





REVIEW


Re-weighting the 5% tagging recommendation: assessing the potential impacts of tags on the behaviour and body condition of bats


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ABSTRACT

1. Considerable advances and breakthroughs in wildlife tracking technology have occurred in recent years, allowing researchers to gain insights into the movements and behaviours of a broad range of animals. Considering the accessibility and increase in use of tracking devices in wildlife studies, it is important to better understand the effects on these on animals.
2. Our endeavour revisits a guideline established in 1988, which proposes that bats may encounter body condition or health problems and alter their behaviour when carrying tags weighing more than 5% of their body mass. Through a systematic literature review, we conducted a meta-analysis to identify the impacts of tags on bats, including 367 papers from 1976 to 2023 that discussed, mentioned, employed, or quantified tagging of bats.
3. We noted that the proportion of studies exceeding the 5% rule has not changed in recent years. However, the impact of tags was quantified in few studies for behaviour ($n=7$) and body condition ($n=10$) of bats. We were unable to assess whether tags weighing less or more than 5% of the bat's body mass impacted bats, but our meta-analysis did identify that tags, irrespective of mass, affect the behaviour and body condition of bats.
4. Although the overall magnitude of measured effects of tags on bats was small, progress has been made to advance our understanding of tag mass on bats. Naturally, there is a bias in reporting of significant results, illustrating the need of reporting results when there is no apparent effect of tags on bats. Our findings highlight the need for rigorous reporting of behaviour and body condition data associated with tagging of animals and illustrate the importance for studies comparing how tracking devices of different dimensions and masses may impact bat species to ensure research meets rigorous ethical standards.

INTRODUCTION

Wildlife is facing a difficult world in the Anthropocene (Otto 2018) and thus it is key to understand how they interact with their environment. This understanding started with simple behavioural observations decades ago and has

since benefited from recent rapid advances in technologies, greatly impacting ways in which scientists can study and understand the natural world. Indeed, tracking and monitoring of wildlife has provided invaluable information on many research topics across the tree of life—from advancing our knowledge of behaviour and movements of marine

animals (e.g. Hussey et al. 2015) to terrestrial animals (e.g. Kays et al. 2015). The resulting information has revolutionised our understanding of how animals interact with other animals and with their environment, which aids development of sound decision-making and conservation strategies (Pimm et al. 2015). During these technological advances, it is increasingly important to ensure that tracking devices do not alter behaviour and that high standards of animal welfare are maintained.

Tracking devices have decreased in mass and size, allowing for a broader array of animals to be monitored (Kays et al. 2015). For instance, GPS tracking devices have seen a significant decrease in mass from 250 g down to 1 g in just over 30 years (Kays et al. 2015). Further, recent advances have led to some GPS devices now weighing under 1 g (e.g. Krainer et al. 2017). ATLAS tags with reverse GPS, for example, weigh as little as 0.8 g (Toledo et al. 2022) and 0.9-g tags have been successfully deployed on bats (Roeleke et al. 2022). These advancements have broadened the range of species that can be effectively monitored, from large mammals such as elephants to small animals such as hummingbirds (e.g. Kays et al. 2015). Yet the size of the device still limits which animal species can be safely monitored (Wikelski et al. 2007) as these devices need to be appropriately fitted to ensure that normal behaviours, and the wellbeing of the animal in question, are not impacted (e.g. Aldridge & Brigham 1988, Fenton et al. 2000).

Due to the small size of some bats, their cryptic habits, and nocturnal flight, research on these animals has benefited greatly from the use of tracking devices (Speakman & Thomas 2003). However, it is difficult to attach devices given the small size of bats, limiting the types of devices and attachment methods available for use (O'Mara et al. 2014). Further, increasing mass during foraging (e.g. due to intake of food) results in an increase in frequency of wingbeats (O'Mara et al. 2019). Therefore, externally attached tags are expected to have the same or stronger effects (Pennycuik et al. 2012). Still, the need to understand the behaviour of these cryptic animals is of importance considering the threats they face (e.g. Arnett & Baerwald 2013, Frick et al. 2020, Cheng et al. 2021), resulting in many species listed as threatened by The International Union for Conservation of Nature's Red List of Threatened Species (IUCN 2024). Thus, it is important to understand limitations of tagging bats and establish recommendations based on empirical evidence to balance the tradeoff between animal welfare and conducting rigorous and unbiased research that advances basic and applied research of this taxon (Soulsbury et al. 2020).

Discourse about the mass that a bat can carry has been around for decades. While some researchers have recommended that devices should not exceed 10% body mass

(Wilkinson & Bradbury 1988, Wilson et al. 1996, Sikes 2016), the standard is that bats should not carry devices heavier than 5% of their body mass (Aldridge & Brigham 1988, Fig. 1). This guideline was based on the study of manoeuvrability of a single bat species and was suggested to be used for bats weighing <70 g, following a recommendation to use the calculation developed for birds by Caccamise and Hedin (1985) for bats weighing more than 70 g. This is not broadly applicable as there are more than 1400 species of bats, varying widely in their wing morphology and foraging niche which likely influences how much mass a bat can carry (Norberg 1994). In addition, body mass of bats varies strongly over the day, between movements, between seasons and during reproduction (Weller et al. 2023). Further, external factors that may affect the bat such as disturbance or resource distribution cannot be teased apart from the effects of tagging and the effect of drag produced by the device (Kelling et al. 2024). Therefore, while the 5% guideline appears straightforward in application, there is likely nuance as to its effects on bats. For example, there may be tradeoffs between tag mass and duration of attachment, or threshold values may differ among foraging guilds, life history stage, or for sensitive species (Fig. 1). O'Mara et al. (2014) attempted to rectify this situation via a meta-analysis to evaluate the 5% rule; however, they were unable to source enough studies that quantified the impacts of tag mass on bats. This illustrated a powerful message that although devices are frequently used, their impacts on the behaviour and body condition of bats are understudied.

Herein, we attempt to answer the question first posed by Aldridge and Brigham (1988) with a more recent synthesis conducted by O'Mara et al. (2014): are there negative effects on the behaviour and body condition of bats when attached tags exceed 5% of the mass of the bat? It has now been more than 35 years since the first attempt at answering this question. During this period, technology has advanced resulting in decreases in tag size and increases in types of tags and attachment methods. Thus, following similar methods as those used by O'Mara et al. (2014), we undertook a systematic literature review across the large body of publications focused on tagging and tracking of bats attempting to quantify the effects of attaching tags on bats with a meta-analysis. We designed our efforts to develop a quantitative understanding of the number of studies that evaluate (or do not evaluate) the 5% guideline, and to gain a global understanding of current practices in tagging bats. Our goal was to determine the measured degree to which tags may or may not impact the behaviour and body condition of various groups of bats to increase awareness of ethical considerations of this work while advancing our understanding of bat behaviour and ecology.

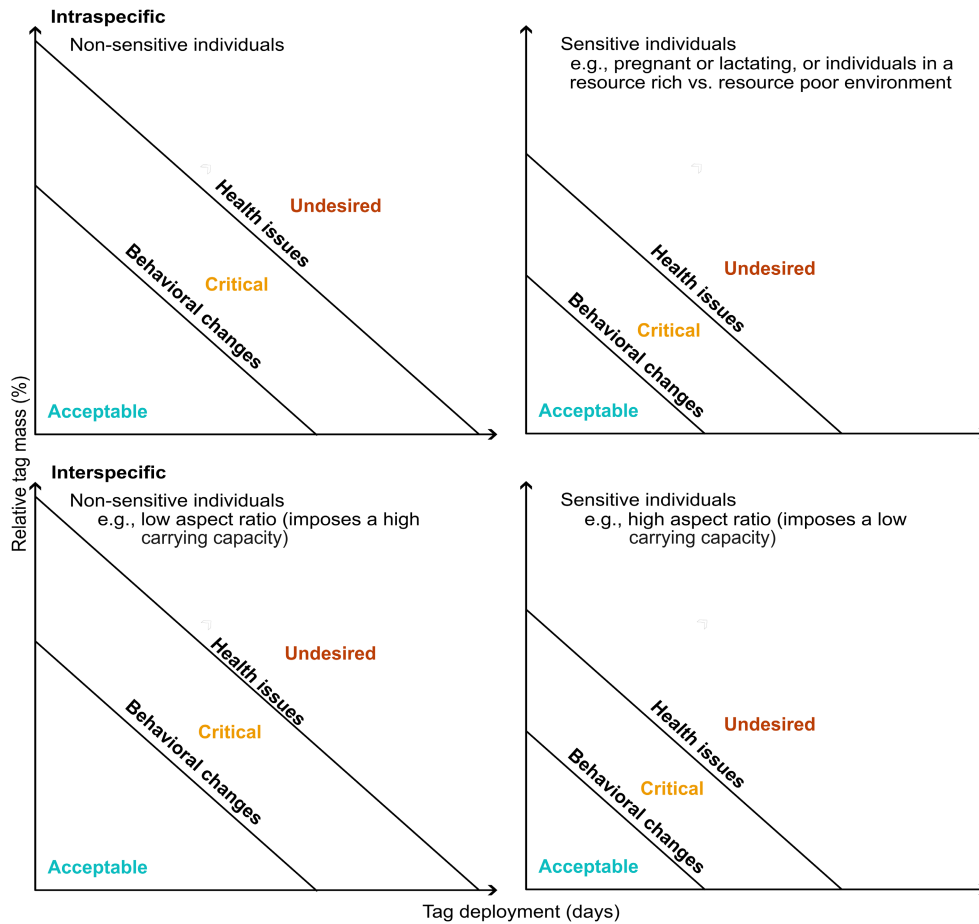


Fig. 1. Depiction of the 5% guidance which illustrates the three-way interaction between relative tag mass, deployment time, and species sensitivity to tag attachment and acceptable tradeoff of disturbance to animals for both intraspecific and interspecific levels. Note that sensitivity is not static within species or even individuals. Figure is for illustrative purposes only and not based on existing data.

MATERIALS AND METHODS

Inclusion criteria

We conducted a systematic literature review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocols (Moher et al. 2009, Page et al. 2021) to compile publications that discussed and/or tested the effects of attaching devices to bats. We included studies: 1) statistically testing the impacts of devices on bats based on quantitative variables describing the status of bat species (e.g. behaviour, recovery); 2) using devices on bats without testing impacts; and 3) discussing the use of devices for bats based on the 5% rule. We excluded studies: 1) using only passive integrated transponder (PIT) devices, as they have very low mass and are often the method used (along with bands/rings) as a control relative to tags of greater mass; 2) proposing

or mentioning devices without using or testing on bats, and 3) summarising data from literature reviews.

We based our systematic search on the database of original tagging papers provided by O'Mara et al. (2014) which included the collation of data from 223 publications on the tracking of bats using a standardised literature search in the Clarivate Analytics Web of Science (WoS). We only included full texts from the O'Mara et al. (2014) database that met our criteria ($n=221$). We performed an additional search to include more recent studies, especially which account for more recent advances in technology. Thus, on 15 October 2022, we performed an additional standardised literature search in WoS to supplement the original search from O'Mara et al. (2014). We used the following search string designed to target new tracking technologies developed in the last eight years (Search #1): $ALL = ("bats" OR "bat" OR "Chiropter*") AND ALL = ("datalogger" OR "data-logger" OR "accelerometer"$

OR “telemetry” OR “radio-telemetry” OR “Knowles microphone” OR “altimeter” OR “tag” OR “geolocator” OR “transceiver” OR “sensor” OR “collar” OR “on-board”).

Our search returned 1961 papers, of which 85 were previously captured by O’Mara et al. (2014) and thus were already screened. We screened the remaining papers ($n=1876$) for eligibility to be included in the review by making independent selections based on titles and abstracts. To test our selection criteria, two authors independently classified the first 100 papers and we then calculated inter-rater agreement using Cohen’s kappa. The value of kappa was 0.8, above the standard threshold of acceptable inter-rater agreement of 0.4 (Cohen 1960). As a result, we used these criteria to screen the remaining papers based on their titles and abstracts and discarded those ($n=1691$) that did not address our key research questions. We then examined the full text of the 185 references retained from the screening to determine if they addressed our research questions, including 137 of those references in the final database. Finally, we opportunistically included papers known to us that were not captured in the initial search ($n=9$). This resulted in a total of 367 studies in the final database.

Metadata extraction

Given the number of articles for review, we trained our international team of experts on data extraction methodology to ensure systematic reporting, and then a second person assessed their data entries. More specifically, for all articles, our team extracted the type of publication, year of study, geographic and taxonomic scope, including family and genus where applicable, wing loading, device type, and device mass in relation to body mass of the bat (%).

When available, we collected all statistical tests used to measure impact, their test statistic, degrees of freedom, number of observations, P -value, and direction of effect. When studies presented partial statistics, we contacted corresponding authors of these studies to request the missing information. We converted all test statistics within each study that measured the impact of devices on a bat to Pearson’s r (Lajeunesse 2013)—a measure of effect (ranging from 1.0 to -1.0)—which expresses the strength and direction of a given linear association between a predictor and response variable.

From the literature where testing occurred, we documented the following measures which compared impacts of different masses of devices (untagged or light mass compared to heavy mass tag) on: emergence time, flight distance, flight duration, foraging time, night activity, manoeuvrability, roost use, body condition index (BCI), body mass, percent (%) body condition, and pup condition. From the documented responses of bats to tags, which varied across studies, we identified two response categories for the purpose of analyses

and visualisation: behaviour (emergence time, flight distance, flight duration, foraging time, night activity, manoeuvrability, roost use) and as a proxy for body condition (body condition index (BCI), body mass [denoted by letters a–f below in ‘Definition of extracted estimates as provided within associated studies’ for interpretation of results of the meta-analysis for body condition], percent (%) body condition, pup condition, and pup mass). The curated literature database supporting this study is available on Zenodo (<https://doi.org/10.5281/zenodo.11183572>). R code to reproduce the analyses is available on GitHub (<https://github.com/melisameierhofer/Meta-5-Rule.git>).

Definition of extracted estimates as provided within associated studies

BEHAVIOUR

Emergence time was the time at which a bat leaves from the roost (Fenton et al. 2000). Flight distance was measured as the furthest distance travelled from the roost whereby the relative transmitter loading (transmitter mass/body mass) was tested (Entwistle et al. 1997). Flight duration was measured as the time spent outside of the roost (Goldshtein et al. 2020). Foraging time was defined as the total amount of time spent foraging each night (Barclay et al. 2000). Manoeuvrability was defined as the minimum-negotiable interstring distance as measured in a flight cage with an arrangement of strings at varying distances (Aldridge & Brigham 1988). Night activity (activity through the night) was measured as hourly capture rates conducted during the first 3 h of the evening (Chruszcz & Barclay 2003). Roost use was measured as the time spent within 0.5 km of the roost (Entwistle et al. 1997).

BODY CONDITION

Body condition index (BCI), measured as mass/forearm length, of hibernating bats captured 55 days post device attachment compared to newly captured hibernating bats (Jonasson & Willis 2012). Body mass change (body mass [a, b]) was defined as the change in body mass (i.e. without tag mass) between capture and recapture at the same time of day with tags still attached, including instances where previously tagged bats were recaptured without their tag (Roeleke et al. 2016, Voigt et al. 2020). Mass loss (body mass [c]) was controlled for by the number of days tracked, with a comparison between a lightweight telemetry and heavier GPS tagged bat (Hurme et al. 2019), (body mass [d–f]) was compared for telemetry or GPS tagged bats, and was controlled for time period a device remained on the bat (d), or was controlled for time since first capture and estimated loss of weight per day (e, f)

(Egert-Berg et al. 2018). Percent body condition was defined as the percent loss of condition between surveys, with radio-tagged bats compared to bats without tags during the same period (Park et al. 2000). Pup condition was calculated as mass/forearm length and was compared to pups whose mothers were either telemetry or GPS tagged (Hurme et al. 2019). Pup mass was measured as the mass loss from before lactating females were tagged to after the study period (Egert-Berg et al. 2018).

Meta-analysis

Where available, we extracted estimates from studies testing the overall effect of devices on bats, allowing us to conduct a meta-analysis to understand the direction and magnitude of the effect of the tag on bats. We conducted this meta-analysis in R 4.1.0 (R Core Team 2021) with the R package metafor 2.4.0 (Viechtbauer 2010). We constructed a meta-analytic linear mixed-effects model (metafor: rma.mv) for behaviour and body condition to assess the extent to which devices impact bats. For each model, we specified a publication-level nesting factor to account for non-independence as both models contained papers where multiple estimates were extracted. We converted Pearson's r to Fisher's z to approximate normality for each model (Rosenberg et al. 2013), and back transformed to Pearson's r for visualisation. We interpreted model-derived estimates of Pearson's r as the magnitude of the standardised effect. We considered it significant when the 95% confidence interval did not overlap zero.

We evaluated publication bias using the fail-safe number analysis (metafor: fsn). We used Rosenthal's method (Rosenthal 1979, Rosenberg 2005) to calculate the number of studies. We averaged the negative results that would need to be added to the given set of observed outcomes to reduce the combined significance level to alpha level 0.05. We found no evidence of publication bias (Table 1).

RESULTS

Summary statistics

In total, 367 studies were entered into the final database. Of those, 321 studies (87.5%) reported the percent mass of the device (either exact or indicated greater/less than 5%) and 46 studies (12.5%) did not. Among those

reporting percent mass, 184 studies (57.3%) reported some or all bats tagged exceeding 5%, and 137 studies (42.7%) <5%. From studies reporting percent mass before and including the year of publication of O'Mara et al. (2014) ($n=206$, 1999–2014), 114 studies (55.3%) reported some or all bats tagged exceeding 5%, and 92 studies (44.7%) <5%. From studies published after O'Mara et al. (2014) ($n=80$, 2015–2022), 46 studies (57.5%) reported some or all bats tagged exceeding 5%, and 34 studies (42.5%) <5%.

Tagging and tracking studies predominantly occurred in the Nearctic (31.7%) and Palearctic (30.6%) biogeographic regions, with 14.8% studies from the Neotropical region and 14.2% from the Australasian region (Fig. 2a). Limited studies occurred both in the Indomalayan (4.8%) and Afrotropical (3.8%) regions. Over time, the number of studies exceeding 5% did not significantly differ from those <5%, although a downward trend is apparent (Fig. 2b,c). When considering Very High Frequency (VHF) devices only, significantly fewer studies exceeded 5% (GLM ($n=24$): -0.06 ± 0.02 , $P=0.007$).

VHF devices were the most common type of device being used in 268 studies (82.8%), followed by GPS (7.5%, 25 studies) and microphones (4.0%, 13 studies) (Fig. 2d). All other device types documented from studies accounted for <2% in the literature (Fig. 2d). Of the number of times that VHF devices were used in studies, 56.0% (150 out of 268 studies) exceeded the 5% guidance, followed by GPS (60.0%, 15 out of 25 studies) and microphones (46.2%, six out of 13 studies) (Fig. 2d).

Vespertilionidae were the most common family tagged in 200 studies (60.2%), followed by Pyllostomidae (12.7%, 42 studies), Pteropodidae (12.0%, 40 studies), Rhinolophidae (3.6%, 12 studies), and Molossidae (3.3%, 11 studies) (Fig. 2e). All other families used in tagging and tracking studies accounted for <2% in the literature. Of the number of times that Vespertilionid bats were used in studies, 63.0% (126 out of 200 studies) exceeded the 5% guidance, followed by Pyllostomidae (54.8%, 23 out of 42 studies), Molossidae (54.5%, six out of 11 studies), Rhinolophidae (41.7%, five out of 12 studies), and Pteropodidae (40.0%, 16 out of 40 studies) (Fig. 2e).

Meta-analysis

We identified 12 studies with 17 estimates that quantified the impacts of tracking devices on bats, which represents

Table 1. Estimated model parameters and evaluation of publication bias using the fail-safe number

Response	Sample size (# studies)	Beta (SE)	95% CI (ub to lb)	z	P	Fail-safe n	P
Behaviour	7 (6)	-0.424 (0.149)	-0.133 to -0.715	-2.857	0.0043	356	<0.0001
Body condition	10 (6)	-0.378 (0.050)	-0.280 to -0.477	-7.500	<0.0001	131	<0.0001

Table 2. Descriptive information of species from studies where tags were tested on behaviour or body condition of the bat. Body mass (g), wing aspect ratio, and wing loading gathered from Rhodes (2002) for *M. moluocarum* and Norberg and Rayner (1987) for all other species. Body mass in parentheses represents values extracted from citation and reported either as mean or min–max. N.R.: Not Reported. BCI: Body Condition Index. Tag mass (g) reported in the study either as minimum–maximum or as a specific mass

Category tested	Taxonomic information	Geography	Body mass (g)	Tag mass (g)	Foraging guild	Wing aspect ratio	Wing loading, Mg/S Nm ⁻²	Citation
Emergence time	<i>Sturnia liliium</i>	Neotropical	15.0 (13.0–15.8)	0.47	Frugivore	6.5	12.2	Fenton et al. (2000)
Flight distance	<i>Plecotus auritus</i>	Palaearctic	9.0	0.65	Gleaner/aerial hawk	5.7	7.1	Entwistle et al. (1997)
Flight duration	<i>Leptonycteris yerbabuenae</i>	Neotropical	5.9 (6.0)	N.R.	Nectarivorous	5.9	10.6	Goldshtein et al. (2020)
Foraging time	<i>Myotis moluocarum</i>	Australasian	10.6	N.R.	Trawler	6.1	7.5 N/m ²	Barclay et al. (2000)
Manoeuvrability	<i>Myotis yumanensis</i>	Nearctic	5.2 (6.0)	N.R.	Aerial hawk	6.3	7.8	Aldridge and Brigham (1988)
Night activity	<i>Myotis evotis</i>	Nearctic	7.3 (6.3–8.4)	0.54	Gleaner	6.0	6.1	Chruszcz and Barclay (2003)
Roost use	<i>Plecotus auritus</i>	Palaearctic	9.0	0.65	Gleaner/aerial hawk	5.7	7.1	Entwistle et al. (1997)
Body condition index (mass/forearm length)	<i>Myotis lucifugus</i>	Nearctic	7.1	0.64–0.8	Aerial hawk (hibernating in study)	6.0	7.5	Jonasson and Willis (2012)
Body mass (a)	<i>Nyctalus noctula</i>	Palaearctic	26.5	3.8–4.5	Aerial hawk	7.4	16.1	Voigt et al. (2020)
Body mass (b)	<i>Nyctalus noctula</i>	Palaearctic	26.5 (32.0)	3.4–4.2	Aerial hawk	7.4	16.1	Roeleke et al. (2016)
Body mass (c)	<i>Myotis vivesi</i>	Neotropical	25.0 (29.4–38.3)	4.4–4.7	Trawler	7.4	9.0	Hurme et al. (2019)
Body mass (d)	<i>Myotis myotis</i>	Palaearctic	26.5	4.3	Gleaner	6.3	11.2	Egert-Berg et al. (2018)
Body mass (e)	<i>Myotis vivesi</i>	Neotropical	25.0	4.3	Trawler	7.4	9.0	Egert-Berg et al. (2018)
Body mass (f)	<i>Myotis myotis</i>	Palaearctic	26.5	4.3	Gleaner	6.3	11.2	Egert-Berg et al. (2018)
% body condition	<i>Rhinolophus ferrumequinum</i>	Palaearctic	22.6	1.3–1.8	Aerial hawk	6.1	12.2	Park et al. (2000)
Pup condition	<i>Myotis vivesi</i>	Neotropical	25.0 (29.4–38.3)	4.4–4.7	Trawler	7.4	9.0	Hurme et al. (2019)
Pup mass	<i>Myotis vivesi</i>	Neotropical	25.0	4.3	Trawler	7.4	9.0	Egert-Berg et al. (2018)

mass, which increased when devices were attached to their mothers. Results of the meta-analysis suggest that devices on bats had an overall negative impact on bats for both behaviour and body condition (Fig. 3). However, we interpreted the meta-analysis with caution due to the low fail-safe *n* (Table 1).

DISCUSSION

We revisited the 5% rule for tagging of bats established in 1988 (Aldridge & Brigham 1988) to understand whether progress has been made since the first systematic evaluation by O'Mara et al. (2014). Whereas a meta-analysis was not possible at the time for O'Mara et al. (2014), our systematic literature review with 10 additional years of published data enabled us to evaluate the magnitude

and direction of effect of devices on aspects of behaviour and body condition of bats. Further, we were able to understand any differences in trends in attaching devices >5% before and after the time of publication of O'Mara et al. (2014), noting that VHF devices are the most used and that tagging and tracking studies commonly use vespertilionid bats. In both cases, studies using VHF devices and studies using vespertilionid bats commonly exceeded the 5% guidance. This is important to note as overall, devices do impact the behaviour and body condition of bats, but caution should be taken when interpreting these results. Only 17 estimates from 11 species in three families were available from the literature for the meta-analysis, highlighting the need to conduct more testing of the impacts of devices on bats and for the rigorous reporting of statistics. It is commonplace to report significant results

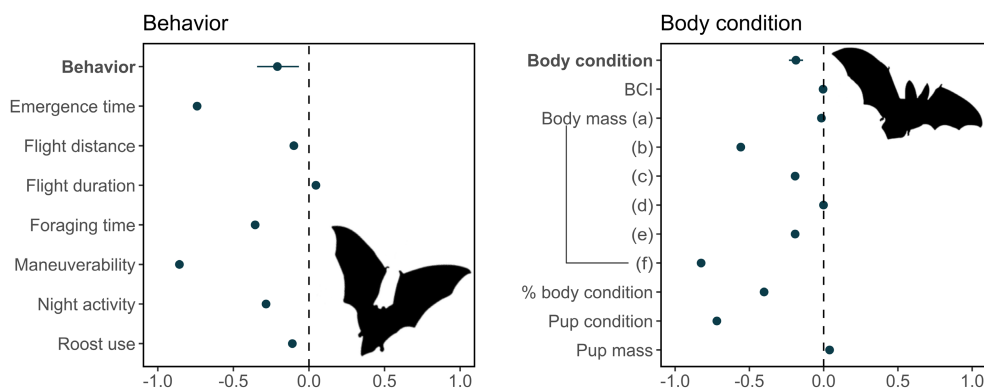


Fig. 3. Estimates of the effect size from the meta-analysis of the impact of tracking devices on Behaviour (bold) and body condition (bold), expressed as standardised Pearson's r and the upper and lower 95% confidence interval (CI). See Table 1 for model estimates and P values. Points without CIs represent the observed estimates from individual studies. Emergence time is the test statistic from a study where animals were tagged under 5%; all other test statistics were taken from studies where some or all bats were tagged >5%. Letters represent data defined within the same category (body mass). Please see the section 'Definition of extracted estimates as provided within associated studies' for more information about the estimates for Behaviour ($n=7$) and Body condition ($n=10$).

of analyses and relatively uncommon to report statistics associated with nonsignificant or neutral findings, which in this case, are important for understanding the impact of devices on the behaviour and body condition of bats. Anecdotal information on the impacts of bats was occasionally given in the form of a sentence, e.g., stating that no behavioural changes were noted between tagged and untagged individuals, usually without providing data in support of this observation. Due to limited data, we were unable to explore differences that are inherent across bat species resulting from their morphological differences.

Our data do suggest that there are potentially highly variable responses to devices attached to bats, both within the same measure (e.g. body mass), and responses across behaviours (e.g. emergence time, foraging time) (see Fig. 3). Indeed, the effects of devices on bats may be highly variable and dependent on factors both associated with the device and with the animal being studied, as was concluded for birds (Burger & Shaffer 2008) and suggested for bats (Aldridge & Brigham 1988). For example, the duration of the device attachment is an important factor to control for in studies measuring impacts of devices on bats, as this may impact the variable (e.g. body mass) being studied depending on when the measure is collected (Kelling et al. 2024). Thus, it is important to carefully consider factors being accounted for and measured, and the systematic data collection of these factors within studies (Cleasby et al. 2021). Finally, from the estimates that were extracted from studies, only two estimates were statistically significant: time of emergence for *Sturnira lilium* (Fenton et al. 2000) and manoeuvrability of *Myotis yumanensis* (Aldridge & Brigham 1988, see Fig. 3 and Table 2). Thus,

while devices impact the bats as depicted in our meta-analysis, the overall magnitude of the impact may be negligible in terms of its potential to significantly affect the behaviour or body condition of the studied individuals.

Considering additional factors that may impact the measured effects of devices on bats

Of course, there are additional factors of consideration when understanding and testing for the potential impacts of devices on bats. Anthropogenic disturbance, for instance, may underlie some of the measured effects of devices on bats (Kelling et al. 2024). In a study on the emergence of *Nyctalus noctula* (Voigt et al. 2020), body mass changes were also noted for untagged bats, which suggests that the disturbance associated with the capturing and handling of bats, regardless of being tagged, might be a confounding factor causing (or adding to) any tag effects. This underscores the need to conduct studies which compare the impacts of tagged versus untagged bats, specifically at the same time of the day. In GPS studies, initial capture is often done early in the morning, e.g., by using bats from artificial bat boxes, while bats are recaptured when emerging. Body mass differences are then affected by daily weight losses. Nonetheless, the measured impact of tagging of bats is of importance as over the last 23 years, only a non-significant downward trend in the proportion of studies exceeding the 5% rule was revealed. Thus, roughly half of the work published on tagging bats includes some or all bats with tags exceeding the previously conservative 5% threshold suggested by Aldridge and Brigham (1988)

and suggests that no real changes have been made since O'Mara et al. (2014). However, when analysing studies only using VHF devices, the downward trend was significant, likely reflecting advances (i.e. reductions in the size and weight of devices) in technology. Nevertheless, our exploration has advanced the recent work of O'Mara et al. (2014). Through measuring the impacts of tags on behaviour and body condition of bats via a meta-analysis, we identified what responses are being measured when testing devices and illustrated where further research is needed to better the tagging guidance.

Advances in technology and the design of future studies of tagging and tracking of bats

Overall, the lower margin of used tag mass has declined in recent years (Kays et al. 2015), due to improved battery technology and lesser energy demands of new designed hardware. This facilitates the broadening of research endeavours and species that can be studied. In our dataset, we identified that VHF devices were the most used devices, which is not surprising as they have been used in research since the 1960s (Cochran et al. 1965) and have continued to reduce in size. However, under certain scenarios, it may be justifiable to attach tags exceeding 5% of bat body mass given the scientific and conservation value of the study (see Fig. 1). Such studies have often resulted in forwarding our knowledge of bat behaviour and ecology. Yet, given the current limited knowledge on the effects of tags exceeding 5% of a bat's mass, it is recommended to minimise the time that tags of this size are attached (Kelling et al. 2024).

Despite technological advances, however, development and reassessment of acceptable mass of devices to attach on bats are still lacking in published literature for both laboratory and field studies (see also O'Mara et al. 2014), hindering the ability to understand more thoroughly the short- and potentially long-term impacts of different tags on bats (Fenton 2003, but see Melber et al. 2013). Although these data are not always accessible from studies, this information is sorely needed at the species level or, at least according to foraging guild and wing morphology. Broad-winged, manoeuvrable gleaners differ profoundly from narrow-winged, fast-flying open-air foragers in their flight performance and behaviour. For example, a large wing area is generally advantageous for a bat carrying an extra load, such as a pup (Norberg & Rayner 1987). Thus, one could hypothesize that tag mass may differentially impact species based on morphology, especially related to the wing shape and foraging niche. Manoeuvrability was impacted when tag mass exceeded 5% for a manoeuvrable species with around 6.45 wing-aspect ratio (Aldridge &

Brigham 1988), but the degree of this impact across different foraging guilds and different tag masses has yet to be explored. Further, differences in life history status of the tagged bats within a species should also be considered variables in this endeavour to identify the impacts of tags on bats. For example, different reproductive states require different energy intakes (Speakman & Racey 1987, Kurta et al. 1989) and alter the baseline mass of the animal. Similarly, age or more difficult to assess parameters, such as parasite loads, or food availability could have an effect. Theoretically, both an increase in the relative tag mass and deployment time are associated with an escalation in behavioural changes and furthermore, health issues as exemplified in Fig. 1. A tag with a higher relative mass attached for a short duration of time can therefore be expected to have similar cumulative impacts as a lighter tag attached for a longer duration. Moreover, the attachment method (e.g. glue, suture, collar), shape, or placement on the body might have unintentional consequences (e.g. Curk et al. 2021, Longarini et al. 2023). Thus, it is important to take caution and minimise any impacts imposed by the tag (see Kay et al. 2019). As some species are more susceptible than others to the negative effects of increased tag mass, it may be plausible that perhaps only certain individuals or species are meaningfully impacted when tag mass exceeds 5% of body mass (i.e. in birds the standard is 3% as in studies that exceeded the threshold documented extended trip durations, a high rate of nest desertion, or both; Phillips et al. 2003). Taking these variables into account, designing studies on bats using tags requires assessing a three-way interaction between relative tag mass, deployment time and species sensitivity (e.g. low vs. high aspect ratio) and individual sensitivity (non-reproductive vs. pregnant or lactating) to tag attachment (Fig. 1).

A call for systematic data reporting in tagging and tracking studies

Aldridge and Brigham (1988) initially provided recommendations for attaching devices to bats, and O'Mara et al. (2014) reviewed the past 50 years of literature to understand device attachment, use and changes in guidelines, and any fitness or health impacts due to devices. Despite the decade since O'Mara et al. (2014), our endeavour found that the reporting of bat (e.g. mass) and device information is still not systematic even though O'Mara et al. (2014) encouraged that these data be reported systematically. Depending on the goal of the research, body mass is not always reported. If body masses are reported, masses might not be reported at individual level which precludes the ability to understand the effects of tags on different ages, sexes, and reproductive classes.

Nonetheless, 87% of papers stated whether the percent body mass of the tag on the bat exceeded 5%, or provided the calculated percentage for the individual, thus demonstrating the impact of Aldridge and Brigham (1988) recommendation despite the underlying information originating from a single species in a laboratory setting.

We conclude from our study that more information is needed on the potential impacts of tags on the behaviour and wellbeing of bats. Our systematic literature review precluded our ability to weigh the pros and cons of <5% to >5% tags, similar to findings reported by O'Mara et al. (2014). Therefore, we plead for the systematic reporting of the following parameters either in the manuscript or in the supplemental material: mass and dimension of the tags, attachment method (e.g. collar, skin glue), individual body masses in relation to tags attached, time of year of tag deployment and recapture, duration of tag deployment, information about whether or not tags were removed when inactive, and reporting on health issues (e.g. inflammations at the site of tag deployment, Soulsbury et al. 2020). As technology advances to allow for a breadth of new research avenues, understanding how these new devices may impact bats, and to what degree, will be important for the justification of gathering new information for conservation efforts. While these data are not always important for the study at hand, they are nonetheless important for our continued pursuit in understanding potential impacts of tagging on bats.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest related to this publication.

DATA AVAILABILITY STATEMENT

The database supporting this study is available on Zenodo (<https://doi.org/10.5281/zenodo.11183572>). R code to reproduce the analyses is available on GitHub (<https://github.com/melissameierhofer/5-Rule.git>).

REFERENCES

- Aldridge HDJN, Brigham RM (1988) Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *Journal of Mammalogy* 69(2): 379–382. <https://doi.org/10.2307/1381393>
- Arnett EB, Baerwald EF (2013) Impacts of wind energy development on bats: implications for conservation. In: Adams RA, Pedersen SC (eds) *Bat Evolution, Ecology, and Conservation*, 435–456. Springer, Cham, Switzerland.
- Barclay RMR, Chruszcz BJ, Rhodes M (2000) Foraging behaviour of the large-footed myotis, *Myotis moluccarum* (Chiroptera: Vespertilionidae) in south-eastern Queensland. *Australian Journal of Zoology* 48(4): 385–392. <https://doi.org/10.1071/zo00036>
- Burger AE, Shaffer SA (2008) Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *The Auk* 125(2): 253–264. <https://doi.org/10.1525/auk.2008.1408>
- Caccamise DF, Hedin RS (1985) An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97(3): 306–318.
- Cheng TL, Reichard JD, Coleman JTH, Weller TJ, Thogmartin WE, Reichert BE et al. (2021) The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology* 35(5): 1586–1597. <https://doi.org/10.1111/cobi.13739>
- Chruszcz BJ, Barclay RMR (2003) Prolonged foraging bouts of a solitary gleaning/hawking bat, *Myotis evotis*. *Canadian Journal of Zoology* 81(5): 823–826. <https://doi.org/10.1139/z03-056>
- Cleasby IR, Morrissey BJ, Bolton M, Owen E, Wilson L, Wischniewski S, Nakagawa S (2021) What is our power to detect device effects in animal tracking studies? *Methods in Ecology and Evolution* 12(7): 1174–1185. <https://doi.org/10.1111/2041-210X.13598>
- Cochran WW, Warner DW, Tester JR, Kuechle VB (1965) Automatic radio-tracking system for monitoring animal movements. *Bioscience* 15(2): 98–100. <https://doi.org/10.2307/1293346>
- Cohen J (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* 20(1): 37–46. <https://doi.org/10.1177/001316446002000104>
- Curk T, Scacco M, Safi K, Wikelski M, Fiedler W, Kemp R, Wolter K (2021) Wing tags severely impair movement in African cape vultures. *Animal Biotelemetry* 9(1): 11. <https://doi.org/10.1186/s40317-021-00234-2>

- Egert-Berg K, Hurme ER, Greif S, Goldstein A, Harten L, Herrera M et al. (2018) Resource ephemerality drives social foraging in bats. *Current Biology* 28(22): 3667–3673. <https://doi.org/10.1016/j.cub.2018.09.064>
- Entwistle AC, Racey PA, Speakman JR (1997) Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351(1342): 921–931. <https://doi.org/10.1098/rstb.1996.0085>
- Fenton MB (2003) Science and the conservation of bats: where to next? *Wildlife Society Bulletin* 31(1): 6.
- Fenton MB, Vonhof MJ, Bouchard S, Gill SA, Johnston DS, Reid FA, Riskin DK, Standing KL, Taylor JR, Wagner R (2000) Roosts used by *Sturnira lilium* (Chiroptera: Phyllostomidae) in Belize. *Biotropica* 32(4a): 729–733. <https://doi.org/10.1111/j.1744-7429.2000.tb00521.x>
- Frick WF, Kingston T, Flanders J (2020) A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences* 1469(1): 5–25. <https://doi.org/10.1111/nyas.14045>
- Goldstein A, Handel M, Eitan O, Bonstein A, Shaler T, Collet S et al. (2020) Reinforcement learning enables resource partitioning in foraging bats. *Current Biology* 30(20): 4096–4102.e6. <https://doi.org/10.1016/j.cub.2020.07.079>
- Hurme E, Gurarie E, Greif S, Herrera MLG, Flores-Martínez JJ, Wilkinson GS, Yovel Y (2019) Acoustic evaluation of behavioral states predicted from GPS tracking: a case study of a marine fishing bat. *Movement Ecology* 7(1): 21. <https://doi.org/10.1186/s40462-019-0163-7>
- Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT et al. (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348(6240): 1255642. <https://doi.org/10.1126/science.1255642>
- IUCN (2024) IUCN Red List of Threatened Species. <https://www.iucnredlist.org/>
- Jonasson KA, Willis CKR (2012) Hibernation energetics of free-ranging little brown bats. *The Journal of Experimental Biology* 215(Pt 12): 2141–2149. <https://doi.org/10.1242/jeb.066514>
- Kay WP, Naumann DS, Bowen HJ, Withers SJ, Evans BJ, Wilson RP, Stringell TB, Bull JC, Hopkins PW, Börger L (2019) Minimizing the impact of biologging devices: using computational fluid dynamics for optimizing tag design and positioning. *Methods in Ecology and Evolution* 10(8): 1222–1233. <https://doi.org/10.1111/2041-210X.13216>
- Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348(6240): aaa2478. <https://doi.org/10.1126/science.aaa2478>
- Kelling M, Currie SE, Troxell SA, Reusch C, Roeleke M, Hoffmeister U, Teige T, Voigt CC (2024) Effects of tag mass on the physiology and behaviour of common noctule bats. *Movement Ecology* 12(1): 38.
- Krainer VK, Mixanig H, Wiser D, Reiter G (2017) Die Nutzung von GPS-Telemetrie zur Analyse der Lebensraumnutzung von Mausohren (*Myotis myotis*) in Kärnten. *Carinthia II* 207/127: 565–576.
- Kurta A, Bell GP, Nagy KA, Kunz TH (1989) Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62(3): 804–818. <https://doi.org/10.1086/physzool.62.3.30157928>
- Lajeunesse M (2013) Recovering missing or partial data from studies: a survey of conversions and imputations for meta-analysis. In: Koricheva J, Gurevitch J, Mengersen K (eds) *Handbook of Meta-Analysis in Ecology and Evolution*, 195–206. Princeton University Press, Princeton, New Jersey, USA.
- Longarini A, Duriez O, Shepard E, Safi K, Wikelski M, Scacco M (2023) Effect of harness design for tag attachment on the flight performance of five soaring species. *Movement Ecology* 11(1): 39. <https://doi.org/10.1186/s40462-023-00408-y>
- Melber M, Fleischmann D, Kerth G (2013) Female Bechstein's bats share foraging sites with maternal kin but do not forage together with them – results from a long-term study. *Ethology* 119(9): 793–801. <https://doi.org/10.1111/eth.12123>
- Moher D, Liberati A, Tetzlaff J, Altman D (2009) Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Annals of Internal Medicine* 151(4): 264–269. <https://doi.org/10.7326/0003-4819-151-4-200908180-00135>
- Norberg U (1994) Wing design, flight performance, and habitat use in bats. In: Wainwright PC, Reilly SM (eds) *Ecological Morphology: Integrative Organismal Biology*, 205–239. The University of Chicago Press, Chicago, Illinois, USA.
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 316(1179): 335–427. <https://doi.org/10.1098/rstb.1987.0030>
- O'Mara MT, Wikelski M, Dechmann DKN (2014) 50 years of bat tracking: device attachment and future directions. *Methods in Ecology and Evolution* 5(4): 311–319. <https://doi.org/10.1111/2041-210X.12172>
- Otto SP (2018) Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences* 285(1891): 20182047. <https://doi.org/10.1098/rspb.2018.2047>
- O'Mara MT, Wikelski M, Kranstauber B, Dechmann DKN (2019) Common noctules exploit low levels of the atmosphere. *Royal Society Open Science* 6(2): 181942. <https://doi.org/10.1098/rsos.181942>
- Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD et al. (2021) The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 372: n71. <https://doi.org/10.1136/bmj.n71>

- Park KJ, Jones G, Ransome RD (2000) Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Functional Ecology* 14(5): 580–588.
- Pennycuik CJ, Fast PLF, Ballerstädt N, Rattenborg N (2012) The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. *Journal of Ornithology* 153(3): 633–644. <https://doi.org/10.1007/s10336-011-0781-3>
- Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. *The Auk* 120(4): 1082–1090. <https://doi.org/10.1093/auk/120.4.1082>
- Pimm SL, Alibhai S, Bergl R, Dehgan A, Giri C, Jewell Z, Joppa L, Kays R, Loarie S (2015) Emerging technologies to conserve biodiversity. *Trends in Ecology & Evolution* 30(11): 685–696. <https://doi.org/10.1016/j.tree.2015.08.008>
- R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.
- Rhodes MP (2002) Assessment of sources of variance and patterns of overlap in microchiropteran wing morphology in southeast Queensland, Australia. *Canadian Journal of Zoology* 80(3): 450–460. <https://doi.org/10.1139/z02-029>
- Roeleke M, Blohm T, Kramer-Schadt S, Yovel Y, Voigt CC (2016) Habitat use of bats in relation to wind turbines revealed by GPS tracking. *Scientific Reports* 6(1): 28961. <https://doi.org/10.1038/srep28961>
- Roeleke M, Schlägel UE, Gallagher C, Pufelski J, Blohm T, Nathan R, Toledo S, Jeltsch F, Voigt CC (2022) Insectivorous bats form mobile sensory networks to optimize prey localization: the case of the common noctule bat. *Proceedings of the National Academy of Sciences of the United States of America* 119(33): e2203663119.
- Rosenberg MS (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* 59(2): 464–468. <https://doi.org/10.1111/j.0014-3820.2005.tb01004.x>
- Rosenberg MS, Rothstein HR, Gurevitch J (2013) Effect sizes: conventional choices and calculations. In: Koricheva J, Gurevitch J, Mengersen K (eds) *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton University Press, Princeton, New Jersey, USA. <https://doi.org/10.23943/princeton/9780691137285.003.0006>
- Rosenthal R (1979) The file drawer problem and tolerance for null results. *Psychological Bulletin* 86(3): 638–641. <https://doi.org/10.1037/0033-2909.86.3.638>
- Sikes RS (2016) Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97(3): 663–688. <https://doi.org/10.1093/jmammal/gyw078>
- Soulsbury CD, Gray HE, Smith LM, Braithwaite V, Cotter SC, Elwood RW, Wilkinson A, Collins LM (2020) The welfare and ethics of research involving wild animals: a primer. *Methods in Ecology and Evolution* 11(10): 1164–1181. <https://doi.org/10.1111/2041-210X.13435>
- Speakman JR, Racey PA (1987) The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus*. In: Fenton MB, Racey PA, Rayner JMV (eds) *Recent Advances in the Study of Bats*. Cambridge University Press, London, UK.
- Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat Ecology*, 430–490. The University of Chicago Press, Chicago, Illinois, USA.
- Toledo S, Mendel S, Levi A, Vortman Y, Ullmann W, Scherer LR et al. (2022) Vildehaye: a family of versatile, widely-applicable, and field-proven lightweight wildlife tracking and sensing tags. In: *2022 21st ACM/IEEE International Conference on Information Processing in Sensor Networks (IPSN)*, 1–14. IEEE, Milano, Italy. <https://doi.org/10.1109/IPSN54338.2022.00008>
- Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* 36: 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Voigt CC, Scholl JM, Bauer J, Teige T, Yovel Y, Kramer-Schadt S, Gras P (2020) Movement responses of common noctule bats to the illuminated urban landscape. *Landscape Ecology* 35(1): 189–201. <https://doi.org/10.1007/s10980-019-00942-4>
- Weller TJ, Clerc J, Lau MJ, Johnson NG (2023) Rates of seasonal fuel loading do not differ by sex or overwintering strategy in three species of bats. *Journal of Mammalogy* 104: 1246–1256. <https://doi.org/10.1093/jmammal/gyad088>
- Wikelski M, Kays RW, Kasdin NJ, Thorup K, Smith JA, Swenson GW Jr (2007) Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology* 210(2): 181–186. <https://doi.org/10.1242/jeb.02629>
- Wilkinson G, Bradbury J (1988) Radio telemetry: techniques and analysis. In: Kunz TH (ed) *Ecological and Behavior Methods for the Study of Bats*, 105–124. Smithsonian Institution Press, Washington, DC, USA.
- Wilson DE, Cole FR, Nichols JD, Rudran R, Foster MS (eds) (1996) *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*. Smithsonian Institution Press, Washington, DC, USA. <https://pubs.usgs.gov/publication/5200145>