

Short-term thermal anomalies are associated with increased use of localized water resources by a montane bat community

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Research Article

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Abstract

Short-term thermal anomalies are becoming increasingly frequent under climate change, yet their influence on how animal communities use spatially restricted resources remains poorly understood. I evaluated whether variation in thermal anomalies was associated with changes in the use of localized water resources by a montane bat community using pond-based monitoring data collected from ten species in La Malinche National Park, central Mexico. Because ambient temperature (T_a) was strongly seasonally structured, analyses focused on within-month thermal anomalies, defined as deviations in minimum T_a from the long-term nightly monthly mean. Pond-based capture activity was analyzed using negative binomial generalized linear mixed-effects models together with phylogenetically informed frequentist and Bayesian models. Bat capture increased significantly during anomalously warm conditions, with the negative binomial model estimating an approximately 39% increase in expected activity for each one standard deviation increase in thermal anomaly. Frequentist and Bayesian phylogenetic analyses yielded qualitatively similar positive associations while revealing substantial interspecific variation in thermal responses. Although the observational design precludes causal inference, these results suggest that short-term climatic anomalies are associated with shifts in the use of localized water sources by free-ranging animal communities. Such changes may increase the ecological importance of spatially restricted resources during unusually warm periods and should be considered when predicting ecological responses to increasing climatic variability.

Introduction

Environmental variability is a major driver of ecological processes because it modifies both the availability of resources and the energetic demands experienced by organisms. Among environmental drivers, water availability plays a central role by influencing ecosystem productivity, species distributions, and animal activity across terrestrial ecosystems (Mishra 2023). Water cycling also contributes to local weather and regional climate through evaporation, condensation and precipitation (Trenberth et al. 2007; Oki and Kanae 2006). Consequently, temporal variation in water variability shapes numerous biological processes, including plant phenology, breeding, migration, and animal activity (Parmesan and Yohe 2003; Cohen et al. 2018). In animals, water consumption becomes essential for maintaining water balance and sustaining physiological functions (Schmidt-Nielsen 1997; Bradshaw 2003). Therefore, variation in both water availability and ambient temperature (T_a) can strongly influence animal physiology, behavior, and ecological activity patterns.

Ambient temperature strongly influences biological processes by regulating rates of energy expenditure and water turnover (Nagy 1987; Speakman 1999). Low T_a generally increases metabolic rate in mammals (Scholander et al. 1950; Heldmaier et al. 2004), whereas higher T_a increases evaporative water loss (Tieleman and Williams 2000; Gerson et al. 2014). These thermal conditions strongly affect behavioral and physiological responses in animals. Under cold conditions, individuals must increase energy intake to maintain thermoregulation. However, low T_a is frequently associated with reduced food

availability (Turner 2002; Humphries et al. 2004). Under these energy-restricted conditions, many species migrate and/or employ energy-saving strategies such as torpor or hibernation (Geiser 2004; Ruf and Geiser 2015; Ayala-Berdon and Medina Bello 2024). Conversely, warmer conditions often increase food availability and foraging opportunities in many ecosystems. However, warmer environments also increase water turnover, forcing animals to consume water more frequently (Savage et al. 2008). In some environments, animals may additionally use torpor as a water-saving strategy (Nowack et al. 2017). Consequently, environmental variation modifies both the energetic demands experienced by organisms and the availability of essential resources, forcing animals to balance energy acquisition with water requirements through behavioral and physiological adjustments. Because energetic and water demands are strongly temperature dependent, thermal anomalies –defined as short-term deviations in T_a relative to the average thermal conditions expected for a given season or month– may substantially alter animal activity and resource use beyond typical seasonal patterns.

Most ecological studies examine predictable seasonal climatic variation. However, organisms are also exposed to short-term thermal anomalies that generate conditions substantially warmer or colder than expected for a given season (Ummenhofer et al. 2017). These variations may alter animal activity and resource use over short time scales, potentially influencing ecological processes such as energetic demands, species interactions, and ecosystem energy flow (Kearney and Porter 2009). Consequently, the study of thermal anomalies is important for understanding how short-term climatic variation influences animal ecology (Jentsch et al. 2007). Understanding ecological responses to short-term thermal anomalies is becoming increasingly important because climate change is expected to increase both the frequency and intensity of climatic extremes rather than simply increasing average temperatures (Walther et al. 2002; Humphries et al. 2004). These processes may be especially important in montane ecosystems, which remain comparatively understudied and often impose high metabolic and water demands on organisms because of their marked seasonal and short-term climatic variation (McCain and Colwell 2011; Şekercioğlu et al. 2012).

Water sources represent predictable resource patches for many terrestrial animals, particular volant insectivores such as bats whose energetic and water demands are exceptionally high because powered flight and echolocation (Speakman and Thomas 2003; Acosta-Luzuriaga et al. 2026). Consequently, bats provide an excellent model system for examining how short-term climatic variability influences the use of spatially restricted resources. In these animals, both T_a and water availability strongly influence drinking and foraging activity (Lisón and Calvo 2011; Stahlschmidt et al. 2012; Sirami et al. 2013; Salvarina 2016). Notably, many insectivorous bat species inhabit montane ecosystems worldwide (Ayala-Berdon et al. 2017; Arias-Aguilar et al. 2020; Bogoni et al. 2021), where seasonal variation and spatially restricted water availability may intensify energetic and water constraints.

Using a montane bat community as a model system, I evaluated whether short-term thermal anomalies were associated with changes in the use of localized water resources. Specifically, I quantified pond-based capture activity at artificial water sources La Malinche National Park, central Mexico, and tested whether anomalously warm or cold conditions relative to expected monthly temperatures were

associated with changes in community. Because warmer conditions are expected to increase both evaporative water loss and insect activity, I predicted greater use of localized water sources during positive thermal anomalies.

Methods

Study system and data collection

The study was conducted in La Malinche National Park (LMNP) (Fig. 1), a temperate montane ecosystem in central Mexico where artificial ponds provide localized water sources for wildlife during the dry season. Bat capture data were compiled from standardized surveys previously reported by Ayala-Berdon et al. (2017), Acosta-Luzuriaga (2025), and Acosta-Luzuriaga and Ayala-Berdon (2026), corresponding to two annual monitoring periods (2014–2015 and 2023–2024). Data were compiled from two standardized annual monitoring periods. Bats were captured monthly during the new moon period over three consecutive nights using mist nets placed around artificial ponds used by bats for drinking and foraging activity. For each capture, minimum T_a were obtained from the nearest meteorological station maintained by the National Water Commission (CONAGUA) (<https://smn.conagua.gob.mx/es/climatologia/temperaturas-y-lluvias/resumenes-mensuales-de-temperaturas-y-lluvias>). These measurements were used to characterize regional climatic conditions rather than the microclimatic conditions immediately surrounding individual ponds. Consequently, thermal anomalies represent regional climatic conditions rather than the microclimate of individual ponds. Sampling effort consisted of standardized combinations of 3 x 2 m and 6 x 2 m mist nets operated from dusk to 01:00. Individuals were temporarily marked to avoid duplicate records within sampling nights.

Statistical analyses

All analyses were conducted in R version 4.5.2 (2025-10-31) with the RStudio interface version 2026.01.1 + 403 (R Core Team, 2025). Because the number of sampled ponds differed slightly among surveys (three ponds during 2014–2015 and four ponds during 2023–2024), all models included the logarithm of the number of sampled ponds as an offset to account for differences in sampling effort. To assess the relationship between thermal conditions and pond-based capture activity, monthly capture counts were analyzed using a generalized linear mixed-effects model. Capture counts were treated as indices of community use of localized water resources rather than direct estimates of abundance.

Thermal anomalies

Preliminary exploration revealed that raw minimum ambient temperature (T_a) was strongly seasonally structured and that monthly sampling coverage differed slightly between periods (see above). To minimize confounding between seasonality and temperature, analyses focused on within-month thermal

anomalies rather than raw temperatures. Thermal anomalies were calculated as deviations between the observed monthly minimum T_a and the long-term mean minimum temperature for the corresponding calendar month across all surveys. Consequently, positive anomalies represented months that were warmer than the expected for that time of year, whereas negative anomalies represent colder-than-average months. Because the objective of thermal anomaly analysis was to evaluate changes in pond-based activity during periods when species were locally active, species-month combinations with no captures were excluded from anomaly analyses, resulting in 187 observations used in subsequent analyses (see Results). Because these absences were continuous for relatively long periods of time, they likely reflected seasonal inactivity rather than short-term responses to thermal anomalies and therefore represented structural rather than sampling zeros. This approach reduced the influence of structural zeros associated with seasonal absence and allowed evaluation of thermal responses during periods in which species were locally active. Thermal anomalies were subsequently standardized (z-scored) prior to modeling. Standardization facilitated model convergence and allowed effect sizes to be interpreted per one standard deviation change in thermal anomaly. The effectiveness of the anomaly transformation in removing seasonal structure was evaluated using an analysis of variance between standardized thermal anomalies and month.

I first fitted a generalized linear mixed model with a negative binomial error distribution using the “glmmTMB” package to evaluate the effect of thermal anomalies on pond-based capture activity while accounting for overdispersion in count data (McGillucuddy et al. 2025). In this model, standardized thermal anomaly was included as a fixed effect, species identity as a random intercept, and the logarithm of sampling effort as an offset term. Species identity was included to account for interspecific variation in baseline pond-based capture activity. This model estimated the average community-wide response to anomalous thermal conditions.

Phylogenetic analysis

To account for phylogenetic non-independence among species, a phylogenetically informed generalized linear mixed-effects model was implemented using the “pglmm” function in the “phyr” package (Ives et al. 2020). This model used a Poisson error distribution and incorporated phylogenetic covariance among species based on the phylogeny published by Amador et al. (2018). Thermal anomaly was included as a fixed effect and sampling effort as an offset term. Because pglmm currently does not implement a negative binomial distribution, this analysis was used to evaluate whether accounting for phylogenetic relatedness altered the estimated association between thermal anomalies and pond-based capture activity as sensitivity analysis rather than the primary inferential model.

To account for phylogenetic relatedness while estimating interspecific variation in thermal responses, I additionally fitted a Bayesian phylogenetic generalized linear mixed-effects model using the “brms” package. This model used a negative binomial error distribution and included species-specific random intercepts and random slopes for thermal anomaly structured by phylogenetic covariance matrices. This

model was used to estimate the community-wide association between thermal anomalies and pond-based capture activity while quantifying interspecific variation in thermal responses after accounting for phylogenetic relatedness. Four Markov chain Monte Carlo chains were run for 4000 iterations each, with 2000 warm-up iterations. Convergence was assessed using trace plots, Rhat statistics, and effective sample sizes.

Model diagnosis

Model fit and distributional assumptions were evaluated using simulated residual diagnostics implemented in the “DHARMA” package (Hartig 2024). Dispersion and zero-inflation tests were used to assess the adequacy of count distributions for both frequentist and phylogenetic models.

Results

The dataset compiled 231 capture records from 10 bat species collected during 2014–2015 ($n = 110$) and 2023–2024 ($n = 121$) survey periods. After excluding species-month combinations with no captures, thermal anomaly analyses were based on 187 observations (110 from 2014–2015 and 77 from 2023–2024; see Supplementary Material). Standardized thermal anomalies showed no residual association with month (ANOVA: $F_{6, 180} = 0.00$, $p = 1$), indicating that the anomaly transformation effectively removed seasonal structure from the temperature predictor. The negative binomial generalized linear mixed model revealed a significantly positive association between thermal anomalies and pond-based capture activity ($\beta = 0.33 \pm 0.14$, $Z = 2.35$, $p = 0.018$), corresponding to an approximately 39% increase in expected capture activity for each one standard deviation increase in thermal anomaly (Fig. 2). Species identity accounted for substantial variation in baseline pond-based capture activity (random intercept SD = 1.69). DHARMA diagnostics indicated no evidence of overdispersion (dispersion test: $p = 0.77$) or zero inflation (zero-inflation test: $p = 0.66$). The phylogenetically informed Poisson model yielded qualitatively similar results, showing a positive association between thermal anomalies and capture activity after accounting for phylogenetic relatedness among species ($\beta = 0.44 \pm 0.13$, $Z = 3.39$, $p < 0.001$), corresponding to an approximately 55% increase in expected capture activity per one standard deviation increase in thermal anomaly. Although this model showed no evidence of overdispersion ($p = 0.48$), residual diagnostics indicated mild zero inflation ($p = 0.024$), likely reflecting the low capture frequencies of several rare species.

The Bayesian phylogenetic negative binomial model produced posterior estimates consistent with a positive association between thermal anomalies and the use of water sources (posterior mean $\beta = 0.33 \pm 0.25$ SD, 95% credible interval = -0.19 to 0.85). In addition, the model estimated substantial interspecific variation in both baseline pond-based capture activity (random intercept SD = 2.46) and the magnitude of thermal responses (random slope SD = 0.33). All model parameters showed satisfactory convergence (Rhat = 1.00). Species-specific posterior estimates revealed marked interspecific variation in responses to thermal anomalies. The probability of a positive response was highest for *Eptesicus fuscus* and *Myotis*

californicus, whereas responses were more uncertain for less frequently captured species (Table 1). Together, the frequentist and Bayesian analyses consistently supported a positive association between thermal anomalies and pond-based capture activity despite interspecific variation in the magnitude of the response.

Table 1
Posterior probabilities of positive thermal responses ($P(\beta > 0)$) and 95% credible intervals (CI) for species-specific thermal anomaly coefficients estimated from the Bayesian phylogenetic negative binomial model.

Species	$P(\beta > 0)$	Lower 95% CI	Upper 95% CI
<i>Eptesicus fuscus</i>	0.988	0.806	5.02
<i>Myotis californicus</i>	0.982	0.0323	4.70
<i>Myotis volans</i>	0.850	-0.476	4.30
<i>Corynorhinus mexicanus</i>	0.803	-1.330	2.63
<i>Myotis velifer</i>	0.736	-1.500	2.61
<i>Myotis thysanodes</i>	0.668	-2.280	1.84
<i>Idionycteris phyllotis</i>	0.606	-2.640	1.59
<i>Myotis lucifugus</i>	0.596	-2.870	1.50
<i>Lasiurus cinereus</i>	0.542	-3.580	1.42
<i>Myotis auriculus</i>	0.532	-3.610	1.24

Discussion

The results indicate that short-term climatic variability may influence how free-ranging animal communities use spatially restricted resources. By isolating thermal anomalies from predictable seasonal variation, the analyses revealed that anomalously warm conditions were consistently associated with greater pond-based activity in a montane bat community. Because capture activity reflects the use of localized water sources rather than abundance, these findings suggest that climatic anomalies may modify patterns of resource use independently of normal seasonal cycles, likely through physiological and ecological mechanisms associated with increased energetic and water demands. More broadly, these findings suggest that localized water sources may function as ecological focal points whose importance changes with short-term climatic variation.

Both frequentist models and Bayesian analysis yielded qualitatively similar positive associations between thermal anomalies and pond-based capture activity. The positive association is consistent with ecological expectations that warmer-than-average conditions increase both physiological water demands and the availability of prey resources. For example, high temperatures can increase evaporative water loss (Herreid and Schmidt-Nielsen 1966; Kurta 2014; Muñoz-Garcia et al. 2022), potentially

intensifying the frequency with which bats visit ponds for drinking (Ayala-Berdon et al. 2017). This effect may be especially important in bats, which exhibit high respiratory rates and substantial water loss during flight (Thomas and Suthers 1972). Water loss may be further aggravated during warm nights in seasonally dry montane ecosystems (Lundquist and Loheide 2011). Warmer conditions may also enhance insect activity near water bodies, thereby increasing community use of localized water sources (Turner 2002; Lisón and Calvo 2014; Meyer et al. 2016).

Although the bat community from la Malinche exhibited an overall positive response in pond-based capture with warmer anomalies, species differed in the magnitude of their associations. Such heterogeneity is expected because ecological communities comprise species that differ in morphology, physiology, and life-history traits. Consequently, short-term climatic variability may reorganize community use of localized resources rather than producing uniform responses across species. For instance, body size may influence evaporative water loss, with larger animals generally exhibiting higher total rates of water loss than smaller ones, as has been observed in birds (Williams 1996). In warm, water-restricted environments, some bat species can reduce water loss through huddling behavior, seasonal or long-term reductions in basal metabolic rate, torpor use, or combinations of these strategies (Thomas and Cloutier 1992; Boratyński et al. 2015; Muñoz-Garcia et al. 2016). Within the bat community visiting the ponds, variation in these physiological and behavioral traits may contribute to interspecific differences in activity near water sources. Species-specific physiological strategies for balancing energetic and water demands may therefore partly explain why thermal responses varied among members of the bat community.

Some limitations should be considered when interpreting the results. First, capture activity near ponds was used as an index of localized bat activity rather than direct estimates of abundance or occupancy. Consequently, the observed responses likely reflect changes in the use of water sources under anomalous thermal conditions rather than population-level changes. Second, ambient temperature was obtained from the nearest meteorological station rather than measured directly at individual ponds. Consequently, thermal anomalies represent regional climatic conditions and may not fully capture the microclimatic conditions experienced by bats while foraging and drinking. In addition, unmeasured changes in pond characteristics, such as vegetation cover, water depth, or prey availability, may also have contributed to temporal variation in pond-based capture activity. Third, the anomaly analyses focused on periods in which species were locally active, reducing the influence of structural zeros associated with seasonal absence. Finally, although the proposed mechanisms are consistent with previous studies on bat energetics and water balance, direct physiological measurements were not obtained in this study. Future studies integrating microclimatic measurements, prey availability, and physiological responses would help identify the mechanisms linking thermal anomalies to changes in community use of localized water sources.

Spatially restricted resources often function as ecological hotspots where interactions among species become concentrated. Water sources provide a particularly useful example because they are essential resources whose ecological importance can vary with short-term climatic conditions. Consequently,

thermal anomalies may alter not only the activity of individual species but also patterns of resource use and the frequency of interspecific encounters around these resources. Understanding how climatic variability modifies the use of limiting resources may therefore improve predictions of community responses to environmental change. Artificial and natural water bodies may represent increasingly important microhabitats for bats under warming conditions. Warmer conditions may therefore spatially concentrate bat activity around localized water sources, increasing their ecological importance within montane landscapes. In mountain ecosystems, water availability may be spatially restricted, and seasonal conditions can fluctuate markedly (Viviroli et al. 2011). Notably, in LMNP runoff water has historically been diverted for human use, potentially reducing water availability for wildlife. At this site, Nolasco (2012) implemented artificial ponds that have subsequently supported long-term bat monitoring and are frequently used by other terrestrial mammals. Under these conditions, localized water sources may become increasingly important ecological focal points under climate warming because they concentrate animal activity and potentially reshape interactions within ecological communities.

Conclusion

The results found in this study demonstrate a positive association between anomalously warm conditions and pond-based bat capture activity in a montane ecosystem. Because the analyses were based on short-term deviations from the expected monthly temperatures, the observed associations are independent of regular seasonal changes in bat activity. These findings suggest that short-term thermal anomalies can modify how animal communities use spatially restricted sources. Although responses are likely to differ among species, localized water sources in montane ecosystems may become increasingly important ecological focal points under climate warming. These findings emphasize the need to understand how changing climatic conditions reshape patterns of community resource use and may ultimately improve conservation strategies for montane ecosystems under climate change.

Declarations

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Data availability

The dataset used for thermal anomaly analyses is provided as Supplementary Material.

Authorship

The author conceived the study, conducted data analyses, interpreted the results, and wrote the manuscript.

Ethics statement

This study was based on previously published monitoring data. No additional animal capture, handling, or experimental procedures were conducted for this investigation; therefore, no additional ethical approval or collection permits were required.

Declaration of competing interests

The author declares no competing interests.

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Declaration of generative AI use

ChatGPT version 1.2026.118 (OpenAI) was used exclusively for language editing and grammatical revision. All scientific interpretations, analyses, and conclusions were developed by the author.

References

1. Acosta-Luzuriaga ED (2025) Relación entre características acústicas y rasgos fenotípicos en murciélagos. Master's thesis, Univ. Autónoma de Tlaxcala, Tlaxcala, Mexico
2. Acosta-Luzuriaga ED, Ayala-Berdon J (2026) Seasonal shifts in body mass shape echolocation traits in *Eptesicus fuscus* from central Mexico. *Mammal Res* 71:43. <https://doi.org/10.1007/s13364-026-00862-0>
3. Acosta-Luzuriaga ED, Medina-Bello KI, Ayala-Berdon J (2026) Linking energy metabolism and echolocation: the relationship between basal metabolic rate and peak frequency in bats. *Bioacoustics* 1–17. <https://doi.org/10.1080/09524622.2026.2623235>
4. Amador LI, Moyers Arévalo RL, Almeida FC, Catalano SA, Giannini NP (2018) Bat systematics in the light of unconstrained analyses of a comprehensive molecular supermatrix. *J Mamm Evol* 25:37–70. <https://doi.org/10.1007/s10914-016-9363-8>
5. Arias-Aguilar A, Chacon-Madrigal E, LaVal R, Rodriguez-Herrera B (2020) Diversity and activity patterns of aerial insectivorous bats along an altitudinal gradient in a tropical forest in Costa Rica. *Hystrix* 31:58–63. <https://doi.org/10.4404/hystrix-00244-2019>
6. Ayala-Berdon J, Medina-Bello KI (2024) Torpor energetics are related to the interaction between body mass and climate in bats of the family Vespertilionidae. *J Exp Biol* 227:jeb246824. <https://doi.org/10.1242/jeb.246824>
7. Ayala-Berdon J, Vázquez-Fuerte R, Rodríguez-Peña N, Martinez Gomez M (2017) Bat fauna associated with artificial ponds in La Malinche National Park, a mountain ecosystem of Mexico. *Mammalia* 81:573–581. <https://doi.org/10.1515/mammalia-2016-0055>

8. Bogoni JA, Carvalho-Rocha V, Ferraz KM, Peres CA (2021) Interacting elevational and latitudinal gradients determine bat diversity and distribution across the Neotropics. *J Anim Ecol* 90:2729–2743. <https://doi.org/10.1111/1365-2656.13594>
9. Boratyński JS, Willis CK, Jefimow M, Wojciechowski MS (2015) Huddling reduces evaporative water loss in torpid *Myotis nattereri*. *Comp Biochem Physiol A* 179:125–132. <https://doi.org/10.1016/j.cbpa.2014.09.035>
10. Bradshaw D (2003) *Vertebrate ecophysiology: an introduction to its principles and applications*. Cambridge Univ. Press, Cambridge
11. Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. *Nat Clim Chang* 8:224–228. <https://doi.org/10.1038/s41558-018-0067-3>
12. Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274. <https://doi.org/10.1146/annurev.physiol.66.032102.115105>
13. Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf BO (2014) The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiol Biochem Zool* 87:782–795. <https://doi.org/10.1086/678956>
14. Hartig F (2024) DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.7. <https://CRAN.R-project.org/package=DHARMA>
15. Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and daily torpor in mammals. *Respir Physiol Neurobiol* 141:317–329. <https://doi.org/10.1016/j.resp.2004.03.014>
16. Herreid CF, Schmidt-Nielsen K (1966) Oxygen consumption, temperature, and water loss in bats from different environments. *Am J Physiol* 211:1108–1112. <https://doi.org/10.1152/ajplegacy.1966.211.5.1108>
17. Humphries MM, Umbanhowar J, McCann KS (2004) Bioenergetic prediction of climate change impacts on northern mammals. *Integr Comp Biol* 44:152–162. <https://doi.org/10.1093/icb/44.2.152>
18. Ives A, Dinnage R, Nell LA, Helmus M, Li D (2020) phyr: Model based phylogenetic analysis. R package version 1.1.0. <https://CRAN.R-project.org/package=phyr>
19. Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* 5:365–374. <https://doi.org/10.1890/060097>
20. Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol Lett* 12:334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
21. Kurta A (2014) The misuse of relative humidity in ecological studies of hibernating bats. *Acta Chiropterol* 16:249–254
22. Lisón F, Calvo JF (2011) The significance of water infrastructures for the conservation of bats in a semiarid Mediterranean landscape. *Anim Conserv* 14:533–541. <https://doi.org/10.1111/j.1469-1795.2011.00478.x>

23. Lisón F, Calvo JF (2014) Bat activity over small ponds in dry Mediterranean forests: implications for conservation. *Acta Chiropterol* 16:95–101. <https://doi.org/10.3161/150811014X683309>
24. Lundquist JD, Loheide SP (2011) How evaporative water losses vary between wet and dry water years as a function of elevation in the Sierra Nevada, California, and critical factors for modeling. *Water Resour Res* 47:W00H09. <https://doi.org/10.1029/2010WR010050>
25. McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecol Lett* 14:1236–1245. <https://doi.org/10.1111/j.1461-0248.2011.01695.x>
26. McGillycuddy M, Warton DI, Popovic G, Bolker BM (2025) Parsimoniously fitting large multivariate random effects in glmmTMB. *J Stat Softw* 112:1–19. <https://doi.org/10.18637/jss.v112.i01>
27. Meyer GA, Senulis JA, Reinartz JA (2016) Effects of temperature and availability of insect prey on bat emergence from hibernation in spring. *J Mammal* 97:1623–1633. <https://doi.org/10.1093/jmammal/gyw126>
28. Mishra RK (2023) Fresh water availability and its global challenge. *Br J Multidiscip Adv Stud* 4:1–78. <https://doi.org/10.58489/2836-5933/004>
29. Muñoz-Garcia A, Ben-Hamo M, Pilosof S et al (2022) Habitat aridity as a determinant of the trade-off between water conservation and evaporative heat loss in bats. *J Comp Physiol B* 192:325–333. <https://doi.org/10.1007/s00360-021-01425-2>
30. Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecol Monogr* 57:111–128. <https://doi.org/10.2307/1942620>
31. Nolasco A (2012) Importancia de estanques artificiales para la conservación de la biodiversidad de tres sitios del estado de Tlaxcala. Master's thesis, Univ. Autónoma de Tlaxcala, Tlaxcala, Mexico
32. Nowack J, Stawski C, Geiser F (2017) More functions of torpor and their roles in a changing world. *J Comp Physiol B* 187:889–897. <https://doi.org/10.1007/s00360-017-1100-y>
33. Oki T, Kanae S (2006) Global hydrological cycles and world water resources. *Science* 313:1068–1072. <https://doi.org/10.1126/science.1128845>
34. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42. <https://doi.org/10.1038/nature01286>
35. R Core Team (2025) R: A language and environment for statistical computing. R Found Stat Comput, Vienna, Austria
36. Ruf T, Geiser F (2015) Daily torpor and hibernation in birds and mammals. *Biol Rev* 90:891–926. <https://doi.org/10.1111/brv.12137>
37. Salvarina I (2016) Bats and aquatic habitats: a review of habitat use and anthropogenic impacts. *Mammal Rev* 46:131–143. <https://doi.org/10.1111/mam.12059>
38. Savage DB, Nolan JV, Godwin IR, Mayer DG, Aoetpah A, Nguyen T et al (2008) Water and feed intake responses of sheep to drinking water temperature in hot conditions. *Aust J Exp Agric* 48:1044–1047. <https://doi.org/10.1071/EA08056>

39. Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge Univ. Press, Cambridge
40. Scholander PF, Hock R, Walters V, Johnson F, Irving L (1950) Heat regulation in some arctic and tropical mammals and birds. *Biol Bull* 99:237–258. <https://doi.org/10.2307/1538741>
41. Şekercioğlu ÇH, Primack RB, Wormworth J (2012) The effects of climate change on tropical birds. *Biol Conserv* 148:1–18. <https://doi.org/10.1016/j.biocon.2011.10.019>
42. Sirami C, Jacobs DS, Cumming GS (2013) Artificial wetlands and surrounding habitats provide important foraging habitat for bats in agricultural landscapes in the Western Cape, South Africa. *Biol Conserv* 164:30–38. <https://doi.org/10.1016/j.biocon.2013.04.017>
43. Speakman JR (1999) The cost of living: field metabolic rates of small mammals. *Adv Ecol Res* 30:177–297. [https://doi.org/10.1016/S0065-2504\(08\)60019-7](https://doi.org/10.1016/S0065-2504(08)60019-7)
44. Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. Univ. Chicago, Chicago, pp 430–490
45. Stahlschmidt P, Patzold A, Ressler L, Schulz R, Bruhl CA (2012) Constructed wetlands support bats in agricultural landscapes. *Basic Appl Ecol* 13:196–203. <https://doi.org/10.1016/j.baae.2012.02.001>
46. Thomas SP, Cloutier D (1992) Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. *Physiol Zool* 65:443–456. <https://doi.org/10.1086/physzool.65.2.30158262>
47. Thomas SP, Suthers RA (1972) The physiology and energetics of bat flight. *J Exp Biol* 57:317–335. <https://doi.org/10.1242/jeb.57.2.317>
48. Tieleman BI, Williams JB (2000) The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol Biochem Zool* 73:461–479. <https://doi.org/10.1086/317740>
49. Trenberth KE, Smith L, Qian T, Dai A, Fasullo J (2007) Estimates of the global water budget and its annual cycle using observational and model data. *J Hydrometeorol* 8:758–769. <https://doi.org/10.1175/JHM600.1>
50. Turner VGT (2002) Aspects of the ecology of Daubenton's bats and pipistrelles and their potential prey in relation to altitude. PhD thesis, Univ. Leeds, Leeds, UK
51. Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philos Trans R Soc B* 372:20160135. <https://doi.org/10.1098/rstb.2016.0135>
52. Viviroli D, Archer DR, Buytaert W, Fowler HJ, Greenwood GB, Hamlet AF et al (2011) Climate change and mountain water resources: overview and recommendations for research, management and policy. *Hydrol Earth Syst Sci* 15:471–504. <https://doi.org/10.5194/hess-15-471-2011>
53. Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC et al (2002) Ecological responses to recent climate change. *Nature* 416:389–395. <https://doi.org/10.1038/416389a>
54. Williams JB (1996) A phylogenetic perspective of evaporative water loss in birds. *Auk* 113:457–472. <https://doi.org/10.2307/4088912>

Figures

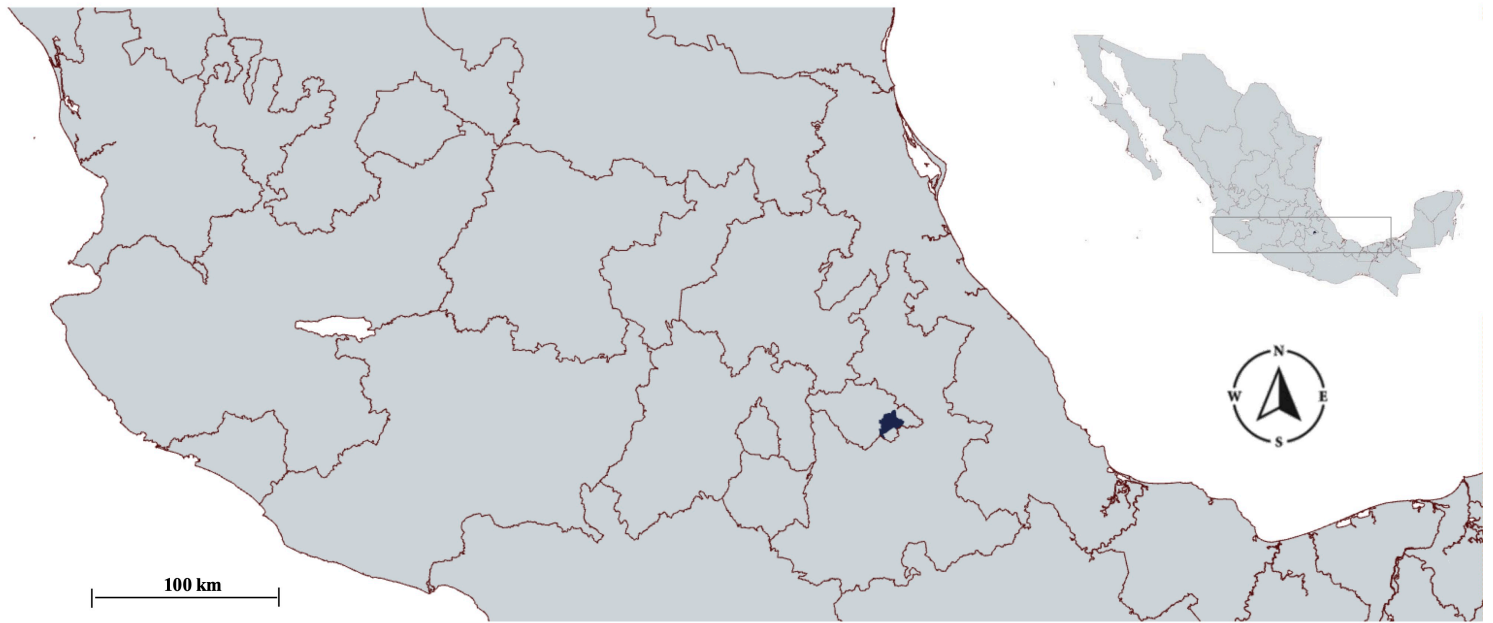


Figure 1

Location of the study area in La Malinche National Park (black polygon), a montane ecosystem in central Mexico, where bat monitoring was conducted during the 2014-2015 and 2023-2024 periods. The inset map shows the location of the study region within Mexico. The base map, including state borders, was generated using MapChart (<https://www.mapchart.net>) and edited with GIMP-2.10 (<https://www.gimp.org>).

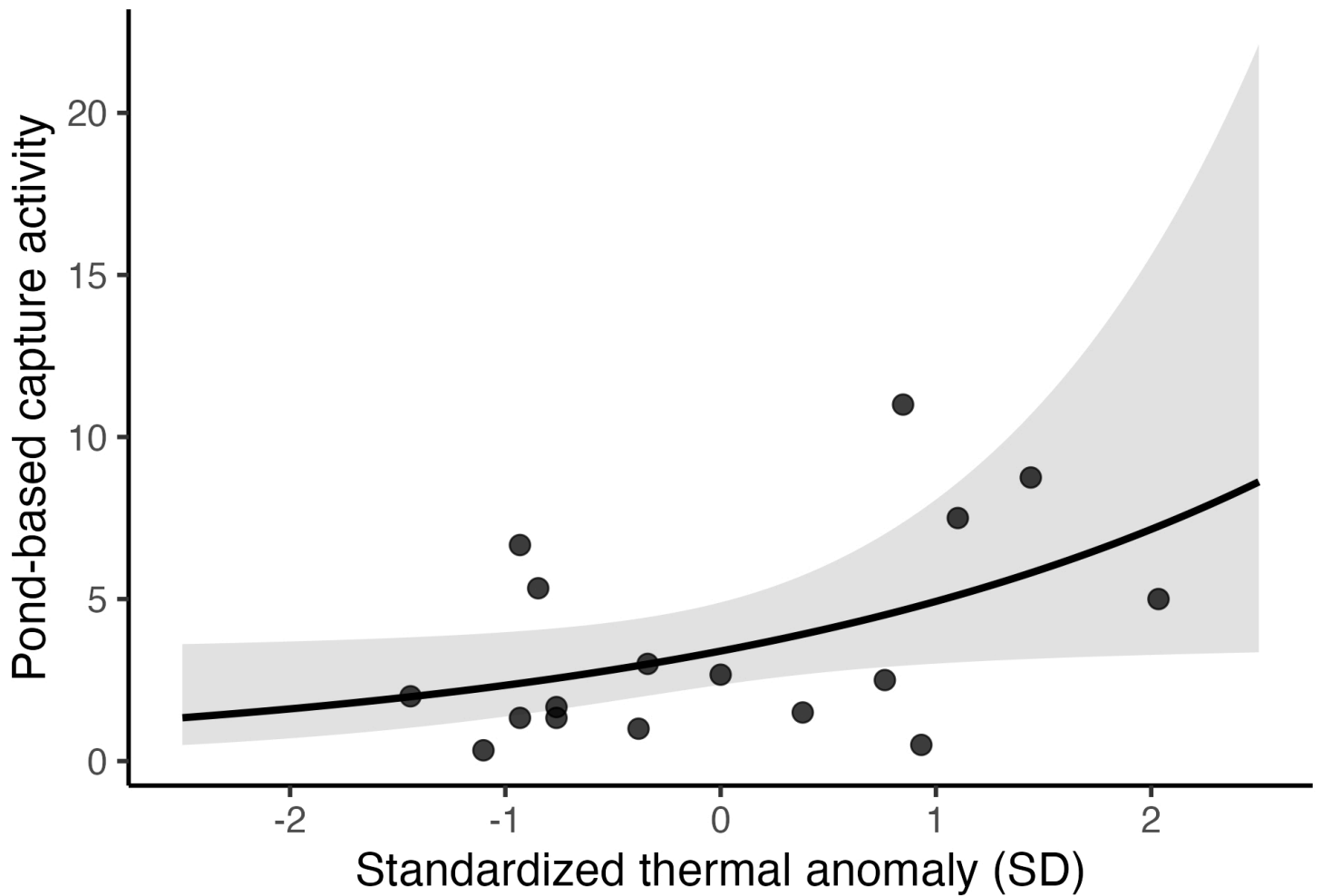


Figure 2

Relationship between standardized thermal anomalies and pond-based bat capture activity. Points represent monthly capture activity standardized by the number of the sampled ponds. The solid line represents the fitted relationship from a negative-binomial model fitted to monthly totals for visualization, and the shaded area indicates the 95% confidence interval.

Supplementary Files

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- [SupplementaryMaterial.xlsx](#)