Received: 15 March 2021 | Revised: 13 August 2021 | Accepted: 19 August 2021

DOI: 10.1111/geb.13393

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology WILEY

An alternative hypothesis for the evolution of sexual segregation in endotherms

Tali Magory Cohen[1,2] | Yosef Kiat[3,4] | Haggai Sharon[5,6] | Eran Levin[1]

[1]School of Zoology, Faculty of Life Sciences, Tel-Aviv University, Tel Aviv, Israel

[2]Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

[3]Department of Evolutionary and Environmental Biology and the Institute of Evolution, University of Haifa, Haifa, Israel

[4]Israeli Bird Ringing Center (IBRC), Israel Ornithological Center (IOC), Society for the Protection of Nature in Israel (SPNI), Tel Aviv, Israel

[5]Sagol Brain Institute and the Institute of Pain Medicine, Tel Aviv Medical Center and Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv, Israel

[6]Pain Management & Neuromodulation Centre, Guy's & St Thomas' NHS Foundation Trust, London, UK

Correspondence
Eran Levin, Tel Aviv, IsraSchool of Zoology, Tel-Aviv University, Tel Aviv 69978, Israel.
Email: levineran1@gmail.com

Funding information
the Tel Aviv University's rector's emergency Corona fellowship; the Council for Higher Education (CHE) postdoctoral fellowship

Handling Editor: Adam Algar

Abstract

Aim: Patterns of separation among males and females, known as sexual segregation, are traditionally correlated with elevation or latitude in animals. Alternatively, in humans, spatial and behavioural segregation is driven by inherent sex-based differences in thermal preference, although the cause and adaptive value of these differences remain unclear. Here, we explore whether, similar to humans, ambient temperature can explain patterns of separation among males and females in endotherms.

Location: Israel.

Time period: 1981–2018.

Major taxa studied: Migratory sexually dimorphic birds (13 species) and bats (18 species).

Methods: We calculated the proportion of males and females at each sampling site for each bird or bat species. We used general linear mixed models (GLMMs) to quantify the variance explained by elevation, latitude, body size and ambient temperature and corrected for phylogeny, site and year. We used model averaging over the best models by comparing the corrected Akaike information criterion.

Results: We found a correlation between geographical separation and temperature that accounted for variance in the data that was not explained by elevation and latitude. We showed that temperature was negatively correlated with the proportion of males in bats and birds, whereas body size explained this response only in birds.

Main conclusions: Our findings suggest that females are found in higher ambient temperatures. We term this differential sex-related thermal preference (DSTP) and propose that it is a broad phenomenon common in many endotherms, acting as a significant force shaping dispersal, sociality and behaviour of animals, and should be explored from this wide perspective.

KEYWORDS

bats, birds, endotherms, sex, sexual segregation, thermal preference, thermal sensing

1 | INTRODUCTION

The phenomenon in which males and females are separated during portions of their life cycle is known as sexual segregation. Although a widely accepted definition of this concept is still under debate, sexual segregation is often defined as the segregation of males and females into different groups (Ruckstuhl, 2007) and has been classified further into segregation by habitat, social segregation or spatial segregation (Conradt, 2005). Several hypotheses have been suggested to explain the adaptive value of sexual segregation in animals, including predator avoidance, reduction of aggression by males towards females and by males towards offspring, different nutritional requirements, niche partitioning, social preferences and different activity patterns (Main, 2008; Main et al., 1996; Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2005). One prominent example of sexual segregation, known as “differential migration” (Cristol et al., 1999), occurs in many migrating bird species and is explained by latitudinal sorting. In this migration pattern, males typically overwinter at cooler, higher latitudes than females, which migrate farther to warmer climates at lower latitudes (but see Gow & Wiebe, 2014). Three main hypotheses are often used to explain the adaptive values of this pattern: the early arrival hypothesis suggests that males experience the most intense intraspecific competition for resources on the breeding grounds and that they should therefore overwinter in more northern latitudes to expedite arrival at the breeding grounds (Myers, 1981); the body size hypothesis or cold tolerance hypothesis (Ketterson & Nolan, 1976; Myers, 1981) stipulates that larger individuals are better suited to survive the colder and less predictable climates at higher latitudes; and the dominance hierarchy hypothesis predicts that the competition for winter resources leads the dominant sex to exclude the subordinate sex, which is forced to move to areas farther away from the breeding grounds (Gauthreaux, 1978).

A similar pattern also appears in bats (order: Chiroptera), in which, unlike birds, sexual segregation has been reported mostly to be related to elevation, with males inhabiting higher elevations than females (Amichai et al., 2013; Barclay, 1991; Cryan & Wolf, 2003; Erickson & Adams, 2003; Levin et al., 2013; McGuire & Boyle, 2013; Nardone et al., 2015; Russo, 2002; Senior et al., 2005). Separation of males and females in bats is most common during the periods of parturition and lactation. It is made possible during this stage because male bats are rarely involved in pup care; the weaning of the pups and mating usually occur long before parturition, and reproduction is seasonal. In this group, sexual segregation is explained mostly in terms of different energetic requirements of the sexes or the dominance of one sex (often the larger female) excluding the other from the better habitats (often the lowlands, the better foraging sites) (Cryan et al., 2000; Erickson & Adams, 2003; Grindal et al., 1999; Nardone et al., 2015; Senior et al., 2005). However, complete elevational sexual segregation was described in a bat species in which males are larger than females (Amichai et al., 2013; Levin et al., 2012, 2013), suggesting that the dominance hierarchy hypothesis does not necessarily account for some of the variance found. Likewise, in several species of birds, males prefer cooler sites than females outside of the breeding season, even in species in which males are smaller than females (Chapman et al., 2011; Cristol et al., 1999), indicating that the body size hypothesis cannot explain all of the detected pattern. Therefore, in the observed sexual segregation patterns in both birds and bats, there remains a portion of cases that none of the current theoretical frameworks seems to explain.

Most of the hypotheses to explain sexual segregation patterns rely heavily on sexual dimorphism and breeding-related behaviour. Only a few studies have addressed the possible role of differential thermal or climatic sensitivity in dictating sexual segregation (but see Alonso et al., 2016; Conradt et al., 2000; Jackes, 1973). A special case study can be found in humans, where sex-based differences in thermal preference have been described extensively. In general, women prefer higher ambient temperatures than men (Karjalainen, 2012) and feel comfortable at an ambient temperature ~1.1°C higher than that at which men are comfortable (Lan et al., 2008; Schaudienst & Vogdt, 2017). It is known that differences in thermal comfort in humans can lead to behavioural separation (e.g., individualized, time-variant air conditioning in the office; Wang et al., 2018). Conversely, in animals, thermal comfort is difficult to measure precisely and directly because they cannot communicate their thermal preferences verbally. However, if temperature-related separation also occurs between sexes in animals, it might reflect thermal preferences. Thermal preference-related sexual segregation in which males show a preference for lower ambient temperatures than females has been reported in a number of species. For example, male alpine ibexes (*Capra ibex*) migrate to higher elevations than females as temperatures increase during the day (Aublet et al., 2009); males of the western grey kangaroo (*Macropus fuliginosus*) prefer shaded habitats at midday (Garnick et al., 2014); and semi-fossorial marsupial males use burrows more often than females, probably to avoid the heat (MacFarlane & Coulson, 2005). Sexual differences in thermal preference were also reported in non-human primates: female grey dwarf lemurs (*Microcebus murinus*) live in small groups and nest in warmer microhabitats than the solitary males, which choose cooler places (Lahann, 2008; Terrien et al., 2010). However, these studies reported either short temporary patterns or differences relatively small in geographical scale. Should ambient temperature play a significant role in determining the preferred habitats of males and females, it could be detected best in species that have the innate ability to reflect thermal responses and preferences by their locomotion patterns. Therefore, highly mobile species, such as birds and bats, which can respond to environmental cues (e.g., temperature, precipitation) more readily than less mobile species, represent a unique opportunity to test this hypothesis.

In this study, using two large groups of mobile endothermic vertebrates, birds and bats, we perform the most comprehensive analysis to date to test whether thermal preferences can explain sexual segregation in homeothermic mobile species. We explore this by establishing that a general trend of sexual segregation can be detected in these species that can clearly select their habitats under natural constraints (i.e., providing no anthropogenic interferences take place). We then test whether sexual segregation can be explained by elevation, body size or latitude, all of which support previously invoked hypotheses. Alternatively, we test whether ambient temperature can explain spatial separation patterns as a new hypothesis that we offer to expand the current theory. Given the evidence for a sex-based differential thermal preference in humans and the proportion of examples that are not explained by current hypotheses, we hypothesize that female preference for higher temperature, regardless of their elevation, body size or latitude, determines space use, and therefore there would be a higher proportion of females of endothermic species in warmer locations.

2 | MATERIALS AND METHODS

2.1 | Sample collection

We collated records from Israeli birds and bats to form two data sets, respectively (Table 1).

The bird data set included 8,810 individuals from 13 species sampled across 76 locations in Israel (Figure 1) obtained from the Israeli Bird Ringing Centre (IBRC). These data were curated by the IBRC between 1981 and 2018 from trained ringers [permitted by the Israel Nature and Parks Authority (INPA)]. We selected migratory species that showed sexual dimorphism such that the sex of the individual could be recorded conclusively at the time of the ringing. We considered only data that were recorded during wintering (December to February). We focused on migratory birds during wintering, because during this period males and females are not dependent on each other and do not need to defend a breeding territory, and therefore we expected to see the most significant differences in habitat selection during this time of year in these species. Some of the records originated in recaptures of previously ringed birds ($n = 559$). To control for the effect of recaptures, we analysed the data without records of recaptured birds. Given that the results of the subset

TABLE 1 Species of bats and birds used in this study, their taxonomic family classification and their respective sample size (*n*)

Common name	Species	Family	*n*
Bats			
Trident bat	*Asellia tridens*	Hipposideridae	83
Botta’s serotine	*Eptesicus bottae*	Vespertilionidae	28
Serotine bat	*Eptesicus serotinus*	Vespertilionidae	56
Desert pipistrelle	*Hypsugo ariel*	Vespertilionidae	588
Savi’s pipistrelle	*Hypsugo savii*	Vespertilionidae	200
Common bent-wing bat	*Miniopterus schreibersii*	Vespertilionidae	20
Long-fingered bat	*Myotis capaccinii*	Vespertilionidae	29
Geoffroy’s bat	*Myotis emarginatus*	Vespertilionidae	64
Whiskered bat	*Myotis mystacinus*	Vespertilionidae	39
Natterer’s bat	*Myotis nattereri*	Vespertilionidae	11
Common noctule	*Nyctalus noctula*	Vespertilionidae	93
Common pipistrelle	*Pipistrellus*	Vespertilionidae	119
Rüppell’s pipistrelle	*Pipistrellus rueppellii*	Vespertilionidae	22
Geoffroy’s horseshoe bat	*Rhinolophus clivosus*	Rhinolophidae	49
Greater horseshoe bat	*Rhinolophus ferrumequinum*	Rhinolophidae	66
Lesser horseshoe bat	*Rhinolophus hipposideros*	Rhinolophidae	25
Egyptian mouse-tailed bat	*Rhinopoma cystops*	Rhinopomatidae	12
Greater mouse-tailed bat	*Rhinopoma microphyllum*	Rhinopomatidae	991
	Total		2,495
Birds			
European greenfinch	*Chloris chloris*	Fringillidae	380
Palestine sunbird	*Cinnyris osea*	Nectariniidae	498
Hawfinch	*Coccothraustes coccothraustes*	Fringillidae	92
Common chaffinch	*Fringilla coelebs*	Fringillidae	1,494
Brambling	*Fringilla montifringilla*	Fringillidae	131
Bluethroat	*Luscinia svecica*	Muscicapidae	2058
White wagtail	*Motacilla alba*	Motacillidae	698
Black redstart	*Phoenicurus ochruros*	Muscicapidae	251
Penduline tits	*Remiz pendulinus*	Remizidae	265
European stonechat	*Saxicola rubicola*	Muscicapidae	375
European serin	*Serinus serinus*	Fringillidae	449
Eurasian siskin	*Spinus spinus*	Fringillidae	273
Eurasian blackcap	*Sylvia atricapilla*	Sylviidae	1846
	Total		8,810

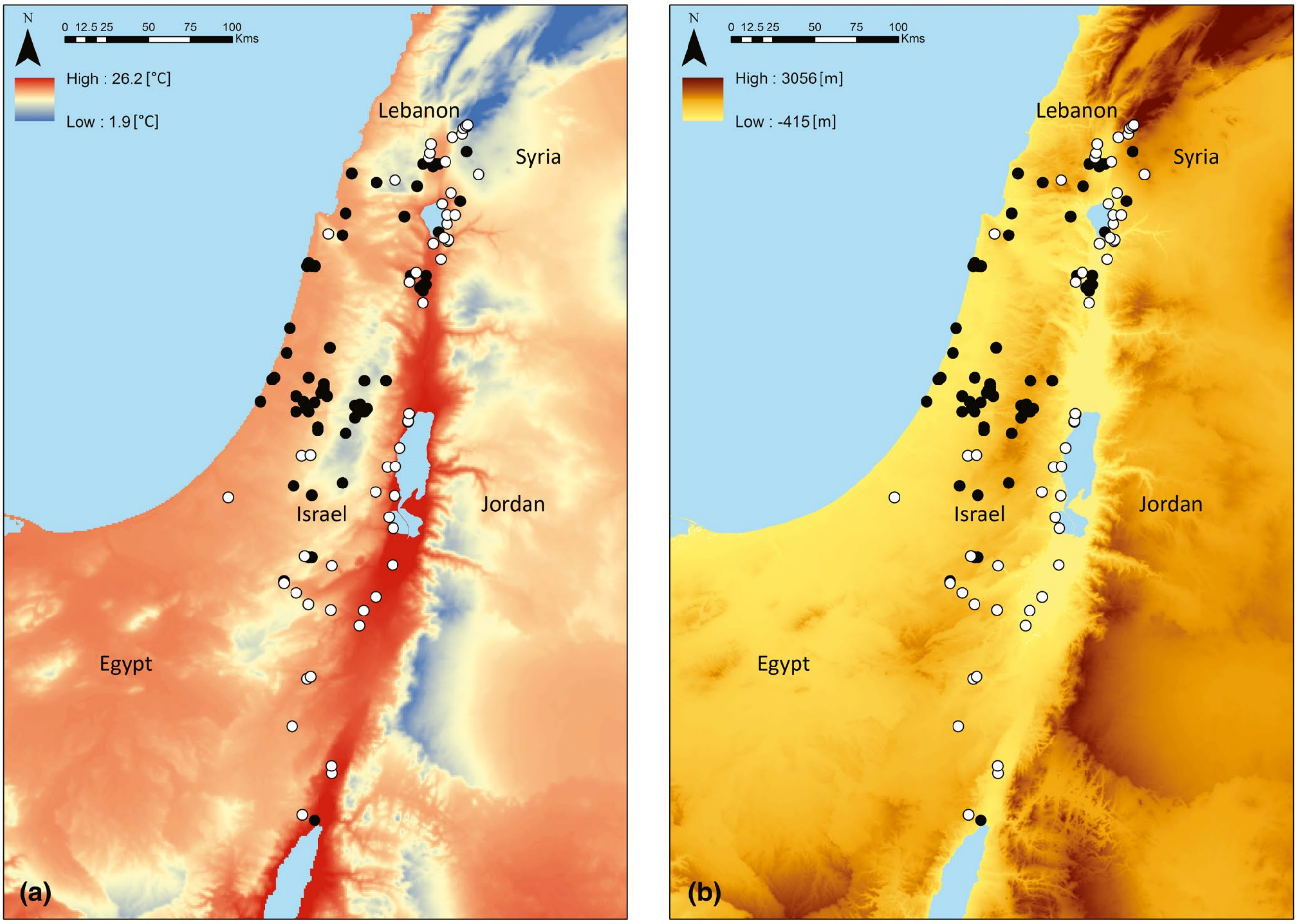

FIGURE 1 Sampling locations used in this study for bats (open circles) and birds (filled circles). (a) Mean ambient temperature (in degrees Celsius; Fick & Hijmans, 2017) and (b) elevation relative to sea level (in metres; METI/NASA, 2011) are represented by continuous colour scales. Data shown here for temperature represent the mean ambient temperature averaged for the years 1970–2000 (spatial resolution of 0.00833333°) to show the general variance in the study area, whereas the data extracted for the analyses were a monthly average per given year (spatial resolution of 1 km^2; CHELSA v.2.1, "tas" data set; Karger et al., 2017)

analysis were very similar to those of the full data set, we carried out the final bird analysis with the complete data set only.

The bat data set included data on 2,495 individuals from 18 species sampled across 53 locations in Israel (Figure 1) obtained from the Society for the Protection of Nature in Israel (SPNI) Centre for Mammals and the Steinhardt Museum of Natural History, collected between 1987 and 2018 by trained bat experts. Most of the bat species were captured at foraging sites. Three species (trident bat, *Asellia tridens*; Egyptian mouse-tailed bat, *Rhinopoma cystops*; and greater mouse-tailed bat, *Rhinopoma microphyllum*) were captured during night emergence from roosts, because they forage high in the air or avoid mist nets. To account for this difference, we verified the results of the bats analysis (all species) by analysing bats from foraging sites or night emergence separately. Given that the results of the separate analysis were very similar to those of the joint analysis, we carried out the final bat analysis with the complete data set only. Sex was determined by examining the external genitalia of the individual. In bats, we considered only data recorded during the weaning season and before wintering (June–October), because mating occurs before this period, and therefore spatial segregation can be maximal (parental care is carried out only by females). Data compiled for both data sets included species, coordinates, location, sex, mass and wing or forearm length.

2.2 | Environmental variables

We used three environmental predictor variables to explain variance in sex proportion: elevation, temperature and latitude. We extracted elevation for every pair of coordinates from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 3 (GDEM 003) (METI/NASA, 2011). Elevation was used to test exclusion by the dominant sex over competition for resources, because in bats, primarily, insect prey is more common at lower altitudes (Nardone et al., 2015), and a similar prediction can be made for the availability of resources for birds. We obtained mean daily air temperature (in degrees Celsius, with a spatial resolution of 1 km^2) recorded for the month and year of the time

TABLE 2 General linear mixed models relating the proportion of males to mean daily air temperature (in degrees Celsius), latitude, body size (the ratio between mean male forearm or wing length and mean female forearm or wing length) and elevation (in metres)

	Bats					Birds				
				Confidence interval					Confidence interval	
Parameter	Estimate	*SE*	*z*-value	2.5%	97.5%	Estimate	*SE*	*z*-value	2.5%	97.5%
Elevation						0.12	0.08	1.448	−0.041	0.274
Latitude						0.10	0.06	1.718	−0.014	0.213
Body size	0.21	0.14	1.487	−0.067	0.489	−0.08	0.04	1.993	**−0.152**	**−0.001**
Temperature	−0.53	0.22	2.478	**−0.946**	**−0.111**	−0.13	0.06	2.383	**−0.242**	**−0.024**

Note: Models were used with standardized temperature, latitude, body size (in bats and birds) and elevation (only in birds) as fixed factors and with species nested in family, year and location as random factors. Results shown here were obtained after model averaging of the best models [change in corrected Akaike information criterion (ΔAICc) < 2] after AICc-based model selection. Statistical significance is marked in bold (confidence interval ≠ 0).

of sampling at every location (CHELSA v.2.1, "tas" data set; Karger et al., 2017), recorded at 2 m hourly and averaged over a month. Latitude was converted from Israeli Transverse Mercator (ITM) or Israel Cassini Soldner (ICS) (original data sets) to the World Geodetic System (WGS). We used latitude as a proxy for distance travelled (in the absence of known origin of the individual), because intrasexual competition often leads to males occupying wintering territories closer to the breeding grounds (Myers, 1981).

2.3 | Statistical analysis

To test the correlation between temperature, elevation, body size or latitude and sex ratio, we aggregated the number of males and the number of females of each species at each location for every year as the response variable. The final data sets after aggregation by location, species and year included 337 sampling events in bats and 1,049 in birds. We estimated body size as the ratio between male and female forearm or wing length in bats and birds, respectively. We selected this measure over body mass because, in small vertebrates such as birds and bats, body mass can change significantly throughout the day, depending largely on food consumption, whereas forearm or wing length remains stable. In sites where no individuals of a particular sex were captured, we used the mean body size of the specific sex of a species to calculate the ratio. We standardized continuous predictor variables by subtracting the mean and dividing by the standard deviation using the "stdize" function in R package "pls" v.2.7-0 (Mevik & Wehrens, 2007), and fitted the models based on the Shapiro–Wilk test of normality (Shapiro & Wilk, 1965). We used Pearson's *r* test to evaluate the correlation between environmental variables in each data set. We used general linear mixed models (GLMMs) with the binomial distribution and the logit link function to model the proportion of males as a response, standardized mean temperature, elevation and latitude as fixed factors, with "species" nested in "family", year and location as random factors to account for variance stemming from phylogenetic correlation, time-series sampling and site identity, respectively. These models are considered appropriate for the analyses of proportion data (Bolker et al., 2009). We selected "species" as a random factor because we are describing a general phenomenon across multiple species, in which case the identity of the species should not affect the response directly. However, to address the possibility that each species responds in a different manner to the predictor variables chosen, we also modelled each species separately. Subsequently, we ran all the possible models (including the null model) and selected the best models (ΔAIC ≤ 2) by comparing corrected Akaike information criterion (AICc; Burnham & Anderson, 2002). We then used model averaging over the best models that were selected using the "MuMIn" R package v.1.43.15 (Barton, 2019). We described the statistical significance of the predictor variables by calculating 95% confidence intervals over 100 permutations (R Core Team, 2019). We computed the goodness-of-fit of each model as a coefficient of determination (marginal R^2 and conditional R^2; Nakagawa & Schielzeth, 2013) via the "r.squaredGLMM" function in the "MuMIn" R package v.1.43.15 (Barton, 2019). We also assessed multicollinearity by computing the variance inflation factor (VIF) to measure how much the variance of the predictors used in the model is inflated owing to multicollinearity using the "vif" function in the R package "car" (Fox & Weisberg, 2019). To assess model adequacy, we inspected the residuals versus fitted plot for nonlinearity, unequal error variances and outliers. In addition, we checked for deviations from multivariate normality and homoscedasticity by visual observation of a scatter plot (Q–Q plot). Additionally, in order to recover estimates of the relative size of each sex in each species, we calculated the mean and standard deviation of forearm length and wing length of bats and birds, respectively. We used the Wilcoxon rank sum test to determine whether these measurements were statistically different between males and females.

3 | RESULTS

Mean daily air temperature and body size were significant factors in explaining the models in birds, whereas only temperature was significant in bats (Table 2). Elevation and latitude were not significant in either model (confidence intervals overlapped zero; Table 2).

Given that the response variable (proportion of males) departed significantly from normality in both bats and birds (bats, $W = 0.791$, $p < .001$; birds $W = 0.863$, $p < .001$; Shapiro–Wilk normality test), we ran GLMMs with all four variables for both data sets. Most of the environmental variables were not highly correlated (Pearson's $|r| \leq .68$; Supporting Information Tables S1 and S2; bats, VIF < 1.32; birds, VIF<1.82; Supporting Information Table S3), except for elevation and temperature in the bat data set (Pearson's $|r| = .90$). Therefore, in bats, we compared models that included elevation with models that included temperature and selected the models that included temperature based on their better AICc scores (Supporting Information Table S4). In addition, we ran the models without temperature and without elevation and used model selection and model averaging on each. In the final averaged models that included temperature (but not elevation), temperature was a significant explanatory variable (estimate ± SE = −0.53 ± 0.21; CI: −0.946, −0.111), whereas no explanatory variable was significant in models that included elevation (but not temperature). Ultimately, we used model averaging only for the models that did not include elevation after model selection (ΔAICc ≤ 2), which included two models in bats (Supporting Information Table S4), and model selection over all of the best models (ΔAICc ≤ 2) in birds, resulting in six models (Supporting Information Table S5). The proportion of variance explained in each of the individual bat models (conditional $R^2 = .73–.75$, marginal $R^2 = .00–.02$) and bird models (conditional $R^2 = .29–.32$, marginal $R^2 = .00–.01$) was relatively low.

In both bats and birds, the proportion of males increased as a function of a decrease in mean daily air temperature (bats, estimate ± SE = −0.53 ± 0.21; birds, estimate ± SE = −0.13 ± 0.06; Figure 2a,b; Supporting Information Figure S1a,b), and in birds as a function of a decrease in body size (estimate ± SE = 0.08 ± 0.04; Figure 2c; Supporting Information Figure S1c). Conversely, latitude overlapped with zero in both models, as did body size in bats and elevation in birds, suggesting that they were not statistically significant (Table 2). When modelled separately, some models did not converge for certain species, most probably owing to small sample size or low geographical variance. The patterns detected for the individual species were diverse (Figure 3).

The larger sex in most species of bats was the female, although males were significantly larger in *A. tridens* and *R. microphyllum* (Supporting Information Table S6). In birds, males were larger than females in all the species for which statistical significance was achieved (Supporting Information Table S7).

4 | DISCUSSION

In this study, we explored whether ambient temperature preference can explain patterns of sexual segregation among east Mediterranean birds and bats. We found a correlation between geographical separation and ambient temperature that accounts for variance in the data that is not explained by the remaining cofactors (body size, elevation and latitude), suggesting an alternative explanation for sexual segregation that relies on thermal sensing terminology rather than on an energetic–metabolic (Angilletta et al., 2010) or dominance-based perspective alone. We propose that sexual segregation can also be driven by an inherent preference of ambient temperature that is different in males and females, which we suggest terming differential sex-related thermal preference (DSTP).

Our results indicate a negative correlation of temperature with the proportion of males in both bats and birds, irrespective of body size, suggesting that, as in humans, females prefer higher ambient temperatures. We therefore propose that sexual segregation in endothermic animals can also be driven by differential thermal preferences in males and females. Our results correspond to previously reported laboratory-controlled experiments, in which female rats (*Rattus norvegicus*) were more sensitive than males to a cold stimulus (Vierck et al., 2008), and female mice (*Mus musculus*) preferred higher ambient temperatures than males, regardless of gonadectomy and probably unrelated to the ovarian cycle (Kaikaew et al., 2017). Ross et al. (2018) showed that female mice display greater thermal responsiveness than males, which might be related to sex-dependent changes in gene expression within the affected dorsal root ganglia. Both Ross et al. (2018) and Kaikaew et al. (2017) suggested that this neurobiological mechanism develops before sexual maturity. Although no equivalent experimental data are available for bats or birds, the existing reported data in these species and others might provide the preliminary background to suggest that similar results would be expected in controlled experiments in these groups. Admittedly, such results would provide the next stepping stone for corroborating DSTP in endotherms. Nonetheless, given the scope of direct (laboratory studies) and indirect (sexual segregation) evidence of this phenomenon across multiple species, we suggest that thermal sensing and processing mechanisms might be sex specific in endothermic species.

In addition to temperature, our findings support only body size in birds as a significant explanatory variable of sexual segregation. This finding provides additional support to the body size hypothesis, according to which larger individuals are better suited to survive in colder areas (Ketterson & Nolan, 1976; Myers, 1981), although evidence for latitudinal support is missing. Moreover, although non-significant, a similar trend can be seen in bats, where females are larger in most of the species studied here, and therefore the trend is reversed (see Table 2). Conversely, elevation, introduced previously as a proxy for the quality of foraging sites in bats (McGuire & Boyle, 2013; Nardone et al., 2015; Russo, 2002), was not a significant explanatory variable in bats, even when temperature was excluded from the models. Given that most of the dominance hierarchy hypothesis refers to the dominant larger females excluding males from the better foraging sites, possibly owing to different energetic requirements, it is possible that including a more direct measurement of foraging quality would yield different results. However, elevation alone does not seem to explain the spatial pattern we found. Likewise, latitudinal segregation was not detected in our models, and therefore could not support the early arrival hypothesis, according to which the proportion of males increased with latitude

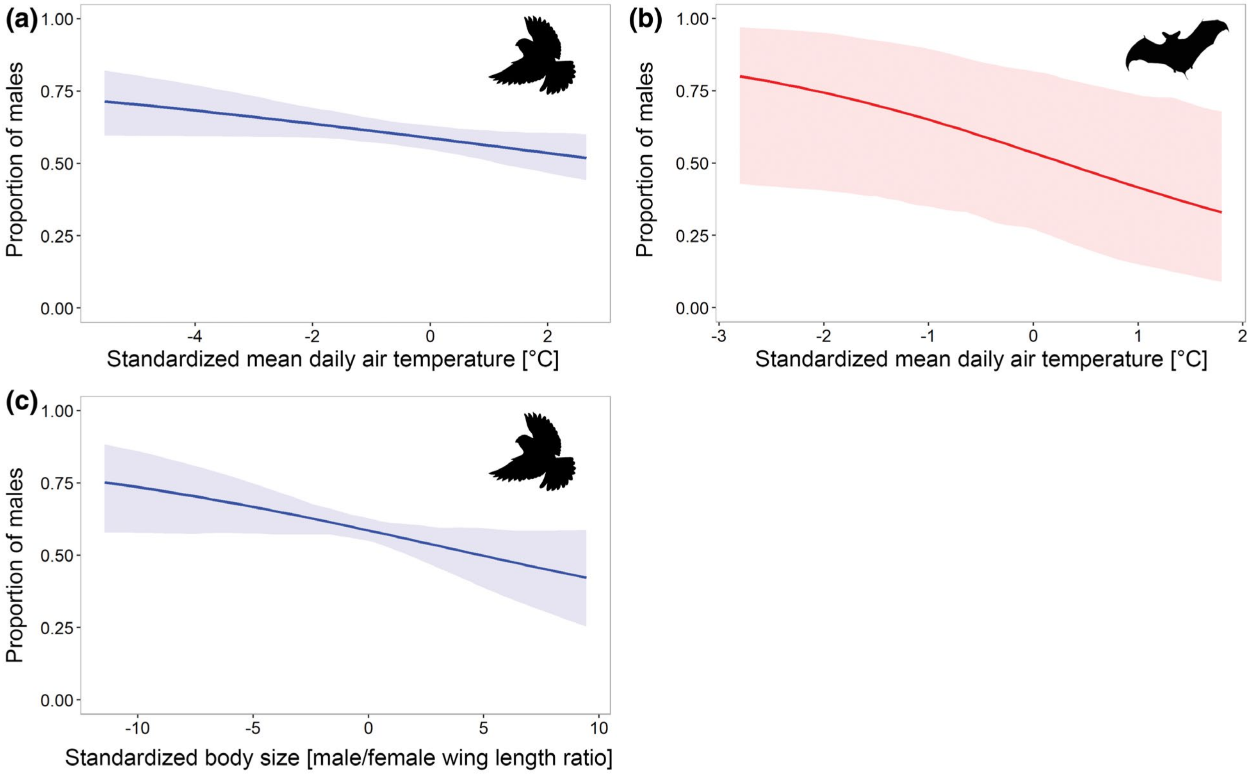

FIGURE 2 Proportion of males as a function of standardized mean daily air temperature (in degrees Celsius) in (a) birds and (b) bats and (c) as a function of body size in birds, as predicted by general linear mixed models that were run with the other fixed predictors as constant at their respective means and random factors of species nested in the family, location and year. Bat models were run without elevation as a fixed factor because of high Pearson's *r* correlation with temperature. Shaded areas are upper and lower 95% confidence intervals. Models were run with 250 bootstraps (with the function "bootMer" from the "lme4" R package; Bates et al., 2015) over an expanded grid. Body size in bats, latitude and elevation are not shown because they were not statistically significant according to the final averaged models (they overlapped with zero)

(Chapman et al., 2011). However, we could not measure increased intrasexual competition, as suggested by the early arrival hypothesis, in detail within the scope of the present study, and therefore cannot contend its relevance. These discrepancies suggest that another mechanism might be in place that does not depend on morphological dimorphism or sex-based dominance. We put forward the idea that DSTP can account for some of the remaining variance.

A clue to the mechanism of DSTP in animals can be found in evidence obtained in humans, where differential sex-related preference can be reported directly by subjective verbal reports and be assigned to measured sensory sensitivity. A significant body of evidence suggests that women have a different baseline sensitivity to ambient temperature, greater sensitivity to small changes in temperature, and display different temperature- and pain-related processing compared with men. For example, several studies have found that women are significantly more sensitive than men to changes in ambient temperature, in that they are able to detect and report smaller manipulations in temperature in the same environment (Chow et al., 2010; Hashiguchi et al., 2010) or when such changes are performed in a stepwise manner (Xiong et al., 2015). Likewise, Golja et al. (2003) and Waller et al. (2016) found that women are more sensitive to cold thresholds than men in an experimental setting. Taken together, these observations attest to different sensory processing of temperature in women relative to men, with a clear preference for slightly higher ambient temperatures in women. Similar to the body size hypothesis in animals, DSTP in humans has been hypothesized to stem from morphological or physiological differences between the two sexes, such as a larger ratio of surface area to body mass in males and greater subcutaneous fat composition and lower exercise capacity in females (Anderson et al., 1995). However, in humans too, body surface area has been shown to provide only a small contribution to the ability of models to predict the metabolic responses to low body temperature (Tikuisis et al., 1987, 2000). Therefore, it seems plausible that a new explanation, relying more on sensory attributes rather than metabolic/energetic considerations, might explain differences in ambient temperature preference and sensitivity to temperature changes better. Such explanations would be discussed in terms of factors influencing cutaneous temperature sensation, either indirectly (e.g., mechanisms related to variations in skin thermoregulatory vasoreflexes by female steroid hormones modifying cutaneous vascular control) or directly [e.g., difference in cutaneous sensory properties, such as decreased intraepidermal nerve fibres in females compared with males (Collongues et al., 2018), with additional greater age-dependent reductions compared with males

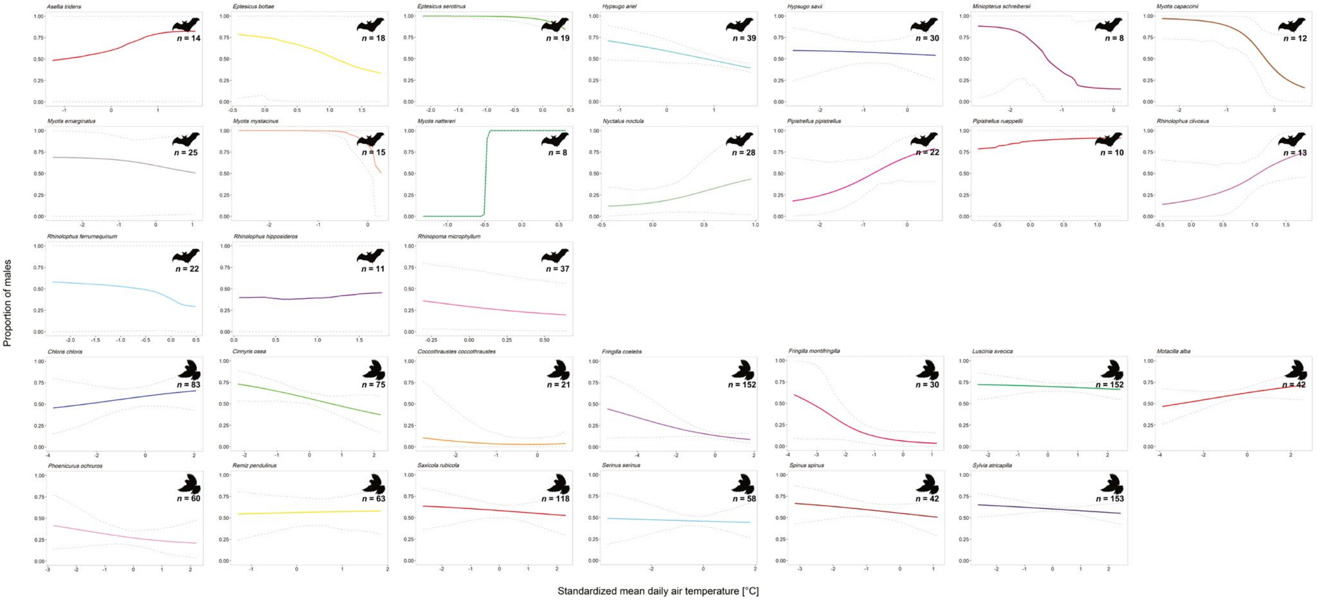

FIGURE 3 Proportion of males as a function of standardized mean daily air temperature (in degrees Celsius) in bats and birds, as predicted by general linear mixed models that were run with the other fixed predictors as constant at their respective means and a random factor of species nested in the family. Dashed lines are upper and lower 95% confidence intervals. Models were run with the function "glmer" from the "lme4" R package (Bates et al., 2015) over an expanded grid. Sample sizes (sites per species per year) are marked with 'n'

(Provitera et al., 2016)]. Another intriguing possible mechanism for altered sensation would be a difference not in sensory neuronal density per se, but rather sex-related differences in the expression of ion channels belonging to the transient receptor potential (TRP) family, known to be activated by non-noxious warmth or cold, and therefore plausible candidates for thermal detectors. It has recently been suggested, for example, that transient receptor potential cation channel subfamily M member 2 (TRPM2) composition and expression might underlie such sex-dependent differences in thermal sensation (Tan & McNaughton, 2016, 2018). Alternatively, endocrine functions, such as the menstrual cycle, elevated progesterone or oestrogen levels, might contribute to the sex differences in heat production and thermoregulation (Charkoudian, 2001; Kaciuba-Uscilko & Grucza, 2001; Kolka & Stephenson, 1989), although they describe short-term changes and might not explain patterns of more extended periods. Although none of these hypotheses explains the entirety of DSTP, these mechanisms possibly act in synergy or complement other underlying processes, such as those related to differential thermal sensing. However, further research is needed to determine the underlying mechanism of sex-related thermal sensing in animals (e.g., identifying patterns of differential neural gene expression; Ross et al., 2018).

Understanding the adaptive value of female preference for higher ambient temperatures can help in determining its evolutionary significance and context. This phenomenon might potentially shape numerous aspects of social behaviour, including, for example, reduction of intraspecific aggression, huddling, differential parental care, and niche partitioning. Additionally, it might have significant physiological implications for female-specific functions that require thermal sensing, such as incubation or infant thermoregulation, and therefore females prefer higher temperatures and not the opposite. We postulate that these behaviours might have been optimized by the selection of warmer habitats by females, which might have resulted in selection for DSTP on an evolutionary scale. Although our results provide support for the studied bat and bird species as a group, individually, some species might not present the same pattern (Figure 3). There might be several reasons for this, such as insufficient sample size, limited variation in one or more explanatory variables (e.g., if records were collected in a small area), or possibly by stronger mechanisms acting on habitat selection and sexual segregation. In addition, the R^2 values of the individual models (Supporting Information Tables S4 and S5) were low, suggesting that the detected relationship is weak and requires additional work to establish the importance of these factors in structuring these patterns in nature. Testing this hypothesis in other species and groups might provide a better understanding of the scope of this phenomenon and help to identify its evolutionary origins.

In the present study, we suggest an alternative driver for sexual segregation in endotherms that is generated through female preference of higher ambient temperatures. In lack of direct experimental evidence, we provide the most extensive evidence to date of the prevalence of sexual segregation in two main groups of highly mobile endothermic animals and show that it can be explained by differential sex-related thermal preference. Given that DSTP has been studied mainly in humans, it remains to be explored whether other endothermic groups or poikilothermic species exhibit DSTP. The data analysed in the present study are limited by species and scope, but provide certain support to the theoretical scaffolding that we wish to put forward, and we look forward to seeing this theory tested in future studies on larger, more diverse groups. In addition, we hope to see our theory examined in species where sexual segregation takes other forms, such as behavioural segregation or microscale adjustments to temperature shifts within a small habitat (e.g., selection of a specific location within a cave in which temperatures shift significantly). Here, we suggest that DSTP might be a broader evolutionary phenomenon and a significant force shaping dispersal, sociality and behaviour of animals and should be explored from this wide perspective.

ACKNOWLEDGMENTS

We wish to thank William Karasov, Arnon Lotem and Jonathan Belmaker for their helpful comments on this manuscript. We are grateful to the bird ringers and bat specialists who obtained the data used in this study and to the Society for the Protection of Nature in Israel for availing the data to us. We also thank Orr Spiegel, Ofir Levy, Adi Barocas and Hezi Buba for their help with analysis and programming and Sol Magory and Ronit Tzach for their fruitful discussion. T.M.C. was supported by the Tel Aviv University's rector's emergency Corona fellowship and the Council for Higher Education (CHE) postdoctoral fellowship.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

T.M.C. carried out the analyses and drafted the manuscript; Y.K. contributed to data collection and drafted the manuscript; H.S. drafted the manuscript; and E.L. developed the original concept, contributed to data collection and drafted the manuscript. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data pertaining to the samples used in this study are deposited in Dryad: https://doi.org/10.5061/dryad.bg79cnp92.

ORCID

Tali Magory Cohen https://orcid.org/0000-0001-7341-2901

REFERENCES

Alonso, J. C., Salgado, I., & Palacín, C. (2016). Thermal tolerance may cause sexual segregation in sexually dimorphic species living in hot environments. *Behavioral Ecology*, *27*, 717–724. https://doi.org/10.1093/beheco/arv211

Amichai, E., Levin, E., Kronfeld-Schor, N., Roll, U., & Yom-Tov, Y. (2013). Natural history, physiology and energetic strategies of *Asellia tridens* (Chiroptera). *Mammalian Biology*, *78*, 94–103. https://doi.org/10.1016/j.mambio.2012.06.006

Anderson, G. S., Ward, R., & Mekjavić, I. B. (1995). Gender differences in physiological reactions to thermal stress. *European Journal of Applied Physiology and Occupational Physiology*, *71*, 95–101. https://doi.org/10.1007/BF00854965

Angilletta, M. J. Jr., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience*, *2*, 861–881.

Aublet, J. F., Festa-Bianchet, M., Bergero, D., & Bassano, B. (2009). Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*, *159*, 237–247. https://doi.org/10.1007/s00442-008-1198-4

Barclay, R. M. R. (1991). Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *Journal of Animal Ecology*, *60*, 165–178. https://doi.org/10.2307/5452

Barton, K. (2019). *MuMIn: Multi-model inference*. R package version 1.43.15. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference – A practical information-theoretic approach*, 2nd edition. Springer.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*, 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Charkoudian, N. (2001). Influences of female reproductive hormones on sympathetic control of the circulation in humans. *Clinical Autonomic Research*, *11*, 295–301. https://doi.org/10.1007/BF02332974

Chow, T. T., Fong, K. F., Givoni, B., Lin, Z., & Chan, A. L. S. (2010). Thermal sensation of Hong Kong people with increased air speed, temperature and humidity in air-conditioned environment. *Building and Environment*, *45*, 2177–2183. https://doi.org/10.1016/j.buildenv.2010.03.016

Collongues, N., Samama, B., Schmidt-Mutter, C., Chamard-Witkowski, L., Debouverie, M., Chanson, J.-B., Antal, M.-C., Benardais, K., de Seze, J., Velten, M., & Boehm, N. (2018). Quantitative and qualitative normative dataset for intraepidermal nerve fibers using skin biopsy. *PLoS One*, *13*, e0191614. https://doi.org/10.1371/journal.pone.0191614

Conradt, L. (2005). Definitions, hypotheses, models and measures in the study of animal segregation. In K. E. Ruckstuhl, & P. Neuhaus (Eds.), *Sexual segregation in vertebrates: Ecology of the two sexes* (pp. 11–32). Cambridge University Press.

Conradt, L., Clutton-Brock, T. H., & Guinness, F. E. (2000). Sex differences in weather sensitivity can cause habitat segregation: Red deer as an example. *Animal Behaviour*, *59*, 1049–1060. https://doi.org/10.1006/anbe.2000.1409

Cristol, D. A., Baker, M. B., & Carbone, C. (1999). Differential migration revisited: Latitudinal segregation by age and sex class. *Current Ornithology*, *15*, 33–88.

Cryan, P. M., Bogan, M. A., & Altenbach, J. S. (2000). Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy*, *81*, 719–725.

Cryan, P. M., & Wolf, B. O. (2003). Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *The Journal of Experimental Biology*, *206*, 3381–3390.

Erickson, J. L., & Adams, M. J. (2003). A comparison of bat activity at low and high elevations in the Black Hills of western Washington. *Northwest Science*, *77*, 126–130.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression*, 3rd edition. Sage.

Garnick, S., Di Stefano, J., Elgar, M. A., & Coulson, G. (2014). Inter- and intraspecific effects of body size on habitat use among sexually-dimorphic macropodids. *Oikos*, *123*, 984–992. https://doi.org/10.1111/oik.00861

Gauthreaux, S. A. (1978). The ecological significance of behavioral dominance. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Social behavior. Perspectives in ethology* (Vol. *3*, pp. 17–54). Springer.

Golja, P., Tipton, M. J., & Mekjavic, I. B. (2003). Cutaneous thermal thresholds—The reproducibility of their measurements and the effect of gender. *Journal of Thermal Biology*, *28*, 341–346. https://doi.org/10.1016/S0306-4565(03)00010-X

Gow, E. A., & Wiebe, K. L. (2014). Males migrate farther than females in a differential migrant: An examination of the fasting endurance hypothesis. *Royal Society Open Science*, *1*, 140346. https://doi.org/10.1098/rsos.140346.

Grindal, S. D., Morissette, J. L., & Brigham, R. M. (1999). Concentration of bat activity in riparian habitats over an elevational gradient. *Canadian Journal of Zoology*, *77*, 972–977. https://doi.org/10.1139/z99-062

Hashiguchi, N., Feng, Y., & Tochihara, Y. (2010). Gender differences in thermal comfort and mental performance at different vertical air temperatures. *European Journal of Applied Physiology*, *109*, 41–48. https://doi.org/10.1007/s00421-009-1158-7

Jackes, A. D. (1973). *The use of wintering grounds by red deer in Ross-shire* (Doctoral dissertation). University of Edinburgh, Scotland.

Kaciuba-Uscilko, H., & Grucza, R. (2001). Gender differences in thermoregulation. *Current Opinion in Clinical Nutrition and Metabolic Care*, *4*, 533–536. https://doi.org/10.1097/00075197-200111000-00012

Kaikaew, K., Steenbergen, J., Themmen, A. P. N., Visser, J. A., & Grefhorst, A. (2017). Sex difference in thermal preference of adult mice does not depend on presence of the gonads. *Biology of Sex Differences*, *8*, 1–10. https://doi.org/10.1186/s13293-017-0145-7

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122. https://doi.org/10.1038/sdata.2017.122

Karjalainen, S. (2012). Thermal comfort and gender: A literature review. *Indoor Air*, *22*, 96–109. https://doi.org/10.1111/j.1600-0668.2011.00747.x

Ketterson, E. D., & Nolan, V. J. (1976). Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology*, *57*, 679–693. https://doi.org/10.2307/1936182

Kolka, M. A., & Stephenson, L. A. (1989). Control of sweating during the human menstrual cycle. *European Journal of Applied Physiology and Occupational Physiology*, *58*, 890–895. https://doi.org/10.1007/BF02332224

Lahann, P. (2008). Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *International Journal of Primatology*, *29*, 117–134. https://doi.org/10.1007/s10764-007-9138-4

Lan, L., Lian, Z., Liu, W., & Liu, Y. (2008). Investigation of gender difference in thermal comfort for Chinese people. *European Journal of Applied Physiology*, *102*, 471–480. https://doi.org/10.1007/s00421-007-0609-2

Levin, E., Ar, A., Yom-Tov, Y., & Kronfeld-Schor, N. (2012). Summer torpor and sexual segregation in the subtropical bat *Rhinopoma microphyllum*. In T. Ruf, C. Bieber, W. Arnold, & E. Millesi (Eds.), *Living in a seasonal world* (pp. 167–174). Springer.

Levin, E., Roll, U., Dolev, A., Yom-Tov, Y., & Kronfeld-Shcor, N. (2013). Bats of a gender flock together: Sexual segregation in a subtropical bat. *PLoS One*, *8*, e54987. https://doi.org/10.1371/journal.pone.0054987

MacFarlane, A. M., & Coulson, G. R. (2005). *Sexual segregation in Australian marsupials*. Cambridge University Press.

Main, M. B. (2008). Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology*, *89*, 693–704. https://doi.org/10.1890/07-0645.1

Main, M. B., Weckerly, F. W., & Bleich, V. C. (1996). Sexual segregation in ungulates: New directions for research. *Journal of Mammalogy*, *77*, 449–461. https://doi.org/10.2307/1382821

McGuire, L. P., & Boyle, W. A. (2013). Altitudinal migration in bats: Evidence, patterns, and drivers. *Biological Reviews*, *88*, 767–786. https://doi.org/10.1111/brv.12024

METI/NASA (2011). *ASTER global digital elevation. model V002*. NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center.

Mevik, B.-H., & Wehrens, R. (2007). The pls package: Principal component and partial least squares regression in R. *Journal of Statistical Software*, *18*, 1–23.

Myers, J. P. (1981). A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology*, *59*, 1527–1534. https://doi.org/10.1139/z81-207

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

Nardone, V., Cistrone, L., Di Salvo, I., Ariano, A., Migliozzi, A., Allegrini, C., Ancillotto, L., Fulco, A., & Russo, D. (2015). How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat *Myotis daubentonii*. *PLoS One*, *10*, e0134573. https://doi.org/10.1371/journal.pone.0134573

Provitera, V., Gibbons, C. H., Wendelschafer-Crabb, G., Donadio, V., Vitale, D. F., Stancanelli, A., Caporaso, G., Liguori, R., Wang, N., Santoro, L., Kennedy, W. R., & Nolano, M. (2016). A multi-center, multinational age- and gender-adjusted normative dataset for immunofluorescent intraepidermal nerve fiber density at the distal leg. *European Journal of Neurology*, *23*, 333–338. https://doi.org/10.1111/ene.12842

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Ross, J. L., Queme, L. F., Lamb, J. E., Green, K. J., & Jankowski, M. P. (2018). Sex differences in primary muscle afferent sensitization following ischemia and reperfusion injury. *Biology of Sex Differences*, *9*, 18–26. https://doi.org/10.1186/s13293-017-0163-5

Ruckstuhl, K. E. (2007). Sexual segregation in vertebrates: Proximate and ultimate causes. *Integrative and Comparative Biology*, *47*, 245–257. https://doi.org/10.1093/icb/icm030

Ruckstuhl, K. E., & Neuhaus, P. (2005). *Sexual segregation in vertebrates: Ecology of the two sexes*. Cambridge University Press.

Russo, D. (2002). Elevation affects the distribution of the two sexes in Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae) from Italy. *Mammalia*, *66*, 543–551. https://doi.org/10.1515/mamm.2002.66.4.543

Schaudienst, F., & Vogdt, F. U. (2017). Fanger's model of thermal comfort: A model suitable just for men? *Energy Procedia*, *132*, 129–134. https://doi.org/10.1016/j.egypro.2017.09.658

Senior, P., Butlin, R. K., & Altringham, J. D. (2005). Sex and segregation in temperate bats. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2467–2473. https://doi.org/10.1098/rspb.2005.3237

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591–611. https://doi.org/10.1093/biomet/52.3-4.591

Tan, C.-H., & McNaughton, P. A. (2016). The TRPM2 ion channel is required for sensitivity to warmth. *Nature*, *536*, 460–463. https://doi.org/10.1038/nature19074

Tan, C.-H., & McNaughton, P. A. (2018). TRPM2 and warmth sensation. *Pflugers Archiv - European Journal of Physiology*, *470*, 787–798. https://doi.org/10.1007/s00424-018-2139-7

Terrien, J., Perret, M., & Aujard, F. (2010). Gender markedly modulates behavioral thermoregulation in a non-human primate species, the mouse lemur (*Microcebus murinus*). *Physiology and Behavior*, *101*, 469–473. https://doi.org/10.1016/j.physbeh.2010.07.012

Tikuisis, P., Gonzalez, R. R., & Pandolf, K. B. (1987). *Human thermoregulatory model for whole body immersion in water at 20 and 28 degrees Celsius*. Report no. T23-87. Natick, Massachusetts: US Army Research Institute of Environmental Medicine.

Tikuisis, P., Jacobs, I., Moroz, D., Vallerand, A. L., & Martineau, L. (2000). Comparison of thermoregulatory responses between men and women immersed in cold water. *Journal of Applied Physiology*, *89*, 1403–1411. https://doi.org/10.1152/jappl.2000.89.4.1403

Vierck, C. J., Acosta-Rua, A. J., Rossi, H. L., & Neubert, J. K. (2008). Sex differences in thermal pain sensitivity and sympathetic reactivity for two strains of rat. *Journal of Pain*, *9*, 739–749. https://doi.org/10.1016/j.jpain.2008.03.008

Waller, R., Smith, A. J., O'Sullivan, P. B., Slater, H., Sterling, M., McVeigh, J. A., & Straker, L. M. (2016). Pressure and cold pain threshold reference values in a large, young adult, pain-free population. *Scandinavian Journal of Pain*, *13*, 114–122. https://doi.org/10.1016/j.sjpain.2016.08.003

Wang, Z., de Dear, R., Luo, M., Lin, B., He, Y., Ghahramani, A., & Zhu, Y. (2018). Individual difference in thermal comfort: A literature review. *Building and Environment*, *138*, 181–193. https://doi.org/10.1016/j.buildenv.2018.04.040

Xiong, J., Lian, Z., Zhou, X., You, J., & Lin, Y. (2015). Investigation of gender difference in human response to temperature step changes. *Physiology and Behavior*, *151*, 426–440. https://doi.org/10.1016/j.physbeh.2015.07.037

BIOSKETCH

The Nutritional Ecology lab, led by **Eran Levin** brings together physiology, ecology and nutrition to address questions regarding how form and function enable the adaptation of an organism to changing environments at both ecological and evolutionary time-scales. His team integrates experimental work in the field with hypothesis-driven experimental testing in a laboratory setting, on multiple scales of inquiry, from the broad scale of the natural ecological setting to the fine scale of molecular and biochemical mechanisms, focusing on animal models that display extreme adaptations.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Magory Cohen, T., Kiat Y., Sharon H., & Levin E. (2021). An alternative hypothesis for the evolution of sexual segregation in endotherms. *Global Ecology and Biogeography*, 00, 1–11. https://doi.org/10.1111/geb.13393