Review and meta-analysis of correlates of home range size in bats

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Abstract

Home range is an ecological concept that affects many aspects of the life of vertebrates and hence understanding how it varies between species is crucial. Mammalian home range size has been linked to body size and diet, but these studies were based predominantly on terrestrial species and most specifically excluded bats. As the only group of flying mammals, bats experience distinctly different constraints on movement, and hence home range. However, despite their diversity, relatively little is known about the home ranges of bats, and this is the first global review assessing correlates of their home range size. Our hypothesis is that home range will be impacted by different ecological conditions experienced by the bats and by the biological traits of the bats themselves. We performed a meta-analysis based on published data for 81 bat species to identify variables that contribute most to home range size. Sex, wing loading, functional group, colony size, dietary class, distance from the equator (latitudinal region), habitat type, and the interaction between habitat type and latitudinal region were all important explanatory variables. Wing loading was positively correlated with home range size—while females, open-air foragers, large colony sizes, and bats in temperate regions consistently had large home ranges. Understanding the correlates of home range has important implications, for example, for bat conservation and for assessing the risk of spillover of zoonotic pathogens from bats to humans and livestock.

Key words: Chiroptera, colony size, ecological interactions, functional group, morphology, movement patterns.

Revisión crítica y metanálisis de correlaciones del ámbito de hogar de los murciélagos

Resumen

El ámbito de hogar es un concepto ecológico que influye en muchos aspectos de la vida de los vertebrados, por lo que es fundamental comprender el modo en que varía entre especies. El ámbito de hogar de los mamíferos ha sido relacionado con el tamaño corporal y la alimentación, pero esos estudios se basaban principalmente en especies terrestres y, concretamente, excluían a los murciélagos. Al ser el único grupo de mamíferos voladores, los murciélagos experimentan restricciones de movimiento diferenciales y en consecuencia sus ámbitos de hogar también varían. Sin embargo, a pesar de su diversidad, el conocimiento de los ámbitos de hogar de los murciélagos es escaso, y esta es la primera revisión global que evalúa la variables que se correlación con el tamaño de sus ámbitos hogareños. Nuestra hipótesis establece el ámbito de hogar de los murciélagos está influenciado por sus características biológicas y por las diferentes condiciones ecológicas que experimentan. Desarrollamos un metanálisis en función de la información publicada sobre 81 especies de murciélagos para identificar las variables que más influyen en el tamaño del ámbito de hogar. El sexo, la carga alar, el grupo funcional, el tamaño de la colonia, la clase de alimentación, la distancia hasta el ecuador (zona latitudinal), el tipo de hábitat y la interacción entre este y la zona latitudinal fueron consideradas como variables explicativas importantes. La carga alar mostró una correlación positiva con el tamaño del ámbito de hogar, mientras que las hembras, los murciélagos forrajeadores de espacios abiertos, las colonias de gran tamaño y los murciélagos de zonas templadas tuvieron ámbitos de hogar consistentemente grandes. La comprensión de las variables que se correlacionan con el ámbito de hogar tiene repercusiones importantes, por ejemplo, para la conservación de los murciélagos y el estudio del riesgo de propagación de patógenos zoonóticos de los murciélagos hacia los humanos y el ganado.

Palabras clave: Chiroptera, grupo funcional, interacciones ecológicas, morfología, patrones de movimiento, tamaño de colonia.

Movements of animals within and between different areas occur daily while searching for inter alia food, mates, water sources, or resting sites. Various factors may influence the decision to remain in an area, but whether animals show fidelity to 1 area or move frequently varies between species. A home range is defined as an animal showing a degree of site fidelity, remaining in a restricted area for prolonged periods (Powell 2000; Powell and Mitchell 2012). The concept of home range was initially introduced by Burt (1943:351) defining it as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." The establishment of a home range is generally to provide benefits to the individual, such as access to reliable resources. However, home ranges are not equivalent among all species or individuals of the same species (Gompper and Gittleman 1991), and it has been hypothesized that a myriad of factors, ranging from seasonal food availability to body mass, are responsible for variability in home range sizes (McLoughlin and Ferguson 2000).

Being able to quantify the home range is important for understanding its potential ecological role of an animal within the ecosystem (Abedi-Lartey et al. 2016) as well as the negative implications of the presence in an area, for example, as a host to a zoonotic disease (Epstein et al. 2020). The presence of a species that is a known host of zoonotic pathogens may pose a risk of transmission to intermediate hosts and people if there is spatial and temporal overlap with the distribution of the host (Breed et al. 2010; Rulli et al. 2021). Home range analysis can help delineate the extent of the range requirements and the overall range of potential impact of a species, but analyzing patterns of range use within that home range may assist in identifying regions where spatial and temporal overlap may occur (Randhawa et al. 2020; Zhao et al. 2022).

One overarching trend among mammalian species is that home range size scales allometrically with body mass according to the equation $HR = aM^b$ (McNab 1963) where HR represents home range, M represents body mass, a represents a species-specific, normalization constant, and b represents the scaling exponent giving the relationship between body mass and home range size (Swihart et al. 1988; Noonan et al. 2020). Larger animals require more resources to satisfy their energetic requirements and thus generally occupy larger areas (Kelt and Van Vuren 2001). In addition, resource distribution and availability are 2 features—unrelated to body mass—that can also impact home range size (Ford 1983; Boutin 1990). Resource acquisition is an integral component of survival for animals, and they should thus adapt the size of their ranges as resource availability changes. Boutin (1990) reviewed studies looking at the effect of food supplementation on home range size and showed that mammals inhabiting areas with higher resource availability had smaller average home ranges than mammals without food supplementation. This trend supported a model by Ford (1983) that predicted that the home ranges of central-placed foragers would fluctuate in size according to temporal changes in resource availability and density, with home ranges being smaller in resource-rich compared to resource-poor areas. Habitat can also contribute to variation in home range size as open areas with patchily distributed resources require animals to maintain larger home ranges than those living in more homogenous situations (Ofstad et al. 2016). Finally, sex- and species-specific mating strategies also affect home range (Henry et al. 2005), with polygynous males tending to have larger home ranges than females as they travel widely in search of females, with the opposite expected for polyandrous species (Priotto et al. 2002; Henry et al. 2005).

Bats (Order Chiroptera), despite being the second most diverse mammalian order at the species level (Altringham 2011), have received little attention regarding their home ranges. They are unique among mammals as the only group capable of self-powered flight (Gunnell and Simmons 2005); however, flight is energetically costly (Voigt et al. 2017) and bats experience unique energetic constraints associated with movement. In addition, bats exhibit a wide variety of diets including frugivory, insectivory, carnivory, and sanguivory (Kunz 2013a), and exploit a diverse array of habitats and ecological niches. Given their unique ecology and diversity, the home range of bats may be influenced differently by the aforementioned factors compared with other mammals in addition to being constrained by order-specific characteristics.

Body mass is expected to scale with home range size (Swihart et al. 1988; Kelt and Van Vuren 2001), and Fenton (1997) predicted that larger bats would travel further compared to smaller bats. This was based on the observation of a limited number of species, most of which weighed more than 15 g, and therefore excluded many smaller bat species. A recent review reported that home ranges of European and North American bats were positively correlated with body mass (Laforge et al. 2021).

Flight patterns and behavior in bats are dictated by wing aerodynamics (Norberg and Rayner 1987), and 2 important metrics influencing flight patterns are aspect ratio and wing loading. Aspect ratio is the ratio of wingspan to the wing surface area, while wing loading is the ratio between body mass and wing surface area (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). Differences in aspect ratio and wing loading of bats result in a trade-off between the cost of transport, flight speed, and maneuverability and thus determine the habitats available to different species (Norberg and Rayner 1987). For bats with high aspect ratio and wing loading, high-speed flight is an aerodynamic requirement needed to generate sufficient lift (Voigt and Holderied 2012) and, consequently, these bats are restricted to foraging in open areas with few obstacles as maneuvering at lower speeds incurs a high energetic cost (Norberg and Rayner 1987). For example, the Brazilian Free-tailed Bat, *Tadarida brasiliensis*, specifically forages at high altitudes in open areas where it utilizes its high flight speed to hunt aerial insects (Wilkins 1989). Alternatively, bats with low wing loading and aspect ratio, such as the Woolly False Vampire Bat (*Chrotopterus auratus*), have slow flight speeds but maneuver efficiently in cluttered space (Norberg and Rayner 1987), and hunt in wooded situations (Vleut et al. 2019). Wing morphology might also impact home range size (Aldridge and Rautenbach 1987)—a hypothesis supported in a recent review Laforge et al. (2021). Species adapted to open spaces are typically capable of long-distance travel at reduced energetic costs given that "a long, narrow wing works better than a short, wide one with the same area and profile, because it develops more lift, and less induced drag at the same angle of attack" (Pennycuick 2008:68). Hence, these species are more likely to occupy larger home ranges (O'Donnell 2001; Noer et al. 2012), while the opposite appears to be the case for clutter specialists (Monadjem et al. 2009; Abbott et al. 2012).

Kelt and Van Vuren (2001) demonstrated that carnivorous terrestrial mammals have larger home ranges than omnivorous or herbivorous species of comparable body mass (Carbone and Gittleman 2002; Tucker et al. 2014), but this trend remains untested for bats. Given that frugivorous and nectarivorous bats target stationary food items that are located on randomly distributed fruiting or flowering trees, their home ranges typically vary as resources are depleted or renewed (Fahr et al. 2015)—but they may also depend on landscape structure, as fragmented habitats can affect the presence and distribution of fruiting or flowering trees (Quesada et al. 2004). Furthermore, their home ranges may differ between seasons as resource abundance fluctuates (Lučan et al. 2016). Insectivorous and carnivorous species target prey items that—similar to fruit availability—fluctuate in abundance on a seasonal basis, but are also mobile and therefore variable in space and time (Conenna et al. 2019). Therefore, their movement patterns are reliant on the temporal availability of prey items but also differ according to hunting strategies, which may result in variable use of space, distances flown, and home range size (Meyer et al. 2005). Bats are typically assigned to 3 functional groups—clutter, edge, and open-air—based on their foraging habitats, with each group possessing specialized flight characteristics and echolocation systems to best exploit these areas (Schnitzler and Kalko 2001).

Bat species roost in a spectrum of social groups ranging from large colonies—which can number in the tens to hundreds of thousands—to roosting solitarily, with most species falling somewhere in between (Kunz 2013b). A colony has been defined as a group of bats forming a social unit within the confines of a specific roost site or several adjacent roost sites (Kunz et al. 2009). For species roosting in large colonies, higher levels of intraspecific competition are predicted to cause increased dispersal distances during foraging bouts, leading to large home ranges (Meyer et al. 2005). In a study focusing on several colonies of different sizes, flight distances and home ranges were greater for individuals from the larger colonies (Acharya et al. 2015). In contrast, Calderón-Capote et al. (2020) showed that distances traveled by the African Straw-colored Fruit Bat (*Eidolon helvum*) while foraging were not strongly influenced by colony size. Individuals often switched roost site to occupy highly productive areas rather than return to a single roost site and increase commuting distance, although foraging flights still ranged from 10 to 100 km regardless of colony size, representing extensive commuting distances. By comparison, solitary species may defend small areas with key foraging patches (Bonaccorso et al. 2015) resulting in smaller home ranges.

Mammalian home range size is predicted to differ between sexes due to different daily activity patterns and energy requirements, with females more strongly influenced by the energetic constraints of reproduction (O'Donnell 2001; Henry et al. 2002) and males influenced by mate availability—thereby adjusting movement distances in order to defend females or roost sites (Meyer et al. 2005). However, no clear trend is thus far evident for bats, e.g., Safi et al. (2007) provided evidence for the male Particoloured Bat (*Vespertilio murinus*) having significantly larger home ranges than females—while Meyer et al. (2005) suggested that home ranges for the female Long-legged Bat (*Macrophyllum macrophyllum*) are likely significantly larger than males. Dechmann et al. (2014) also provided evidence for no significant differences in home range size or habitat use between males and females, but Mackie and Racey (2007) identified the use of different habitat types by females in different reproductive conditions.

The specific landscape in which a bat occurs can influence its movement patterns through its structure dictating resource abundance and distribution—and also could impose limitations on movements by creating ecological or geographical barriers (Wickramasinghe et al. 2003; Fuentes-Montemayor et al. 2013). Areas that have been fragmented by anthropogenic activities can increase landscape heterogeneity and the corresponding availability of food or roosting sites (Williams et al. 2006; Hahn et al. 2014; Egert-Berg et al. 2021). However, disturbances more commonly result in isolated resource patches, and an overall decrease in the availability of resources might force bats to travel further each night (Quesada et al. 2004).

Latitude may also play a role in movement patterns wherein at higher latitudes (i.e., distances further away from the equator) greater seasonal variation in conditions compared to tropical areas could influence local resource conditions (Fleming and Eby 2003). Dramatic changes between seasons at higher latitudes and seasonal shifts in resource availability may force more pronounced seasonal adjustments in temperate species of bats compared to tropical species (Fleming and Eby 2003) in order to compensate for increased or decreased resource availability (Richter and Cumming 2006; Páez et al. 2018).

Home range size might also be influenced by specific methodological variables such as the ratio of mass of a transmitter relative to the tagged individual (Aldridge and Brigham 1988) because bats burdened with excessively heavy tags might experience difficulties maintaining normal flight patterns (O'Mara et al. 2014). Meanwhile, the number of locations obtained from a transmitter could influence the statistical power of the estimate, whereas different methods could provide different estimates for home range (Laver and Kelly 2008; Noonan et al. 2019).

Home range studies provide insight into the movement patterns of bats and their potential interactions with other species. As key role-players in ecosystems and known hosts for potential zoonotic pathogens, their movements confer importance on ecosystem well-being in addition to affecting the risk of pathogen spread and disease transmission to people (Kunz et al. 2011; Letko et al. 2020). Therefore, understanding how their movements are affected by ecological and biological variables is vital to delineating their importance across different scientific disciplines (Randhawa et al. 2020). Laforge et al. (2021) reviewed variations in bat home range size, but only for North American and European species—and the review only assessed the effects of landscape composition, body mass, and wing morphology but did not include other potentially important variables such as colony size, functional group, or diet. This review includes the assessment of additional variables to understand the correlation between ecological and biological variation in home ranges for bats.

Our hypothesis is that home range will be impacted in a predictable fashion by both a variety of ecological conditions as well as by biological traits of the bats themselves. In particular, we predict that: (i) aspect ratio and wing loading will be positively correlated with home range size; (ii) larger bats will have larger home ranges; (iii) species roosting in larger colonies will have larger home ranges; (iv) open-air foragers will have larger home ranges than edge and clutter foragers; (v) females will have larger home ranges than males; (vi) disturbed landscapes will contribute toward larger home ranges than natural landscapes; and (vii) bats from temperate regions will have larger home ranges than those from tropical regions.

Materials and methods.

Data collection.

We searched for peer-reviewed publications on home range sizes of bats including journal articles, review papers, and book chapters published around the globe until the end of December 2022 in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al. 2009). Searches were performed in order to identify species for which home range size had been reported using the Institute for Scientific Information's Web of Science database, ScienceDirect, Scopus, JSTOR, and Google Scholar with the following keywords: "Chiroptera" OR "bats" AND "home range" OR "foraging range" OR "movement ecology" OR "movements" OR "telemetry" OR "radio-tracking" OR "GPS tracking." We reviewed the publications by reading the abstracts, or full articles where necessary, and excluded articles that did not report home range sizes. Of the publications that did report home range size, we elected to further retain an article for analysis only if home range data were reported for the species at an individual level, rather than as a mean for multiple individuals or as a colony estimate. The decision was to only include home range statistics reported at the individual level in order to allow for meaningful comparisons between sexes, or where studies included multiple study sites with different landscape types or roost structures between study populations. Where needed, further searches were conducted in order to obtain supplementary data including colony size, functional group, and wing morphology metrics for the individual species using the keywords "foraging ecology," "mammalian species," "wing morphology," or "population ecology" paired with the name of the species. Taxonomic classifications for the species included in the data set were confirmed using the Mammal Diversity Database (MDD 2022) and the "Bats of the World" database (Simmons and Cirranello 2022). There were no cases of ambiguous species classifications in our data set because any formerly cryptic species had their taxonomic classification resolved by the time of this study. All searches were performed using the current species name and all previous names if there had been a taxonomic revision. All publications not written in English were translated in order to assess their relevance for the analysis.

Statistical analysis.

We extracted information regarding the habitat and landscape of the study area, the latitudinal region in which the study occurred, body mass, sex, diet, functional group, colony size, wing morphology, and home range size of the bats directly from the selected articles or supplementary files. Alternatively, where body mass values were not available for the individual bats in the study, a species average was used—extracted from papers such as Norberg and Rayner (1987), as well as other papers (Supplementary Data SD1). Home range measurements were reported using either hectares (ha) or square kilometers (km^2) but were all converted to hectares prior to analysis to ensure comparability across the same unit. Habitat type and landscape classifications for the study areas were further supplemented with data from worldwide habitat type ranges (Jung et al. 2020) and by satellite imagery from Google Earth. Landscapes were assessed using the historical imagery feature to determine landscape structure and cover during the respective study periods. Categorical variables were divided into separate classes (Table 1). We had initially wanted to include additional data including reproductive status and age, as well as the season in which each study was performed—however, due to inconsistent reporting among publications, these variables were not included.

The sex of individual bats was obtained from the corresponding articles. Habitats were broadly defined as "arid," "forest," or "savanna" because bats from these biomes tend to display different ecological traits. A more specific definition of habitat was not possible due to the inconsistent way in which it was described in the different papers—however, since the review is focused on a global scale, the use of such broad definitions is necessary because a finer-scale classification would result in too many variables for reliable statistical comparisons. The landscape for the study areas was defined as either "natural" or "disturbed" based on the descriptions given and historical satellite imagery—with areas being considered "disturbed" where agricultural practices were present, intensive vegetation management was ongoing, or urbanization had occurred. Region refers to latitudinal distance from the equator and was defined as "tropical" for studies performed between the latitudes of 23.5°N and 23.5°S, or "temperate" for studies performed further north or south of 23.5°N and 23.5°S, respectively. The diet and functional group for each species were identified from supplementary literature pertaining to that species if information was not included in the home range publication. Dietary classes were broadly defined as "insectivore," "carnivore," "frugivore," and 'nectarivore' (Ingala et al. 2021)—although some species including exhibit generalist dietary requirements (Stevens and Amarilla-Stevens 2021), e.g., the Great Fruit-eating Bat (*Artibeus lituratus*) which is primarily frugivorous, but molecular analysis has revealed the inclusion of insects in the diet (Ingala et al. 2021). The insects included in the diet, however, may not have been specifically targeted by the bat as they might have been attracted to the fruit and ingested by the bat accidentally. Therefore, dietary classifications were based on the primary food items targeted by different species. Bat species were assigned to functional groups according to the original definitions of "clutter," "edge," and "open-air" foragers given by Schnitzler and Kalko (2001). Colony sizes were defined as "solitary," "small" (less than 100 individuals), or "large" (more than 100 individuals)—similar to the classifications used by (Tournant et al. 2013), with the word "colony" used when the relevant publication used this term.

A phylogenetic generalized least-squares (PGLS) regression was run to search for a phylogenetic signal pertaining to home range size in the data set using the mammalian phylogeny generated by Upham et al. (2019). Because we were interested in the potential effect of phylogeny on home range size—given the variables in the data set—we constructed the PGLS using body mass, aspect ratio, wing loading, and all categorical variables (Table 1) as predictors with home range size as the response (Mundry 2014). We ran 2 separate PGLS regressions using the "caper" and "ape" packages in R (Orme et al. 2018; Paradis and Schliep 2019)

Table 1. Summary of the explanatory variables and respective classes used for analysis.

Variable	Classes[a]
Diet	Frugivore; Nectarivore; Insectivore; Carnivore
Functional group	Clutter forager; Edge forager; Open-air forager
Habitat	Arid; Forest; Savanna
Landscape	Disturbed; Natural
Region	Temperate; Tropical
Colony size	Solitary; Small colony; Large colony
Sex	Male; Female
Taxonomic family[b]	Furipteridae; Hipposideridae; Megadermatidae; Miniopteridae; Molossidae; Mystacinidae; Myzopodidae; Noctilionidae; Nycteridae; Phyllostomidae; Pteropodidae; Rhinolophidae; Vespertilionidae
Home range estimator	Minimum Convex Polygon; Kernel Density Estimation; Local Convex Hulls; Anderson Fourier

[a] For more detail on how the variables were defined, refer to methods described in text.

[b] Taxonomic family and home range estimators were included as random effects in the analysis.

to estimate the maximum likelihood of the parameter lambda (λ). Lambda is a metric that scales from 0 to 1 (0 representing no phylogenetic signal, 1 representing a strong phylogenetic signal and one can assume evolution by a Brownian motion model where trait data are fully explained by phylogeny) and is used to determine the extent to which phylogeny explains the variation in a data set (Symonds and Blomberg 2014). The PGLS regressions demonstrated that there was no phylogenetic signal in the estimates of home range ($\lambda = 0$), meaning that the effect of the different covariates on home range size was not biased by phylogeny (Revell 2010). Therefore, we performed linear mixed models (LMMs) to determine which variables had a significant impact on home range size.

Due to the nature of the morphological predictor variables (i.e., body mass, aspect ratio, and wing loading), we would expect phylogenetic relatedness among them. For instance, average body mass for Pteropodidae was higher than that for Vespertilionidae. We included taxonomic family as a random effect in the LMMs to account for trends across the data set due to phylogenetic relatedness. Home range estimates were log-transformed to account for outliers and achieve an approximately normal distribution. Although data were not normally distributed post-transformation (Shapiro–Wilk: $w = 0.997$; $P = 0.008$), regression models with a Gaussian distribution have been shown to be robust to violations of normality (Knief and Forstmeier 2021). Body mass was also log-transformed to account for high variability within the data set. We included wing loading, aspect ratio, log of body mass, diet, functional group, colony size, habitat type, sex, region, and landscape as fixed effects. Interaction terms were considered for inclusion in the models only if they carried biological relevance that may influence home range size variation. Two interaction terms were considered: firstly, between body mass and sex to address the potential effect of sexual dimorphism on home range size; and secondly, between habitat type and latitudinal region due to potential regional variability in vegetation structure and/or resource availability between similar habitat types.

We attempted to investigate whether number of locations, proportional tag mass, or statistical methods influenced home range estimates. Unfortunately, the number of locations obtained for each bat was inconsistently reported among publications and was not available for a large proportion of the data set and, therefore, could not be assessed. Proportional mass of the transmitters deployed on the bats was, however, available and we included it as a covariate in the analysis. The best measure to assess its potential influence was to analyze it for species where multiple studies had been performed. Therefore, a separate analysis was performed using a subset of the data set including only species with multiple separate home range studies.

Four different home range estimation methods had been employed to calculate home range size in the different studies, which can confound comparative assessments given the lack of comparability between different estimation methods (Laver and Kelly 2008). However, because we had multiple species and families represented for each of the different estimation methods, we included home range estimator as a random effect to control for potential variability between the statistical methods.

Taxonomic family was included as a second random effect to account for variability within the morphological variables due to phylogenetic relatedness. Both taxonomic family and home range estimator were included as random intercepts. We assessed for potential collinearity between variables in the full model using generalized variance inflation factors (GVIF) from the "car" package in R. Upon the recommendations by Fox and Monette (1992) we used the squared ratio generalized variance inflation factor, $\text{GVIF}^{1/(2 * df)}$, which enables effective comparisons for variables with multiple coefficients. Model selection was performed using the "AICcmodavg" and "lme4" packages in R (Bates et al. 2015; Mazerolle 2020) by generating all relevant candidate models and assessing the AICc (corrected Akaike Information Criterion) and ΔAICc values. The model with the lowest AICc value was selected as the best model, and any models that were within $\Delta\text{AICc} < 2$ were considered as competing (Burnham and Anderson 2004). To assess for the reliability of the output from the top-ranked model, we performed a Bonferroni test assessing for the presence of outliers (Cook and Prescott 1981), although none were detected, and overall model fit was assessed with the marginal and conditional R^2 values using the "MuMIn" package in R (Barton 2020). Post hoc Tukey tests were also performed for variables with >2 classes using the "emmeans" package (Lenth 2022) to determine interclass differences. All analyses were performed in R v4.0.2 (R Core Team 2021) using the RStudio v1.3.1073 (RStudio Team 2021) interface and statistical significance was assessed using an alpha of 0.05.

Results

The data set.

Our literature search returned 4,239 articles relevant to our search terms. After the removal of duplicate articles, conference results, non-peer-reviewed data sets, off-topic publications, or articles reporting home range sizes at population or colony level, the data set was reduced to 91 publications (all but 1 peer-reviewed plus a single unpublished report). Subsequent searches for species-specific supplementary data included an additional 75 publications resulting in a total of 166 publications encompassing 1,260 individuals from 81 species and 13 families for our final data set with sample size per species ranging from 1 to 83 individuals (Supplementary Data SD1 and SD2).

Summary of species data collected.

The species for which we obtained home range data were distributed across the 6 continents where bats are found: Africa (14); Asia (7); Europe (19); North America (18); Oceania (8); and South America (15)—and included insectivores, frugivores, nectarivores, and carnivores. From the 6 continents, species were distributed across tropical (44) and temperate regions (37). Species collectively belonged to 13 families: Furipteridae (1); Hipposideridae (1); Megadermatidae (2); Miniopteridae (1); Molossidae (2); Mystacinidae (1); Myzopodidae (1); Noctilionidae (1); Nycteridae (1); Phyllostomidae (22); Pteropodidae (17); Rhinolophidae (3); and Vespertilionidae (28). Home range sizes varied from 0.2 ha (Atacama Myotis, *Myotis atacamensis*; Rodriguez-Pinto et al. 2022) to 124,413.8 ha (Straw-coloured Fruit Bat, *E. helvum*; Randhawa et al. 2020).

Home range estimates and model selection.

There was no evidence of collinearity within the data set with all $\text{GVIF}^{1/(2 * df)}$ values < 3 (Supplementary Data SD3), well below previously suggested values of 10 when assessing severe multicollinearity (Hair et al. 1995; O'Brien 2007). Model selection revealed that the best-performing model included sex, wing loading, colony size, the interaction between habitat type and region, functional group, and diet—with taxonomic family and home range estimator as random intercepts ($R^2m = 0.29$; $R^2c = 0.81$; Table 2).

Table 2. Summary of the top 10 candidate models and the full model for comparison with AICc scores, model weight (AICcWt), and parameters (*K*) examining the effect of biological and ecological variables on bat home range sizes.

	Candidate models	K	AICc	ΔAICc	AICcWt
1	S + WL + C + H * R + FG + D	18	4,075.60	0.00	0.24
2	log(m) * S + WL + C + H * R + FG + D	20	4,076.30	0.70	0.17
3	S + WL + C + H * R + FG + D + L	19	4,076.55	0.95	0.15
4	log(m) * S + WL + C + H * R + FG + D + L	21	4,077.13	1.53	0.11
5	log(m) + S + WL + C + H * R + FG + D	19	4,077.55	1.95	0.09
6	log(m) * S + AR + WL + C + H * R + FG + D	21	4,077.98	2.38	0.07
7	log(m) + S + WL + C + H * R + FG + D + L	20	4,078.38	2.78	0.06
8	log(m) * S + AR + WL + C + H * R + FG + D + L	22	4,078.94	3.34	0.04
9	log(m) + S + AR + WL + C + H * R + FG + D	20	4,079.21	3.61	0.04
10	log(m) + S + AR + WL + C + H * R + FG + D + L	21	4,080.17	4.57	0.02
Full	log(m) + S + AR + WL + C + H + R + FG + D + L	19	4,206.50	130.90	0.00

Variable definitions: m = mass; S = sex; AR = aspect ratio; WL = wing loading; C = colony size; H = habitat; D = diet; FG = functional group; R = region; L = landscape; taxonomic family and home range estimator were included as random effects.
*Denotes an interaction between variables.

Residuals were not normally distributed according to statistical tests (Shapiro–Wilk: $w = 0.99$, $P < 0.001$) but Knief and Forstmeier (2021) suggest that these violations of normality do not impact the accuracy of estimates nor the significance of variables if sample sizes are sufficiently large. The separate analysis assessing the influence of proportional tag mass on home range size for the data subset revealed a significant negative relationship with home range size ($\beta = -0.20$; $P < 0.001$). When included in the top-ranked model, the proportional mass of transmitters on the tagged bats still had a significant negative influence on home range size ($\beta = -0.07$; $P = 0.001$), supporting the idea that tag mass may influence movement patterns (Aldridge and Brigham 1988) and may bias home range estimates. However, its inclusion did not change the significance or effects of the remaining variables and therefore, did not influence the overall results (Supplementary Data SD4). There were 4 competing models that included the interaction between body mass and sex, body mass as a separate covariate, and landscape in different combinations (Table 2).

Wing loading, sex, functional group, habitat type, latitudinal region, the interaction between habitat type and region, colony size, and diet all had a significant influence on home range size (Table 3; Supplementary Data SD5). None of the variables included in the competing models had a significant influence on home range size. Their inclusion also did not alter the signs or significance of the other covariate estimates except for models with the interaction between body mass and sex. For these models, sex was no longer significant, and the estimate changed from a negative to a positive value, although its inclusion in the interaction likely caused this difference. Wing loading had a significant, positive influence on home range size (Supplementary Data SD6). Females had significantly larger home ranges than males. Home ranges of bats in the temperate zone were significantly larger than those in tropical regions. Home ranges within savanna habitats were significantly smaller than in arid areas, and pairwise comparison revealed they were also significantly smaller than in forested areas (Table 4). However, since habitat type was involved in a significant interaction with latitudinal region, the interpretation of the pairwise comparisons for the main effects in isolation may not be reliable. Considering the interaction, home ranges were significantly larger within temperate forests and arid areas compared to tropical regions for these 2 habitat types; however, tropical savannas had significantly larger home ranges than temperate savannas. Species roosting in large colonies had significantly larger home ranges than both small colonies or species roosting solitarily, with no difference between small colonies and solitary species. Home ranges for open-air foragers were significantly larger than both edge and clutter foragers, while edge foragers also had larger home ranges than clutter foragers. Finally, carnivores had significantly larger home ranges compared to insectivores and frugivores, but not to nectarivores—the small sample size for carnivores likely influenced these results because there were only 34 individuals from 4 species in our data set. There were no other differences in home range size between the other dietary classes (Table 4).

The results show that individual explanatory variables contribute relatively little to explaining variations in home range size; however, investigating the different variables in conjunction with each other provides a better picture of home range size variation. For example, larger colony size, open-air foraging strategies, and temperate regions all contributed toward larger home ranges. Therefore, we expect species with this combination of variables to have comparably larger home ranges than solitary, clutter foragers from tropical regions. A comparison of home range size for species from our data set with these combinations of variables further supported this trend (Fig. 1), also showing a positive relationship between home range size and wing loading.

Discussion

We found a weak, but positive association between wing loading of bats and home range size. Wing loading is primarily linked to flight speed in bats, with higher wing loading correlating to higher flight speeds to generate sufficient lift (Norberg and Rayner 1987; Voigt and Holderied 2012). Higher flight speeds would enable bats to cover a greater distance in a shorter space of time and could translate to larger range sizes (Laforge et al. 2021). Contrary to our predictions, we did not find an association with aspect ratio, despite higher aspect ratio corresponding with higher aerodynamic efficiency that may facilitate long-distance flight (O'Donnell 2001). Body mass was also predicted to positively correlate with home range size as bats experience unique energetic constraints associated with flight (Thomas and Suthers 1972), which increase with higher body masses (Norberg and Rayner 1987; Fenton 1997).

Table 3. Coefficient estimates, standard error, t-values, and 95% confidence intervals for the best-performing LMM assessing the effects of ecological and biological variables on bat home range sizes. Statistical significance was assessed with an alpha threshold of 0.05.

Variable	Coefficient estimate	Standard error	t-values	95% CI
Intercept	**5.17**	**0.94**	**5.51**	**3.32 to 7.01**
Wing loading	**0.08**	**0.02**	**4.88**	**0.04 to 0.12**
Sex				
Female	Ref lev[a]			
Male	**–0.28**	**0.10**	**–2.72**	**–0.48 to –0.08**
Colony size				
Large	Ref lev			
Small	**–1.34**	**0.15**	**–8.69**	**–1.63 to –1.05**
Solitary	**–1.54**	**0.18**	**–8.67**	**–1.89 to –1.19**
Habitat				
Arid	Ref lev			
Forest	0.00	0.47	0.00	–0.92 to 0.92
Savanna	**–4.31**	**0.52**	**–8.26**	**–5.33 to –3.29**
Region				
Temperate	Ref lev			
Tropical	**–5.60**	**0.90**	**–6.25**	**–7.36 to –3.84**
Functional group				
Clutter	Ref lev			
Edge	**0.41**	**0.12**	**3.37**	**0.17 to 0.65**
Open-air	**1.60**	**0.18**	**9.10**	**1.25 to 1.95**
Diet				
Insectivore	Ref lev			
Frugivore	–0.01	0.28	–0.04	–0.56 to 0.54
Nectarivore	0.68	0.38	1.79	–0.06 to 1.42
Carnivore	**1.72**	**0.32**	**5.36**	**1.09 to 2.35**
Habitat_Forest * Region_Tropical	**4.10**	**0.98**	**4.19**	**2.18 to 6.02**
Habitat_Savanna * Region_Tropical	**10.09**	**1.02**	**10.66**	**8.09 to 12.09**

Variables in bold are significantly different from their respective reference level variables. More detail on the pairwise comparisons for variables with >2 classes is provided in Table 4.

[a] Reference level variable.

Therefore, it seems reasonable that larger bats would occupy larger home ranges to obtain sufficient resources to balance their energy budgets. Yet, body mass did not contribute to the top model and when it was included in competing models, it had no influence on home range size. This contrasts with the findings of Laforge et al. (2021) who reported that wing loading, aspect ratio, and body mass all significantly influenced home range size. A possible reason for this could be due to the global nature of our study, which resulted in a higher number of species and families being used in our analysis. Alternatively, the combination of individual-level and species average body mass values in the data set of Laforge et al. (2021) may have confounded the effect of body mass on home range size through inadvertent pseudoreplication. However, this limitation could not easily be resolved without sacrificing statistical power with significantly smaller sample sizes. Therefore, although our results show that body mass did not significantly influence home range size, we suggest that future studies incorporate individual-level body mass values for this analysis. Regardless, we supported previous results (Laforge et al. 2021) indicating that wing loading was positively correlated with home range size.

Like most mammals, bats are hypothesized to experience sex-specific energetic constraints linked to reproduction that may influence movement patterns and range sizes (Henry et al. 2002). Several previous studies have reported contrasting results regarding sex-specific range requirements (Meyer et al. 2005; Safi et al. 2007; Dechmann et al. 2014), yet females consistently had larger home ranges than males in our data set. Female bats experience stringent energetic constraints during pregnancy and lactation that males do not encounter and therefore may need to alter their movement patterns or behaviors with 1 option being to expand their ranges over a large area to satisfy their increased energetic requirements (O'Donnell 2001; Henry et al. 2002). Similarly, nightly activities that differ between sexes could also influence movement distances. For instance, males have been observed foraging closer to the day roost than females during the breeding season in order to defend females (Meyer et al. 2005).

The 3 functional groups (open-air, edge, and clutter foragers) each have their own unique flight characteristics and patterns imposed by their wing shape and aerodynamic constraints (Norberg and Rayner 1987; Schnitzler and Kalko 2001).

Table 4. Coefficient estimates, standard error, and 95% confidence intervals for post hoc pairwise comparisons of functional group, colony size, and dietary class. Statistical significance was assessed with an alpha threshold of 0.05.

Comparison	Coefficient estimate	Standard error	df	t-ratio	95% CI
Clutter–Edge	**−0.41**	**0.12**	**1,148**	**−3.34**	**−0.65 to −0.17**
Clutter–Open	**−1.60**	**0.17**	**1,150**	**−9.02**	**−1.93 to −1.27**
Edge–Open	**−1.19**	**0.17**	**1,150**	**−6.91**	**−1.52 to −0.86**
Large–Solitary	**1.54**	**0.18**	**1,145**	**8.57**	**1.19 to 1.89**
Large–Small	**1.34**	**0.16**	**1,153**	**8.59**	**1.03 to 1.65**
Small–Solitary	−0.21	0.15	1,151	−1.34	−0.50 to 0.08
Insectivore–Frugivore	0.01	0.28	1,148	0.04	−0.54 to 0.56
Insectivore–Nectarivore	−0.68	0.39	1,122	−1.77	−1.44 to 0.08
Insectivore–Carnivore	**−1.71**	**0.32**	**1,146**	**−5.32**	**−2.34 to −1.08**
Frugivore–Nectarivore	−0.69	0.30	1,148	−2.29	−1.28 to −0.10
Frugivore–Carnivore	**−1.73**	**0.33**	**1,150**	**−5.27**	**−2.38 to −1.08**
Nectarivore–Carnivore	−1.03	0.45	1,142	−2.32	−1.91 to −0.15

Significant comparisons given in bold.

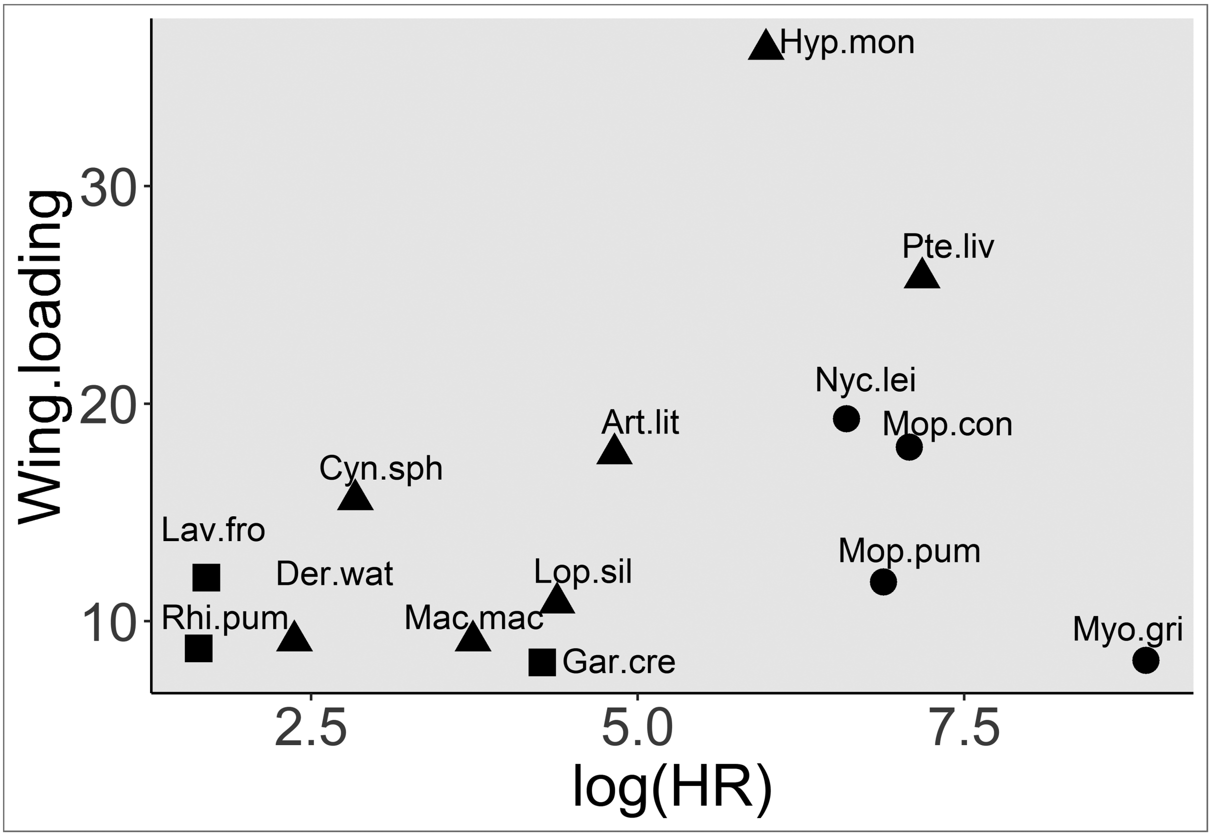

Fig. 1. Graphical representation of the combined effect of colony size, functional group, and latitudinal region on home range size compared against wing loading. Circles represent open-air foragers in large colonies from temperate regions: *Myotis grisescens* (Myo.gri), *Mops condylurus* (Mop.con), *Mops pumilus* (Mop.pum), *Nyctalus leisleri* (Nyc.lei). Triangles represent edge foragers in small colonies from tropical regions: *Hypsignathus monstrosus* (Hyp. mon), *Pteropus livingstonii* (Pte.liv), *Artibeus lituratus* (Art.lit), *Lophostoma silvicolum* (Lop.sil), *Macrophyllum macrophyllum* (Mac.mac), *Cynopterus sphinx* (Cyn. sph), *Dermanura watsoni* (Der.man). Squares represent solitary, clutter foragers from tropical regions: *Gardnerycteris crenulatum* (Gar.cre), *Lavia frons* (Lav. fro), *Rhinophylla pumilio* (Rhi.pum).

Examples for each group include: the Angolan Free-tailed Bat (*Mops condylurus*) that forages in open space over vegetation (Noer et al. 2012); the Soprano Pipistrelle (*Pipistrellus pygmaeus*) that forages along the edge of tree lines (Kirkpatrick et al. 2018); and the Egyptian Slit-faced Bat (*Nycteris thebaica*) that forages in well-vegetated, cluttered areas (Monadjem et al. 2009). There was a trend for home range size to increase in line with increasing requirements for open space. Open-air foragers had the largest home ranges followed by edge and clutter foragers.

There are fundamental differences among habitat types in terms of vegetation structure, density, and heterogeneity that can all influence resource distribution and availability (Egert-Berg et al. 2021). The specific vegetation structure within different habitats may limit the types of species present in these areas which may result in different bat assemblages with traits specifically evolved to exploit a particular habitat type (Fahr and Kalko 2011). As a result, there may be contrasting movement patterns for bats from these different habitats. There were differences in patterns of range size between different habitat types, but this was also influenced by latitudinal region. Movement patterns were more variable within temperate compared to tropical habitats for arid and forested areas in our data set. The small sample size for temperate and tropical arid habitats may have confounded this effect; however, tropical forests are typically densely vegetated with high levels of structural complexity and species diversity (Bonaccorso et al. 2005). The structural complexity of tropical forests limits accessibility to species that are adapted for slower flight and higher maneuverability (Norberg and Rayner 1987; Schnitzler and Kalko 2001) while the dense concentration and diversity of suitable resources may enable species to satisfy their energetic requirements within a smaller area compared to temperate forests (Rothenwoehrer et al. 2011). For savanna habitats there was an interesting trend for home range to be larger in tropical regions than temperate ones. This trend, however, may have been an unintended artifact of sampling bias because all but one of the species from tropical savannas were from parts of South America that have experienced extensive habitat fragmentation and alteration (Bernard and Fenton 2007).

Colony size was an important predictor of variation in home range size. Large colony size was linked to larger home range areas, supporting previous hypotheses that intraspecific competition in colonial species drives wider dispersal to avoid potential resource competition (Meyer et al. 2005; Corman et al. 2016). Acharya et al. (2015) alluded to a similar trend where range size and flight distances were greatest for bats from larger colonies. Dietary class was also linked to home range size variation.

Carnivorous bats had larger home ranges than insectivores and frugivores, although the limited number of carnivores may have masked the true differences between these groups as the small sample size is more sensitive to extreme values. Whether diet influences home range sizes for bats has thus far remained untested and, although our results suggest carnivorous bats may require larger ranges, further investigations are required with greater representation of carnivorous species before such a conclusion can be drawn.

Landscape status did not affect home range size despite predictions that sparsely distributed resources in disturbed areas would force bats to travel further to reach isolated resource patches or to avoid undesirable areas such as urban centers or large, open agricultural fields (Quesada et al. 2004). However, responses to habitat fragmentation may be species-specific because habitat specialists are typically more susceptible to disturbance than generalists (Webala et al. 2019). Furthermore, disturbance may benefit bats through increased habitat heterogeneity that provides greater foraging opportunities year-round, or potential roosting sites that could forego the need for larger ranges and travel distances (Hahn et al. 2014; Egert-Berg et al. 2021; Laforge et al. 2021). Similarly, bats foraging at high altitudes may be less susceptible to fragmentation because their flight paths allow them to circumnavigate areas of disturbance without being affected (Jung and Threlfall 2016).

Limitations and future directions.

Data were available for a relatively limited number of species given their overall diversity (with >1,400 known species; Monadjem et al. 2020), and there was relatively poor representation for species from Asia and Oceania. The different home range estimators used in the different studies brought in further complexity through the lack of comparability between methods (Laver and Kelly 2008). We addressed this by controlling for estimator method across the different studies. Although this may not have accounted for all potential bias inherent between the different statistical methods, it helped to control for some of the variation in the available data without sacrificing statistical power with smaller sample sizes or fewer species in the data set. Regardless, we believe that the findings of this meta-analysis provide important insight as to how the home ranges of bats across the globe are affected by different biological and ecological variables. We included species representation for 13 of the 21 bat families reported by the Mammal Diversity Database (MDD 2022), and therefore, provide good coverage for the taxonomic diversity within the Order Chiroptera despite relatively poor species representation. Future studies should look to build on these findings by focusing on additional species and taxonomic families once home range data become available because the high diversity of bats may potentially provide contrasting trends not observed within our data set. Future efforts will still be constrained by the availability of appropriately size tags that may prevent investigations for smaller species. Small tags are being developed that will increase accessibility to smaller species; however, the costs associated with more compact units may limit the number of bats that can be tracked. The inclusion of reproductive status in general home range studies can also provide important information regarding energetic constraints and movement patterns during these periods, especially for males due to the scarcity of published data regarding home range sizes for males of different reproductive statuses. The inconsistent or lack of reporting for season(s) in which studies were performed prevented the comparison of home ranges and movement patterns across seasonal gradients. However, perhaps a more useful metric may be to report periods of food availability around the study area—this would likely be more informative than season or rainfall periods because habitat dynamics may vary between different ecoregions and such information could allow comparisons of home ranges given an understanding of fluctuating resource availability.

Implications for pathogen risk assessment.

As known viral hosts, the movement patterns of bats are potentially important for their role in pathogen spillover events (Dougherty et al. 2018). Most studies investigating emerging zoonoses in bats, however, do not consider movement data that could highlight potential areas of contact between species (Letko et al. 2020; Randhawa et al. 2020). Home range analysis can help provide a broad overview of the potential range over which contact may occur—however, a more useful measure may be to explore patterns of range use within a home range (Randhawa et al. 2020; McKee et al. 2021). Range use analysis, such as kernel density estimates that identify areas with higher intensity usage, could provide crucial information regarding specific regions of overlap and potential risk of contact for pathogen spillover (Zhao et al. 2022). Additionally, by assessing the patterns of range use within bat home ranges, researchers can gain more specific insight into which habitat features are vital to their survival to make informed conservation decisions (Kunz et al. 2003; Zeale et al. 2012).

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Results of literature search and list of publications used in the analysis including species sample size and study locations.

Supplementary Data SD2.—Summary of data set structure including the number of species per family, number of studies per species, and sample size per study.

Supplementary Data SD3.—Results from collinearity test with generalized variance inflation factors for variables in the full model.

Supplementary Data SD4.—Comparison of the top-ranked model when proportional mass of the transmitter is included as a covariate.

Supplementary Data SD5.—Graphical visualization of statistical outputs from top model detailing the scale of effects for the different covariates on home range size.

Supplementary Data SD6.—Graphical plots detailing the effects on home range size for (A) sex, (B) wing loading, (C) colony size, (D) functional group, (E) diet, and (F) habitat type, latitudinal region interaction.

Supplementary Data SD7.—https://doi.org/10.17605/osf.io/jbc4s.

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Author contributions

MRW and JLdV conceived the study. MRW and AM performed the statistical analyses. All authors drafted, edited, read, and approved the final manuscript.

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Conflict of interest

None declared.

Data availability

The full data set is available from the Open Science Framework online repository: https://doi.org/10.17605/osf.io/jbc4s.

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