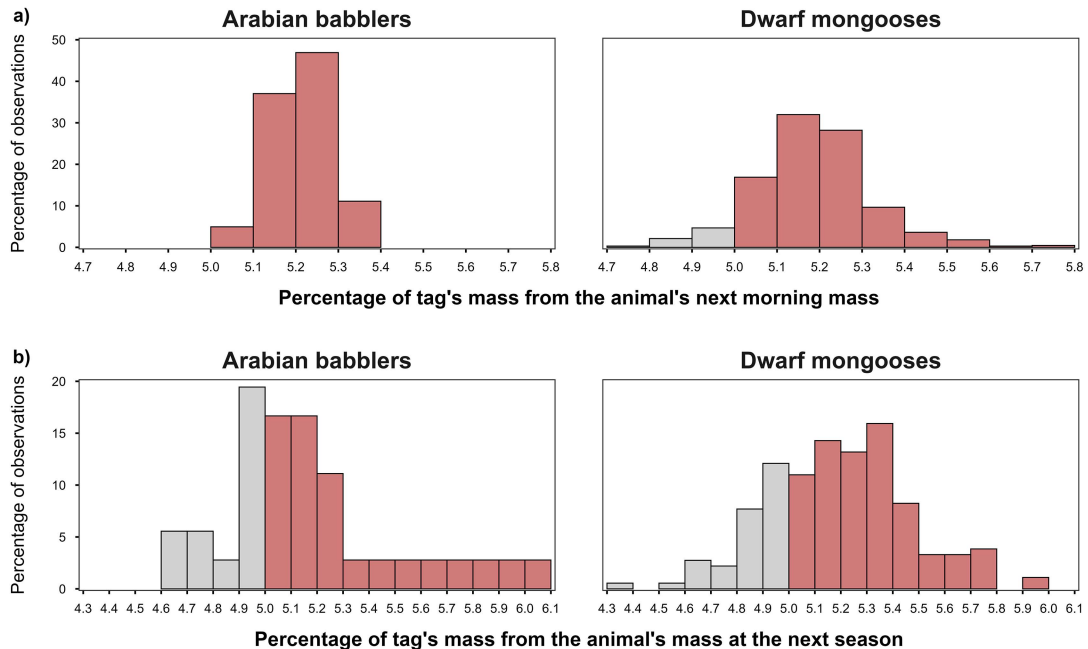


Figure 5. Histogram of the percentage of observations according to the relative percentage of body mass of an animal-borne device when measured (a) the following morning and (b) the following season. Assuming the permissible mass of animal-borne devices was set according to the animal's body mass during the previous midday or previous season, which is typically greater. Observations that exceed 5% of the animal's body mass are in red. See table S2 in the supplementary material for a summary of the information in this figure.

evenings), only approximately 70% of models detected sex difference in body mass (i.e. 30% rate for type-II error).

4. Discussion

4.1. Temporal variation in body

Both study species exhibited temporal variation in body mass (figure 4): (i) mass gain during the day, (ii) mass loss during the night (probably due to metabolic and thermoregulation needs without energetic intake) and (iii) mass gain/loss across parts of the annual cycle. Similar daily and annual patterns were reported in other diurnal birds (kestrels, greenfinches (*Chloris chloris*), yellowhammers (*Emberiza citrinella*), great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), coal tits (*Periparus ater*), marsh tits (*Poecile palustris*), willow tits (*Poecile montanus*) and European nuthatch (*Sitta europaea*) [20,35,68,69]). Temporal terms (time of day and seasonality) accounted for a significant portion of body mass variation in our Arabian babbler and dwarf mongoose models (9.4% and 6.2%, respectively, tables 1 and 2). Hence, ignoring temporal variation in body mass could considerably bias studies among other diurnal birds and mammals, and would potentially result in a similar bias among nocturnal species. The magnitude of temporal variation would also depend on age, sex and social dominance categories, which should thus be accounted for according to the specific animals studied. For instance, temporal variation in body mass seems to be larger in small bird species [35], resulting in greater biases if ignored in smaller than larger species ([16], but see also [24]).

4.2. Temporal body mass variation and animal-borne devices

Temporal variation in body mass represents an under-appreciated cause of error when determining the permissible mass of animal-borne research devices [18,26,70]. Specifically, if the permissible mass of the device is determined according to daily or annual periods where animals tend to be heavier (e.g. evenings and winters), it could be overestimated (figure 5). Even devices within the permissible ranges (1%, 3%

Table 3. Recommended safety margins for deployment of animal-borne research devices on adult Arabian babblers and dwarf mongooses.

species	sex	grams to be deduced from body mass ^a	mean body mass ^b	1%	3%	5%
				of mean body mass (grams)		
Arabian babblers	females	4.8	65.3	0.65	1.96	3.26
	males	5.9	72.1	0.72	2.16	3.16
dwarf mongooses	females	44	272	2.72	8.15	13.16
	males	39	278	2.78	8.35	13.9

^aEach cell presents the mass to be deduced from the body mass measured after midday. Safety margins represent the maximal mass the animals usually gain between onset and termination of daily activity (excluding outliers of the interquartile range: $Q3 + 3 * IQR$, figure 4).

^bAt the onset of daily activity during the season of low mass.

or 5% of body mass) may compromise wildlife behaviour, welfare and survival [16,25,27,30–32]. Hence, deploying additional mass, small as it may seem, will further increase the handicap imposed on the study animal and subsequently compromise data accuracy and animal welfare [25]. The magnitude of this additional mass's negative effects also depends on other characteristics, such as the lifestyle [26] and morphology [28] of the animal. Excess mass may especially impact flying [27,28], diving [33] and breeding animals [27] more severely. Notably, deployment of animal-borne devices on breeding females may be problematic in at least two different ways. First, the device's mass is added to that of the offspring being carried by the female [71]. Second, calculating the permissible mass of a device from the body mass of reproducing females would result in even greater over-estimation of a given percentage mass (e.g. 5%) for that individual.

Neglecting temporal variation in body mass may also result in underestimating the permissible mass of the device if it is determined based on when the animal is usually lighter. Such under-estimation may explain why, in some cases, no negative effect was measured although the animals apparently carried heavy devices. Furthermore, natural decrease or increase in body mass may result in making the attaching harnesses of animal-borne devices too loose or too tight [24,72], with especially significant impacts on flight and dive performance.

4.3. Recommendations for animal-borne devices

First, the total mass of all devices deployed on the animal (e.g. biologgers, harnesses, identification rings/tags) should remain below the target percentage of body mass during the entire research period, not just mass at deployment. To this end, the target mass should be calculated as a proportion of the lowest body mass the animal is expected to attain during the entire study period. If the lowest body mass of the animal is unknown, a 'safety margin' should be deduced from the available mass measurements. Ideally, safety margins would be tailored according to the specific animal. For example, greater safety margins should be used for females during the breeding season to avoid greater handicap during pregnancy [27], egg laying [71] or female and male incubation [73]. Table 3 lists safety margins for Arabian babblers and dwarf mongooses as examples. Given a similar dataset of repeated mass measurements, the R code provided as ESM can be used to map daily and annual variation in body mass of other species and produce population-specific safety margins. In sum, field researchers should tailor the device's mass and form of attachment according to (i) the current condition of the particular individual to whom the device is attached and (ii) its predicted natural variation in body mass during the study period.

A second recommendation is that harnesses used to attach the device to animals should be flexible enough to accommodate the expected change in body mass during the study, avoiding excessive tightness or looseness caused by natural variation in body mass throughout the study period [24,72].

Third, we encourage field studies to include a control group to evaluate the effect that animal-borne devices may cause due to their mass, shape, position, colour or mere presence [25,28,74].

4.4. Within-day body mass variation and comparative research

Body mass is a common and important trait used in comparative studies. For example, masses are often compared between periods (e.g. seasons, before versus after pregnancy/incubation [73,75,76]), categories of individuals (e.g. between sexes, dominance or breeding classes [3,77,78]) and locations [65]. Our simulations demonstrate that even within-day changes in body mass can inflate type-I and type-II error rates if weighing times are not standardized between the compared groups (figure 2). Even if sampling is not imbalanced to the degree of resulting type-I or type-II errors in terms of statistical significance, temporally imbalanced sampling would result in inaccurate estimates of mass in statistical models.

The rates of type-I and type-II errors depend on the ratio between the difference of the compared groups (e.g. between sexes or populations) in body mass (e.g. mean sex difference between Arabian babbler males and females: 7.8%) and the temporal difference in body mass (e.g. mean mass gain between morning and evening in Arabian babblers: 4.8%). The higher the ratio between these factors is in favour of the group difference (i.e. if group-difference > temporal-difference), the more likely that a true group difference will be detected despite a more imbalanced sample. For instance, because the mean sex difference in Arabian babblers is much greater than the daily temporal difference (group-difference/temporal-difference ratio = 1.6), the true sex difference in this species is detectable even if most samples were temporally imbalanced (figure 2c). However, type-II error is expected to be higher when sex differences are subtler. In contrast, the greater this ratio is in favour of the temporal differences (i.e. if group-difference < temporal-difference), the greater the risk that the temporal difference will mask true group differences (i.e. type-II error) or lead to the detection of a false group difference (e.g. type-I error as in the dwarf mongoose simulation in figure 2b). To avoid such erroneous inferences, comparative studies should balance weighing times between the compared groups at the data collection phase and statistically control for weighing times at the data analysis phase.

5. Conclusions

- (1) Leveraging extensive datasets from wild birds and mammals, we demonstrate that neglecting temporal variation in body mass can lead to (i) overestimating the permissible mass of animal-borne research devices (figure 5) and (ii) an increase in type-I and type-II error rates in comparative studies (figure 2).
- (2) We provide further empirical evidence in support of the repeated calls to evaluate the effects of animal-borne devices in research.
- (3) We make practical recommendations to avoid these biases and provide an R code to generate species-specific safety margins when calculating the permissible mass of animal-borne devices.

Ethics. The total mass of three plastic rings and one aluminium ring placed on Arabian babblers was 0.336 g, which is approximately 0.5% of the mean body mass of adult females during summer [5]. It is thus not expected to affect the birds significantly. Research permits were obtained from the Israeli National Parks Authority (2014/40304, 42538/2020, 43151/2022, 43511/2024). Work on dwarf mongooses was conducted under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013), and ethical approval from the University of Pretoria, South Africa (Animal Ethics Committee: NAS321/2022) and the University of Bristol, UK (Animal Welfare and Ethics Review Body: UIN/17/074), and in line with ASAB guidelines for the ethical treatment of animals [79]. No animal-borne devices were deployed on dwarf mongooses as part of this or any other associated study.

Data accessibility. The data and code used for all analyses and all results are provided as R data frames and R code in the supplementary material [80].

Declaration of AI use. AI technology was used to assist in writing and verifying the R code used for this study.

Authors' contributions. Y.B.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review and editing; O.K.: Data curation; A.N.R.: data curation, funding acquisition, writing—review and editing; J.J.A.: data curation, formal analysis, investigation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests

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