

Research Article

Seasonal variation of bat activity in an endangered temperate forest in the Chilean biodiversity hotspot

Martín A. H. Escobar^{1,2}, Nélica R. Villaseñor³¹ Facultad de Ciencias de la Naturaleza, Universidad San Sebastián, Santiago, Chile² Escuela de Medicina Veterinaria, Facultad de Ciencias Médicas, Universidad Bernardo O'Higgins, Santiago, Chile³ Grupo de Ecología, Naturaleza y Sociedad, Departamento de Gestión Forestal y su Medio Ambiente, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Santiago, ChileCorresponding author: Martín A. H. Escobar (marescob@uchile.cl)

Abstract

Bats play an integral key ecological role in forests, but there is limited understanding of how their richness and activity vary over time in temperate forests and the effect of habitat variables on these species. Herein we describe the seasonal variation of bat species richness, activity and assemblage structure during the reproductive season in a sclerophyllous forest, an endangered temperate Mediterranean forest located in Chile's biodiversity hotspot. Additionally, we explored the relationship between bat activity and environmental variables (air temperature, vegetation cover, and proximity to water bodies). Species richness and bat activity varied during the breeding season and exhibited two peaks: spring and summer end, markedly decreasing in mid-summer. During spring, the bat assemblage exhibited greater species richness, diversity and evenness, whereas from the end of summer until autumn, both diversity and evenness decreased. Monthly average air temperatures had a positive association with total bat activity, although there was evidence of a threshold temperature over which bat activity significantly decreased. Canopy cover had a negative influence on the activity of *Tadarida brasiliensis* and *Lasiurus varius*, whereas increasing distance to water bodies was associated with a lower activity of *T. brasiliensis* and *L. villosissimus*. Our study demonstrates that bat diversity and bat activity vary greatly during the reproductive season in an endangered temperate forest, highlighting the importance of knowing seasonal patterns and evidencing that multiple surveys will improve our understanding of bat communities. This study provides relevant information to aid bat monitoring and conservation in the biodiversity hotspot of central Chile.

Key words: Air temperature, Central Chilean winter rainfall-Valdivian forests, Chiroptera, Mediterranean ecosystem, vegetation cover, water body

Introduction

Bats are widely distributed worldwide (Hutson et al. 2001). They are essential in ecosystem processes of terrestrial environments and provide various ecosystem services, such as pest control, seed dispersal and pollination (Ramírez-Fráncel et al. 2022), contributing to food production in agricultural landscapes (Boyles et al. 2011; Rodríguez-San Pedro et al. 2020). In particular,



Academic editor: Piter Boll
Received: 10 July 2024
Accepted: 21 October 2024
Published: 7 November 2024

ZooBank: <https://zoobank.org/555EB2AC-F9F2-44A5-82D7-11E737EADDEB>

Citation: Escobar MAH, Villaseñor NR (2024) Seasonal variation of bat activity in an endangered temperate forest in the Chilean biodiversity hotspot. Neotropical Biology and Conservation 19(4): 475–494. <https://doi.org/10.3897/neotropical.19.e131710>

Copyright: ©
Martín A. H. Escobar & Nélica R. Villaseñor.
This is an open access article distributed under
terms of the Creative Commons Attribution
License (Attribution 4.0 International – CC BY 4.0).

insectivorous bats play a key ecological role in temperate forests (van den Driessche et al. 2000) because they feed on insects that can be considered pests, and may ultimately influence forest health, structure, and composition (Beilke and O'Keefe 2022).

All insectivorous bats are exposed to relatively high energy demands for maintaining flight and echolocation, but in temperate zones, they also require energy for thermoregulation (Ciechanowski et al. 2007; Fjellidal et al. 2021). However, unlike other small epigeal insectivorous, bats can reduce their energetic demands under unfavorable conditions by entering torpor (Speakman and Thomas 2005; Dietz and Kalko 2006), allowing them to concentrate their activity during optimal periods and avoid unfavorable ones (Ciechanowski et al. 2007; Fjellidal et al. 2022). This behavior generates a temporal variation in the pattern of bat activity in temperate environments (Amaral et al. 2020). Temporal activity also varies among bat species, producing structural changes in the assemblage over time (Mello 2009). Therefore, it is important to know the temporal variation of species when carrying out ecological studies to avoid bias in the interpretation of the results.

Temporal variation in bat activity depends on environmental variables such as climate, weather, and habitat conditions (O'Donnell 2000; Koch et al 2023). Among weather factors, air temperature is usually one of the most important variables influencing bat activity (Milne et al. 2005; Ruczynski and Barton 2020). Within habitat elements, vegetation cover (Kusch et al. 2004; Shapiro et al. 2020) and proximity to water bodies have been found to influence bat activity patterns (Ancillotto et al. 2019). Vegetation provides orientation clues, special foraging habitats and shelter from wind and/or predators (Verboom and Huitema 1997), but sites with very dense vegetation reduce foraging efficiency by limiting the movement of species and use of echolocation to detect obstacles and potential prey (Marciente et al. 2015). Water bodies have a high richness, and bat activity around them is usually high because they allow them access to drinking water and a greater abundance of insects (Amorim et al. 2018). This association is particularly strong in arid and semi-arid environments (Korine et al. 2016).

The sclerophyllous forest corresponds to a temperate Mediterranean ecosystem (Gajardo 1994), which is in the middle zone of the "Central Chilean winter rainfall-Valdivian forests" (CCWR-VF) one of the 36 global biodiversity hotspots (Weinzettel et al. 2018). This hotspot contains many endemic plant and animal species and has lost at least 70% of its original coverage (Critical Ecosystem Partnership Fund 2019). Among natural ecosystems, the sclerophyllous forest has suffered one of the greatest losses of surface area and is poorly represented in the national system of protected wild areas (Pliscoff and Fuentes-Castillo 2011). Although the mammal community in this ecosystem is not particularly rich in species (Cofré et al. 2018), it exhibits a high level of endemism (Arroyo et al. 2008).

Mammal studies in the endangered sclerophyllous forest of central Chile have been performed for decades (e.g., Jaksic et al. 1981; Iriarte et al. 1989; Jaksic 2001; Pavez et al 2010). However, bat research in this ecosystem has only been developed recently (e.g. Rodríguez-San Pedro et al. 2018; Escobar et al. 2022). Most of this bat research evaluated the effect of land use change on species richness and abundance (e.g. Rodríguez-San Pedro et al.

2021; Chaperon et al. 2022) whereas the natural history of bat species, such as their temporal activity patterns, has received little attention (e.g. Muñoz et al. 2019; Rodríguez-San Pedro et al. 2024; Vásquez et al. 2020), although this information is important for designing more complex ecological studies. Bat species inhabiting the sclerophyllous forest of central Chile concentrate their activity during the reproductive season (spring-summer) (Ossa 2010; Muñoz et al. 2019). However, it is unknown whether activity patterns change within the reproductive season and if they vary among species in the sclerophyllous forest. This knowledge is essential for bat conservation, as it helps identify the time within the season when it is more likely to record species presence and activity (Law and Dickman 1998).

Herein we present the first study on seasonal variation of bat species richness and their activity during reproductive season in sclerophyllous forest remnants. In the biodiversity hotspot of central Chile, we describe the monthly variation in bat activity and the structural change of bat assemblage during the breeding season. We expect a gradual increase in bat activity as spring progresses and a decrease as summer progresses. Additionally, we explore the relationship between bat activity and environmental variables, including temperature, vegetation cover, and proximity to water bodies. The results of this study will provide relevant information to aid bat conservation in the biodiversity hotspot of central Chile.

Materials and methods

Study area

The study area is located in the biodiversity hotspot of central Chile, in the ecoregion of Sclerophyllous Forest and Scrubland (Gajardo 1994). Anthropogenic activities now dominate central Chile, with agriculture, nonnative tree plantations and urban land uses being widespread, whereas sclerophyllous forests and shrublands are highly threatened (Venegas-González et al. 2023), with some remnants found in the hills (Hernández et al. 2016). So far, six bat species have been found in the sclerophyllous forest of central Chile: Brazilian Free-tailed Bat *Tadarida brasiliensis*, Valparaiso Myotis *Myotis arescens*, Cinnamon Red Bat *Lasiurus varius*, Southern Hoary Bat *L. villosissimus*, Small Big-eared Brown Bat *Histiotus montanus* and Big-eared Brown Bat *H. macrotus* (Díaz et al. 2002), and concentrates an important part of the country's threatened bat species (Galaz et al. 2020).

We carried out our study in Las Torcasas de Pirque Nature Sanctuary, located in the southeast of the Metropolitan Region (33.72°S, 70.50°W) (Fig. 1). The Sanctuary has an area of 827 hectares, comprising altitudes from 900 to 2,500 m.a.s.l. (CMN 2010). The climate is cold temperate with winter rain (di Castri and Hajek 1976), with average monthly temperatures of 7.5 °C as a minimum (July) and 21.5 °C as a maximum (January). The average rainfall is 648 mm per year and is concentrated in the winter months (Dirección Meteorológica de Chile 2016). The southern exposure slopes are dominated by a dense, humid sclerophyllous forest with an understory of native shrubs, while the northern exposure slopes are dominated by a thorny scrub with an herbaceous stratum composed of perennial and annual herbs (Gajardo 1994).

Sampling sites

Twelve sampling sites were selected in remnants of sclerophyllous forest within “Las Torcazas de Pirque Nature Sanctuary” (Fig. 1). The sampling points were located on trails since these are usually used as flight paths by bats (Adams et al. 2009; Webala et al. 2011). Each site was located more than 150 m from any other sampling site to promote its independence (Korine and Pinshow 2004; Rodríguez-San Pedro and Simonetti 2013).

Bat survey and species identification

Bats were surveyed monthly for eight consecutive months (from September 2013 to April 2014), comprising the austral spring, summer and fall seasons. All monthly surveys comprised two sampling nights and avoided the full moon phase. Thus, surveys were not performed from three nights before the full moon phase up to three nights after the full moon phase to avoid the modulating effect of lunar light phobia on bat activity (Saldaña-Vásquez and Munguía-Rosas 2013; Vásquez et al. 2020). Sampling was conducted after sunset and within six hours, matching the period of maximum foraging activity of insectivorous bats (Kuenzi and Morrison 2003). On a given night, we conducted three trails (early, middle and late) to visit the same six sites on each, with a random order of visits within each trail. Bat calls were recorded for 10 minutes in each site visit using an EchoMeter 3 ultrasonic detector (Wildlife Acoustics, USA), totaling 30 minutes of monitoring per site in each monthly survey. The microphone was oriented upward at a 45° angle to the operator and was located 1.5 m above the ground (Weller and Zabel 2002).

The recorded files were processed in the Kaleidoscope program (Wildlife Acoustics, USA) to identify the files corresponding to bat echolocation calls. Each echolocation call was manually identified and assigned to a species by comparing their structure and frequency with reference libraries of bat echolocations recorded in central Chile (e.g., Ossa 2010; Rodríguez-San Pedro et al. 2016).

Environmental variables

We measured environmental variables that might be relevant for bats in our study area: air temperature, vegetation cover, and distance to the nearest water body. Temperature was obtained from the Pirque Meteorological Station, 8 km northeast of the study area. Vegetation cover was calculated for each sampling site at two spatial scales. First, the percentage of woody vegetation coverage at each site was calculated using 100-m-radius plots (Fig. 1A). For this, a 100-m buffer was created around each site and the woody vegetation cover within the buffer was digitized by interpreting high-resolution satellite imagery (WorldView, DigitalGlobe) in ArcGIS. Based on the digitized polygons, the percentage of woody vegetation coverage per plot (100 m radius) was calculated in ArcGIS. Vegetation cover was also assessed at the microhabitat level using two 12 m long transects starting from each edge of the trail towards the forest (Fig. 1B). In each transect, we estimated the canopy coverage every 3 m with a Vertical Cover Tube by visually estimating the percentage of the cylinder area covered by the canopy (Fiala et al. 2006). Then we obtained the average

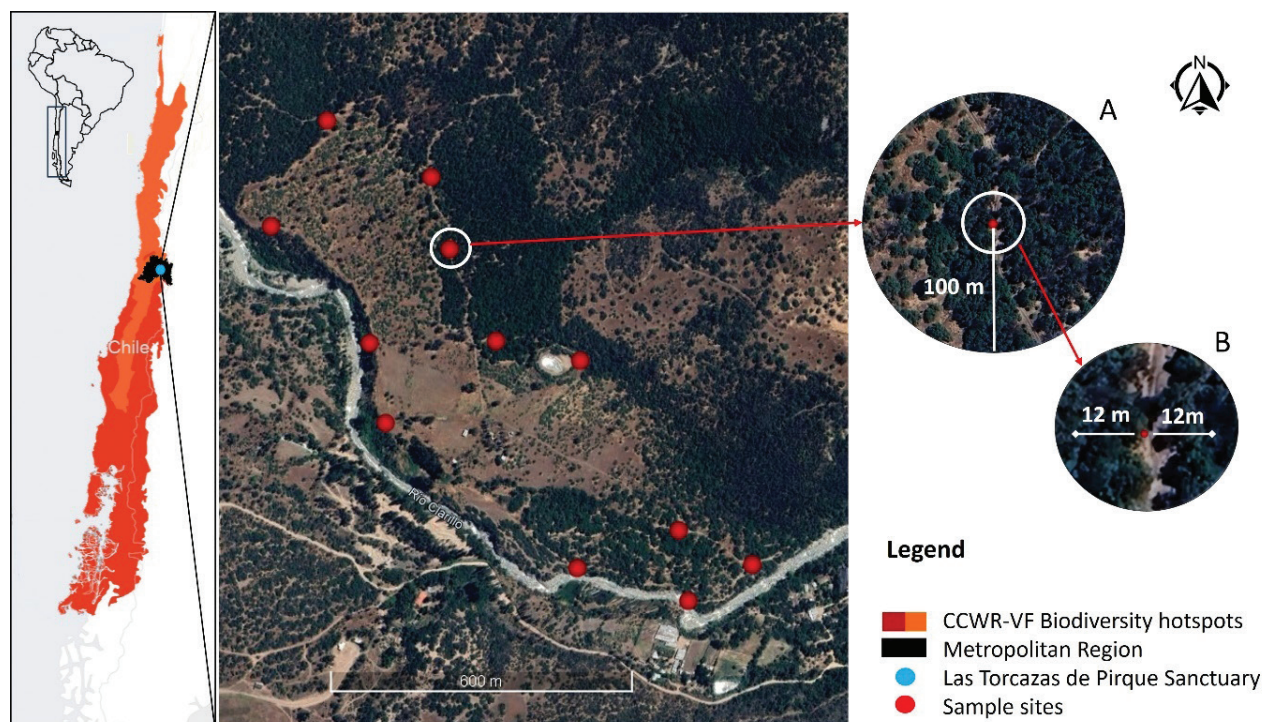


Figure 1. Study area and sampling sites **A** plot for recording woody vegetation coverage (100 m radius) at the habitat level **B** vegetation cover at the microhabitat level was recorded using two transects (12 m long).

percentage of canopy cover at a site using both transects. Finally, to calculate the distance to the nearest water body, we used high-resolution satellite imagery (WorldView, DigitalGlobe) to identify water bodies (such as riverbanks or irrigation dams), and then measured the linear distance from the sampling site to the nearest water body.

Data analysis

Species richness and activity

From echolocation calls identified at the species level, we obtained the total bat species richness per month (considering all 12 sampling points) and used the activity index (passes/hr) to estimate abundance per sampling point (Walsh et al. 2004). A bat pass was considered to be any record with a maximum duration of 15 s where two or more pulses emitted by a bat were identified (Rodríguez-San Pedro et al. 2020) and the activity index was built by quantifying the number of bat passes per hour per sampling point. To establish the seasonal variation in bat activity, we calculated the monthly average activity index for all records and each species.

Additionally, we calculated the monthly proportion of records assigned to each species to determine changes in its relative abundance in the assemblage over the evaluation period. Finally, we calculated for each month the Shannon index (H') and the Pielou evenness index (J') as descriptors of the diversity and degree of homogeneity of the species assemblage (Caballero et al. 2004). For both indices, 95% confidence intervals were calculated by resampling using PAST 3.25 Software (Hammer et al. 2001).

Environmental variables

We first explored the association between the number of passes and the monthly average air temperature (average between the daily minimum and maximum air temperatures) by using the Spearman rank correlation coefficient (Milne et al. 2005).

To identify the habitat variable that best explained each bat species' activity, we used model selection in R 3.5.3 (R Core Team 2019). For each bat species, we first fitted three candidate models using Generalized Linear Models (GLMs) with Poisson distribution (log link). Each model described the total activity recorded over eight months (the response variable) as a function of a habitat variable (predictive variable) for an individual species. Only one habitat variable was included in each model to avoid overparameterizing models because, for each species, we had one variable (total passes) from each sampling point ($n = 12$). Due to over-dispersion in our GLMs, we fitted Generalized Linear Mixed Models (GLMMs) by incorporating an observation-level random effect (sampling point, $n = 12$; Bolker et al. 2009). The best model for each response variable was then selected using the Akaike Information Criterion corrected for small samples (AICc) with the MuMIn package (Barton 2018). Finally, the residuals of the best models (lowest AICc values) were explored to evaluate the model fit. The best models were interpreted, and their 95% confidence intervals were estimated and graphed when there were significant ($p < 0.05$) or near significant ($p \leq 0.1$) effects from predictive variables.

Results

Richness and abundance

We obtained 48 effective hours of acoustic recording and recorded 710 files during surveys. Of these, 330 files were classified as effective bat echolocation calls. All the potential species (six) for the study area were recorded (Table 1) (Díaz et al. 2002). All recorded species are native and one, *Myotis arescens*, is endemic to central Chile. *Myotis arescens* used to be considered a subspecies of *M. chiloensis*, but recently has been recognized as a separate species (see Novaes et al. 2022). The species with the largest number of records were *M. arescens* and *Lasiurus varius*, which together corresponded to 72% of the records (Table 1).

Species richness and bat activity showed seasonal variation during the breeding season. Bats were not recorded in September, whereas the maximum species richness was recorded in October and November (spring). There was a marked decrease in species recorded in January (mid-summer) and then increased richness in February and March (end of summer), although with a slightly lower value than in spring. In April (autumn), only one species was recorded (Fig. 2). Bat activity presented a pattern of monthly variation similar to species richness, with a peak in October and November (spring) and another in March (summer end) (Fig. 2).

Species assemblage varied over time regarding the proportion of records of bat species detected. During spring, the assemblage's composition showed a higher species richness and similar relative abundances (Fig. 3). In fact, during this period, Shannon's diversity (H') and Pielou's evenness (J') indices were sig-

Table 1. Origin (N = native; E = endemic), status (R = resident; PM = possible migratory), foraging groups (OS = open space; CE = clutter edge; C = clutter) and number and percentage of acoustic files of the six bat species recorded in the study area.

Family	Species	Origin	Status	Foraging groups	Files N° (%)
Molossidae	<i>Tadarida brasiliensis</i>	N	PM	OS	46 (14)
Vespertilionidae	<i>Myotis arescens</i>	E	R	C	172 (52)
	<i>Lasiurus varius</i>	N	R	C	65 (20)
	<i>Lasiurus villosissimus</i>	N	PM	OS	29 (9)
	<i>Histiotus montanus</i>	N	R	CE	11 (3)
	<i>Histiotus macrotus</i>	N	R	CE	7 (2)

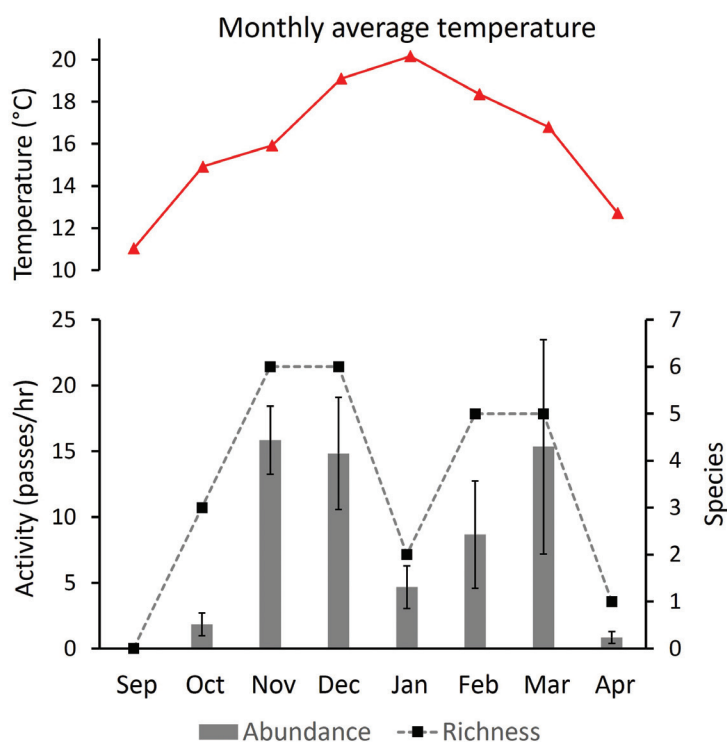


Figure 2. Seasonal variation of species richness (black line) and average monthly activity (passes/hr) (gray bars). The error lines correspond to the standard error. The top shows the monthly average temperatures (red line) in the study area.

nificantly higher (Fig. 4). From the end of summer to autumn, both diversity and evenness decreased significantly (Fig. 4), accounting for a less diverse assemblage initially dominated by *M. arescens* and *L. varius* to end in autumn with the absolute dominance of *M. arescens* (Fig. 3).

There were two peaks of bat activity during the evaluated period, the first at the end of spring and the second at the end of summer (Fig. 2); however, this pattern of activity varies between species. The first peak of activity is very clear for all species and occurs in November for *M. arescens*, *L. varius*, *Histiotus macrotus* and *H. montanus*, whereas for *T. brasiliensis* and *L. villosissimus* it occurs in December (Fig. 5). The second peak of activity is very clear for *M. arescens* and *L. varius* and occurs in March and February, respectively. The rest of the recorded species show a slight increase in activity in March (Fig. 5).

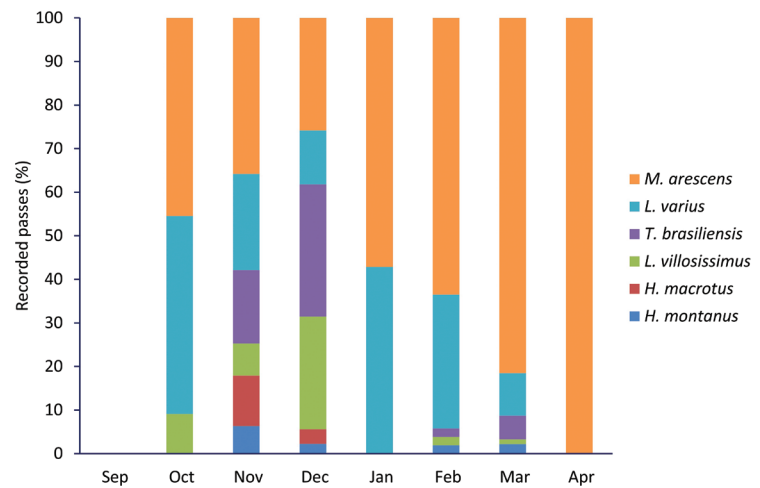


Figure 3. Monthly proportion of each bat species in the number of files recorded as an indicator of their relative abundance.

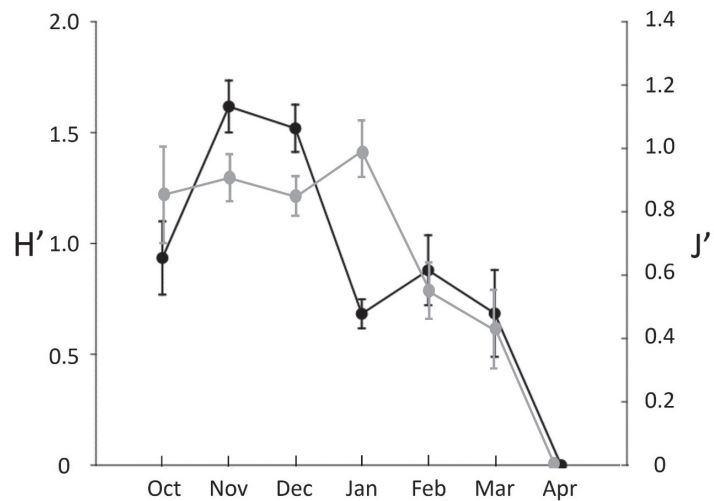


Figure 4. Monthly values of Shannon Diversity Index (H') (black line) and Evenness Index (J') (gray line). Error bars show 95% confidence intervals.

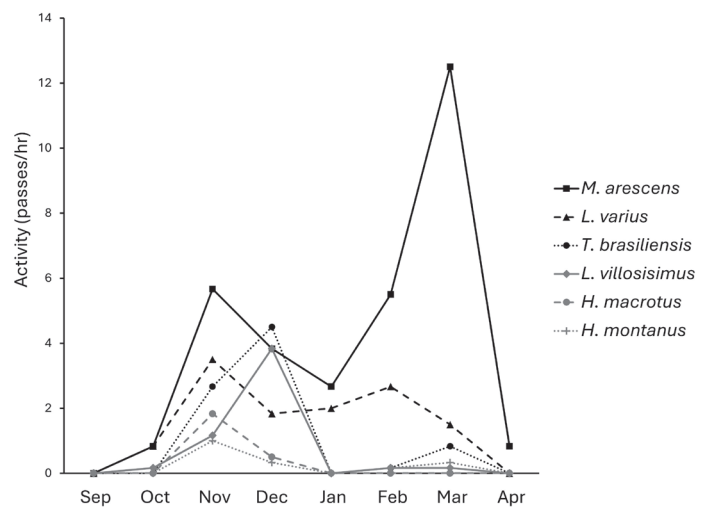


Figure 5. Monthly activity (passes/hr) for each bat species. Line and point symbols differentiate the species.

Environmental variables

Monthly average air temperatures exhibited a positive association with bat activity, except during the hottest month (January) where there was an abrupt decrease in richness and activity (Fig. 2). Total bat activity and average monthly air temperature were positively correlated ($r_s = 0.43$; $p < 0.001$). However, certain temperature thresholds can be identified. With an average monthly temperature above 15 °C, bat activity increased, with the greatest activity concentrated between 16 °C and 19 °C. At higher monthly temperatures, bat activity decreased (Fig. 6).

Best models predicting bat activity included canopy cover and distance to the water body (Appendix 1: Table A1). Canopy cover at the microhabitat level (12 m long transects) only affected *T. brasiliensis* and *L. varius*. The increase in canopy cover was associated with a lower abundance of these species (Fig. 7). The distance to the nearest water body affected two species. Increasing distance to the water body was associated with lower activity of *T. brasiliensis* and *L. villosissimus* (Fig. 7).

Discussion

Our study reveals a marked variation in bat activity and species richness in an endangered sclerophyllous forest of central Chile. Monthly activity patterns vary for each species, causing structural changes in the assemblage of bat species during the season. These seasonal bat activity patterns are associated with temperature. Additionally, habitat variables such as canopy cover and distance to water bodies affected bat activity negatively in the surveyed sites.

Richness and abundance

Although there is still limited understanding of how bat richness and activity vary over time in Mediterranean landscapes (Amorim et al. 2018), it is also well known that bat activity is high during the reproductive season (Swift 1980;

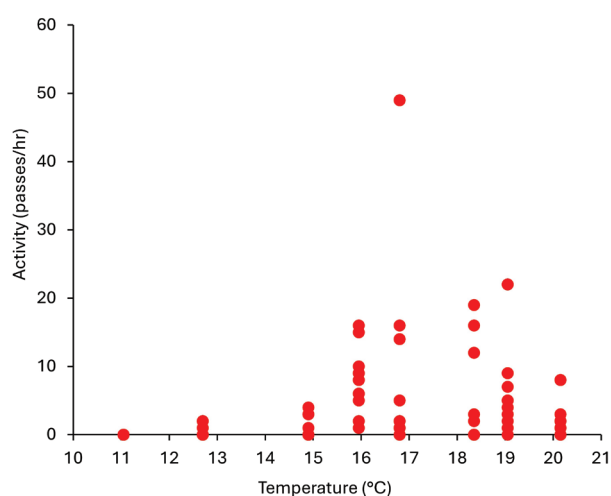


Figure 6. Bat activity (passes/hr) recorded at the sampling sites compared to the monthly average temperature.

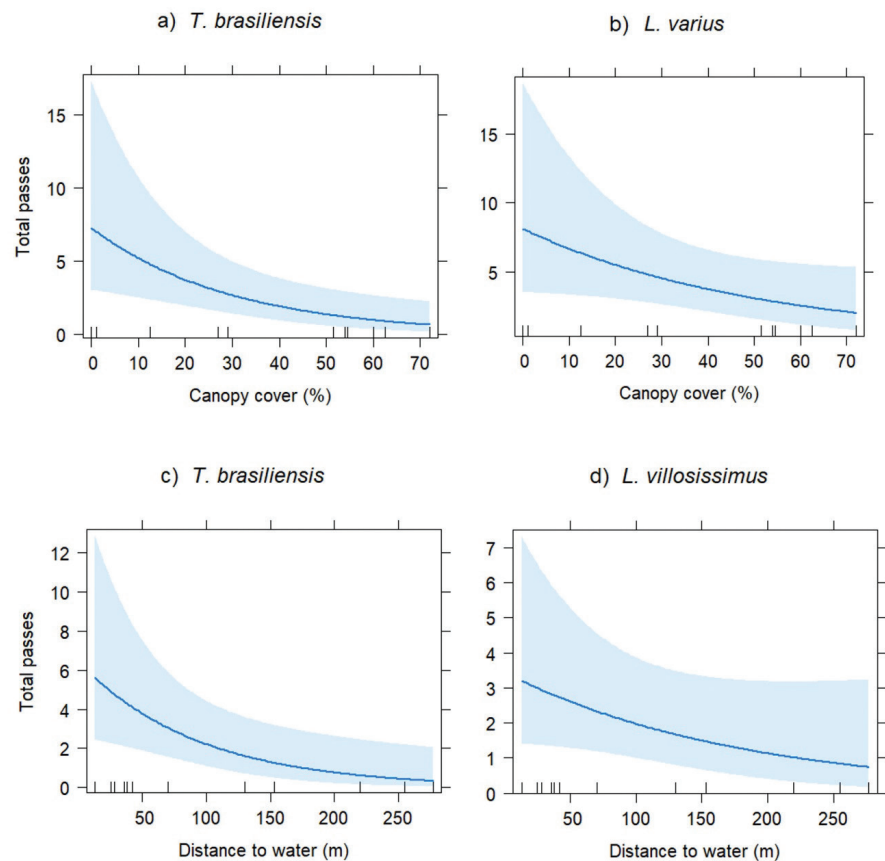


Figure 7. Predicted activity (total passes) for bat species according to habitat variables in the best Generalized Linear Mixed Model. Predicted activity for **a** *T. brasiliensis* **b** *L. varius* **c** *T. brasiliensis* **d** *L. villosissimus*. Shaded areas represent 95% confidence intervals.

Hayes 1997; Korine and Pinshow 2004), which is consistent with our findings. The higher activity recorded in spring (October and November) may be explained by post-torpor restoration of fat body reserves (Ciechanowski et al. 2010) and the increase in the abundance of insects and other prey species (Korine et al. 2020). In addition, we report a high activity at the end of summer (February and March). This may reflect the addition in the population of young bats that likely increase their activity during this period, as well as an increased bat feeding activity to accumulate fat body reserves for the winter torpor period (Barros et al. 2017; Korine et al. 2020).

Bats in temperate regions typically hibernate during the winter to minimize energy expenditure (Miková et al. 2013). However, when temperatures are high enough, torpor interruptions can be quite frequent (Ransome 1971; Daan 1973; Zukal et al. 2005). Although in our study we did not record bat activity during September (late winter), and it was very low in April (autumn), some bat activity has been documented during the non-breeding season in our study area, particularly over water bodies (Ossa 2010). However, this activity is sporadic and associated with days with favorable temperature (e.g., Barros et al. 2017; Mas et al. 2022) since the low temperatures and precipitation during winter in Mediterranean areas generally suppress bat activity (e.g., Kapfer and Aron 2007), possibly due to high thermoregulatory costs (Burles et al. 2009).

Although the structure of the bat assemblage varied over time regarding the proportion of bat species records, overall, the assemblage was dominated by

M. arescens and *L. varius*. Both species live under the canopy (Rodríguez-San Pedro and Simonetti 2014; Novaes et al. 2022), so their acoustic recording is probable given the height of the recording equipment (1.5 m). On the other hand, *T. brasiliensis*, *L. villosissimus*, *H. montanus* and *H. macrotus* fly at high altitudes above the canopy or in open spaces (Canals et al. 2005), so the probability of acoustically recording these species would be lower compared to those species that commonly move within the forest. In future studies, it is necessary to perform acoustic sampling at different heights to confirm our results on the dominance of these species in sclerophyllous forests.

All bat species presented a first peak of activity at the beginning of spring. However, the first peak of activity of *T. brasiliensis* and *L. villosissimus* is later than in the other species. This gap could be due to the greater mass of these species so their torpor period could be longer (Ruf and Geiser 2015). Alternatively, as open space flyers, they may be more sensitive to lower air temperatures at night (e.g. Duval and Campo 2017). We also cannot rule out that this gap reflects the migratory behavior of individuals of these species (see Galaz et al. 2020). Only *M. arescens* exhibited a clear second peak of activity during summer, with twice the activity recorded in the first peak. This greater activity could be due to increased feeding activity to accumulate reserves for the winter torpor as well as due to births (see Korine et al 2020). In fact, capture data for the summer in the study area shows that 45% of *M. arescens* captured corresponded to young bats (M. Escobar, unpublished data).

Environmental variables

We found a positive relationship between bat activity and air temperature, a finding that agrees with recent research by Rodríguez-San Pedro et al. (2024) in agroecosystems in the same study area, and which has been previously described in the literature (e.g. O'Donnell 2000; Vaughan et al. 1997). Environmental temperature is crucial for aerial-insectivorous bats in temperate zones because it largely influences insect activity and bat activity, as bats need to maintain a stable body temperature when out of hibernation or torpor (Agosta et al. 2005; Barros et al. 2014). However, in our case, this relationship between activity and temperature seems to be non-linear, evidencing a reduction in activity above a threshold temperature (e.g., Amaral et al. 2020; Ciechanowski et al. 2007; Kraker-Castañeda et al. 2013). This reduction in activity at high temperatures would avoid the risk of hyperthermia by not dissipating the heat product of flight (Bender and Hartman 2015; Reichard et al. 2010; Voigt and Lewanzik 2011). This response to the increase in temperature would explain the lower activity recorded during the period of highest temperature in the austral summer season (January). In any case, this pattern could present species-specific variations for bats in central Chile (e.g. Rodríguez-San Pedro et al 2024), so that specific studies are needed to identify species that may be more vulnerable to temperature increase.

Tree vegetation cover is an important habitat variable for bat species (Estrada et al. 2004). However, in our study the cover of woody vegetation only influenced the activity (total passes) of *T. brasiliensis* and *L. varius*, presenting a negative relationship. The negative relationship between *T. brasiliensis* and canopy cover may be explained by their low maneuverability and low-frequency calls, which restrict their ability to capture insects in areas with dense canopies

(Bailey et al. 2019). In the case of *L. varius*, although this species lives under the canopy (Rodríguez-San Pedro and Simonetti 2014), it is likely that a cover of woody vegetation that is too dense obstructs the flight paths and does not allow the movement of individuals (Shapiro et al. 2020).

The decrease in activity (total passes) at greater distances from water bodies presented by *T. brasiliensis* and *L. villosissimus* would indicate that water bodies are an important food source for these insectivorous species. Water sources in dry Mediterranean forests are particularly important during the dry summer months (Lisón and Calvo 2014). Some authors have reported that most of the recorded species present greater feeding activity in sites with water bodies (e.g. Lisón and Calvo 2014; MacSwiney et al. 2020). This would be because the life cycles of many insect groups are associated with the aquatic environment and its surrounding vegetation (Escalona 2011; MacSwiney et al. 2020). Additionally, *T. brasiliensis* and *L. villosissimus* present morphological characteristics that allow them to fly fast and in an energetically economical manner (Norberg and Rayner 1987) in open spaces during foraging (Canals et al. 2005; McCracken et al. 2008), which would also explain their greater abundance near water bodies.

Insights for conservation

A better understanding of the seasonal variation of bat diversity and activity, as well as their relationship with habitat variables, improves the knowledge of their natural history and provides valuable information for bat conservation (e.g. Lisón and Calvo 2014; Rodríguez-San Pedro et al. 2024). Our results highlight the need for a profound understanding of bat ecology for sampling and monitoring studies since bat diversity and activity significantly vary with survey date and habitat features. This is relevant and should be considered in the design of short- and long-term studies to determine population trends and phenological changes in behavior or understand the effects of climate change (Forrest 2016; Gottfried et al. 2020; Kerth 2022), but is particularly important in assessing environmental impacts of development projects. In Chile, these assessments are not only deficient in the methodologies they use (e.g. Escobar et al. 2015) but are also extremely limited in time (few nights) and tend to occur in periods that are not favorable for bats (Fernández et al 2016). We hope that the environmental authority considers our results and incorporates recommendations for the design of bat surveys in the context of evaluating development projects, at least in projects with a greater impact on bats such as wind farms (Pereira et al. 2022). For example, based on our results, for this area, it would be appropriate to carry out sampling in spring and not in summer during the reproductive season. This is particularly important to aid protection measures for bat communities that inhabit this biodiversity hotspot in central Chile.

Acknowledgements

We thank Jorge Abarca for his collaboration in file processing, Jaime Gaete for granting access to “Las Torcasas de Pirque Natural Sanctuary” and volunteers who participated in the fieldwork. The authors thank Trevor Walter for editing previous versions of the manuscript and two anonymous reviewers whose comments improved this manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript, and they declare no financial interests.

Author contributions

Escobar, M.A.H.: Funding acquisition, Conceptualization, Investigation, Methodology, Formal analysis, Project administration, Visualization, Writing – original draft. Villaseñor, N.R.: Formal analysis, Visualization, Writing – review & editing.

Author ORCIDs

Martín A. H. Escobar  <https://orcid.org/0000-0001-6009-7025>

Nélica R. Villaseñor  <https://orcid.org/0000-0001-8624-4484>

Data availability

The datasets for the current study will be available from the corresponding author on reasonable request.

References

- Adams MD, Law BS, French KO (2009) Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. *Forest Ecology and Management* 258(9): 2090–2100. <https://doi.org/10.1016/j.foreco.2009.08.002>
- Agosta SJ, Morton D, Marsh BD, Kuhn KM (2005) Nightly, seasonal, and yearly patterns of bat activity at night roosts in the Central Appalachians. *Journal of Mammalogy* 86(6): 1210–1219. <https://doi.org/10.1644/05-MAMM-A-012R1.1>
- Amaral IS, Pereira MJR, Mader A, Ferraz MR, Pereira JB, Oliveira LR (2020) Wind farm bat fatalities in southern Brazil: Temporal patterns and influence of environmental factors. *Hystrix* 31: 40–47.
- Amorim F, Jorge I, Beja P, Rebelo H (2018) Following the water? Landscape-scale temporal changes in bat spatial distribution in relation to Mediterranean summer drought. *Ecology and Evolution* 8(11): 5801–5814. <https://doi.org/10.1002/ece3.4119>
- Ancillotto L, Bosso L, Salinas-Ramos VB, Russo D (2019) The importance of ponds for the conservation of bats in urban landscape. *Landscape and Urban Planning* 190: 103607. <https://doi.org/10.1016/j.landurbplan.2019.103607>
- Arroyo MTK, Marquet P, Marticorena C, Simonetti J, Cavieres L, Squeo F, Rozzi R, Massardo F (2008) El hotspot chileno, prioridad mundial para la conservación. In: Rovira (Ed.) *Biodiversidad de Chile. Patrimonio y Desafíos*. Ocho Libros Editores, Santiago, Chile.
- Bailey AM, Ober HK, Reichert BE, McCleery RA (2019) Canopy Cover Shapes Bat Diversity across an Urban and Agricultural Landscape Mosaic. *Environmental Conservation* 46(3): 1–8. <https://doi.org/10.1017/S0376892919000109>

- Barros MA, Pessoa DMA, Rui AM (2014) Habitat use and seasonal activity of insectivorous bats (Mammalia: Chiroptera) in the grassland of southern Brazil. *Zoologia* 31(2): 153–161. <https://doi.org/10.1590/S1984-46702014000200006>
- Barros PA, Ribeiro C, Cabral JA (2017) Winter activity of bats in Mediterranean peri-urban deciduous forests. *Acta Chiropterologica* 19(2): 367–377. <https://doi.org/10.3161/15081109ACC2017.19.2.013>
- Barton K (2018) Package MuMIn: multi-model inference. R-package version 1.40.4. <https://cran.r-project.org/web/packages/MuMIn/>
- Beilke EA, O’Keefe JM (2022) Bats reduce insect density and defoliation in temperate forests: An exclusion experiment. *Ecology* 104(2): e3903. <https://doi.org/10.1002/ecy.3903>
- Bender MJ, Hartman GD (2015) Bat Activity Increases with Barometric Pressure and Temperature during Autumn in Central Georgia. *Southeastern Naturalist* (Steuben, ME) 14(2): 231–242. <https://doi.org/10.1656/058.014.0203>
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JS (2009) Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24(3): 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Boyles JG, Cryan PM, McCracken GF, Kunz TH (2011) Economic importance of bats in agriculture. *Science* 332(6025): 41–42. <https://doi.org/10.1126/science.1201366>
- Burles DW, Brigham RM, Ring RA, Reimchen TE (2009) Influence of weather on two insectivorous bats in a Temperate Pacific Northwest rainforest. *Canadian Journal of Zoology* 87(2): 132–138. <https://doi.org/10.1139/Z08-146>
- Caballero H, Varona G, García Y (2004) Estructura ecológica de las comunidades de corales de la costa oriental de bahía de cochinos, Cuba. *Revista de Investigación Marina* 25: 23–36.
- Canals M, Grossi M, Iriarte-Díaz J, Veloso C (2005) Biomechanical and ecological relationships of wing morphology of eight Chilean bats. *Revista Chilena de Historia Natural* 78(2): 215–227. <https://doi.org/10.4067/S0716-078X2005000200005>
- Chaperon PN, Rodríguez-San Pedro A, Beltrán CA, Allendes JL, Barahona-Segovia RM, Urra F, Grez AA (2022) Effects of adjacent habitat on nocturnal flying insects in vineyards and implications for bat foraging. *Agriculture, Ecosystems & Environment* 326: 107780. <https://doi.org/10.1016/j.agee.2021.107780>
- Ciechanowski M, Zając T, Biłás A, Dunajski R (2007) Spatiotemporal variation in activity of bat species differing in hunting tactics: Effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology* 85(12): 1249–1263. <https://doi.org/10.1139/Z07-090>
- Ciechanowski M, Zając T, Zielińska A, Dunajski R (2010) Seasonal activity patterns of seven vespertilionid bat species in Polish lowlands. *Acta Theriologica* 55(4): 301–314. <https://doi.org/10.1007/BF03193234>
- CMN [Consejo de Monumentos Nacionales] (2010) Santuarios de la Naturaleza de Chile. CNM, Santiago, Chile, 144 pp.
- Cofré H, Vilina YA, Spotorno A (2018) Mamíferos Terrestres. In: Figueroa A, et al. (Eds) Biodiversidad de Chile. Patrimonio y Desafíos. Ministerio del Medio Ambiente. Tercera Edición, Santiago, Chile.
- Critical Ecosystem Partnership Fund (2019) Impact Report.
- Daan S (1973) Activity during natural hibernation in three species of vespertilionid bats. *Netherlands Journal of Zoology* 23(1): 1–71. <https://doi.org/10.1163/002829673X00193>
- di Castri F, Hajek ER (1976) Bioclimatología de Chile. Ediciones de la Universidad Católica de Chile, Santiago, Chile.

- Díaz IA, Sarmiento C, Ulloa L, Moreira R, Navia R, Véliz E, Peña C (2002) Vertebrados terrestres de la Reserva Nacional Río Clarillo, Chile central: Representatividad y conservación. *Revista Chilena de Historia Natural* 75(2): 433–448. <https://doi.org/10.4067/S0716-078X2002000200013>
- Dietz M, Kalko EK (2006) Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* 176(3): 223–231. <https://doi.org/10.1007/s00360-005-0043-x>
- Dirección Meteorológica de Chile (2016) Anuario climatológico 2010. Santiago, Chile.
- Duval VS, Campo AM (2017) Variaciones microclimáticas en el interior y exterior del bosque de caldén (*Prosopis caldenia*), Argentina. *Cuadernos de Geografía. Cuadernos de Geografía* 26(1): 37–49. <https://doi.org/10.15446/rcdg.v26n1.42372>
- Escalona MG (2011) Papel ecológico de las aguadas para murciélagos insectívoros en un bosque tropical subhúmedo. Tesis de Maestría. El Colegio de la Frontera Sur (ECOSUR), México.
- Escobar MAH, Vidal N, De La Fuente D, Abarca JA (2015) Incorporación de los murciélagos en la evaluación ambiental de parques eólicos y líneas de transmisión eléctrica en Chile: ¿mito o realidad? *Gestión y Ambiente* 29: 11–22.
- Escobar MAH, Puelma-Díez F, Villaseñor NR (2022) "Pit-tag" como marca permanente en *Myotis chiloensis* (Chiroptera: Vespertilionidae) y *Tadarida brasiliensis* (Chiroptera: Molossidae) en Chile central. *Gayana (Concepción)* 86(2): 40–46. <https://doi.org/10.4067/S0717-65382022000200040>
- Estrada A, Jiménez C, Rivera A, Fuentes E (2004) General bat activity measured with an ultrasound detector in a fragmented tropical landscape in Los Tuxtlas, Mexico. *Animal Biodiversity and Conservation* 27: 1–9.
- Fernández I, Yáñez J, Allendes JL, Ossa G, Rodríguez-San Pedro A (2016) Murciélagos de Chile: Lineamientos para su estudio. *Gestión y Ambiente* 32: 5–18.
- Fiala ACS, Garman SL, Gray AN (2006) Comparison of five canopy cover estimation techniques in the western Oregon Cascades. *Forest Ecology and Management* 232(1–3): 188–197. <https://doi.org/10.1016/j.foreco.2006.05.069>
- Fjellidal MA, Wright J, Stawski C (2021) Nightly torpor use in response to weather conditions and individual state in an insectivorous bat. *Oecologia* 197(1): 129–142. <https://doi.org/10.1007/s00442-021-05022-6>
- Fjellidal MA, Sørås R, Stawski C (2022) Universality of Torpor Expression in Bats. *Physiological and Biochemical Zoology* 95(4): 326–339. <https://doi.org/10.1086/720273>
- Forrest JRK (2016) Complex responses of insect phenology to climate change. *Global Change Biology* 17: 49–54. <https://doi.org/10.1016/j.cois.2016.07.002>
- Gajardo R (1994) La Vegetación Natural de Chile: clasificación y distribución geográfica. Editorial Universitaria, Santiago, Chile.
- Galaz J, Yáñez J, Fernández I (2020) Los murciélagos de Chile: Guía para su reconocimiento. CEA Ediciones, Valdivia, Chile.
- Gottfried I, Gottfried T, Lesiński G, Hebda G, Ignaczak M, Wojtaszyn G, Jurczyszyn M, Fuszara M, Fuszara E, Grzywiński W, Błachowski G, Hejduk J, Jaros R, Kowalski M (2020) Longterm changes in winter abundance of the barbastelle *Barbastella barbastellus* in Poland and the climate change – Are current monitoring schemes still reliable for cryophilic bat species? *PLoS One* 15(2): e0227912. <https://doi.org/10.1371/journal.pone.0227912>
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 1–9.

- Hayes JP (1997) Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* 78(2): 514–524. <https://doi.org/10.2307/1382902>
- Hernández J, Acuña MP, Magni CR (2016) The foothills of Santiago and its ecosystem services. University of Chile, Santiago, Chile.
- Hutson AM, Mickleburgh SP, Racey PA (2001) Microchiropteran Bats: Global Status Survey and Conservation Action Plan. IUCN/SSC chiroptera specialist group. IUCN, Gland, Switzerland. <https://doi.org/10.2305/IUCN.CH.2001.SSC-AP.1.en>
- Iriarte JA, Contreras LC, Jaksic FM (1989) A long term study of a small mammal assemblage in the central Chilean matorral. *Journal of Mammalogy* 70(1): 79–87. <https://doi.org/10.2307/1381671>
- Jaksic FM (2001) Patrones de variación espaciotemporal de plantas y animales en San Carlos de Apoquindo, Chile central. *Revista Chilena de Historia Natural* 74: 477–502. <https://doi.org/10.4067/S0716-078X2001000200021>
- Jaksic FM, Yañez JL, Fuentes ER (1981) Assessing a small mammal community in central Chile. *Journal of Mammalogy* 62(2): 391–396. <https://doi.org/10.2307/1380722>
- Kapfer G, Aron S (2007) Temporal variation in flight activity, foraging activity and social interactions by bats around a suburban pond. *Lutra* 50(1): 9.
- Kerth G (2022) Long-term field studies in bat research: Importance for basic and applied research questions in animal behavior. *Behavioral Ecology and Sociobiology* 76(6): 75. <https://doi.org/10.1007/s00265-022-03180-y>
- Koch M, Manecke J, Burgard JP, Münnich R, Kugelschafter K, Kiefer A, Veith M (2023) How weather triggers the emergence of bats from their subterranean hibernacula. *Scientific Reports* 13(1): 6344. <https://doi.org/10.1038/s41598-023-32166-7>
- Korine C, Pinshow B (2004) Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. *Journal of Zoology (London, England)* 262(2): 187–196. <https://doi.org/10.1017/S0952836903004539>
- Korine C, Adams R, Russo D, Fisher-Phelps M, Jacobs D (2016) Bats and water: Anthropogenic alteration threaten global bat populations. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-25220-9_8
- Korine C, Niv A, Axelrod M, Dahan T (2020) Species richness and activity of insectivorous bats in cotton fields in semi-arid and mesic Mediterranean agroecosystems. *Mammalian Biology* 100(1): 73–80. <https://doi.org/10.1007/s42991-019-00002-z>
- Kraker-Castañeda C, Santos-Moreno A, García-García JL (2013) Riqueza de especies y actividad relativa de murciélagos insectívoros aéreos en una selva tropical y pastizales en Oaxaca, México. *Mastozoología Neotropical* 20(2): 255–267.
- Kuenzi AJ, Morrison ML (2003) Temporal patterns of bat activity in southern Arizona. *The Journal of Wildlife Management* 67(1): 52–64. <https://doi.org/10.2307/3803061>
- Kusch J, Weber C, Idelberger S, Koob T (2004) Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zoologica* 53: 113–128.
- Law BS, Dickman CR (1998) The use of habitat mosaics by terrestrial vertebrate fauna: Implication for conservation and management. *Biodiversity and Conservation* 7(3): 323–333. <https://doi.org/10.1023/A:1008877611726>
- Lisón F, Calvo JF (2014) Bat Activity Over Small Ponds in Dry Mediterranean Forests: Implications for Conservation. *Acta Chiropterologica* 16(1): 95–101. <https://doi.org/10.3161/150811014X683309>
- MacSwiney MC, Ávila-Flores R, Pech-Canché JM (2020) Richness and activity of arthropodophagous bats in an arid landscape of central México. *Therya* 11(1): 23–31. <https://doi.org/10.12933/therya-20-900>

- Marciente R, Bobrowiec PED, Magnusson WE (2015) Ground-Vegetation Clutter Affects Phyllostomid Bat Assemblage Structure in Lowland Amazonian Forest. *PLoS One* 10(6): e0129560. <https://doi.org/10.1371/journal.pone.0129560>
- Mas M, Flaquer C, Puig-Montserrat X, Porres X, Rebelo H, López-Baucells A (2022) Winter bat activity: The role of wetlands as food and drinking reservoirs under climate change. *The Science of the Total Environment* 828: 154403. <https://doi.org/10.1016/j.scitotenv.2022.154403>
- McCracken GF, Gillam E, Westbrook J, Lee Y-F, Jensen M, Balsley B (2008) Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae: Chiroptera) at high altitude: links to migratory insect populations. *Integrative and Comparative Biology* 48(1): 107–118. <https://doi.org/10.1093/icb/icn033>
- Mello MAR (2009) Temporal variation in the organization of a Neotropical assemblage of leaf-nosed bats (Chiroptera: Phyllostomidae). *Acta Oecologica* 35(2): 280–286. <https://doi.org/10.1016/j.actao.2008.11.008>
- Miková E, Varcholová K, Boldogh S, Uhrin M (2013) Winter diet analysis in *Rhinolophus euryale* (Chiroptera). *Central European Journal of Biology* 8: 848–853. <https://doi.org/10.2478/s11535-013-0199-9>
- Milne DJ, Fisher A, Rainey I, Pavey CR (2005) Temporal patterns of bats in the top end of the Northern Territory, Australia. *Journal of Mammalogy* 86(5): 909–920. [https://doi.org/10.1644/1545-1542\(2005\)86\[909:TPOBIT\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)86[909:TPOBIT]2.0.CO;2)
- Muñoz AE, Ossa G, Zaviezo T, Bonacic C (2019) Diversity and foraging activity of bats in cultivated and uncultivated areas in agroecosystems of a Mediterranean-climate hotspot. *Neotropical Biodiversity* 5(1): 36–40. <https://doi.org/10.1080/23766808.2019.1621626>
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia, Chiroptera) wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London* 316: 335–427. <https://doi.org/10.1098/rstb.1987.0030>
- Novaes RLM, Rodríguez-San Pedro A, Saldarriaga-Cordoba MM, Aguilera-Acuña O, Wilson DE, Moratelli R (2022) Systematic review of *Myotis* (Chiroptera, Vespertilionidae) from Chile based on molecular, morphological, and bioacoustic data. *Zootaxa* 5188(5): 430–452. <https://doi.org/10.11646/zootaxa.5188.5.2>
- O'Donnell CFJ (2000) Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology* 27: 3. 207–221. <https://doi.org/10.1080/03014223.2000.9518228>
- Ossa G (2010) Métodos bioacústicos: una aproximación a la ecología de comunidades de murciélagos en las eco-regiones mediterránea y el bosque templado de Chile. Tesis Ingeniero Agrónomo. Especialidad Ciencias Animales. Facultad de Ciencias Agronómicas, Pontificia Universidad Católica de Chile, Santiago, Chile.
- Pavez EF, Lobos GA, Jaksic FM (2010) Cambios de largo plazo en el paisaje y los ensamblajes de micromamíferos y rapaces en Chile central. *Revista Chilena de Historia Natural* 83(1): 99–111. <https://doi.org/10.4067/S0716-078X2010000100006>
- Pereira CG, Falcão F, Bernard E (2022) One size doesn't fit all: Singularities in bat species richness and activity patterns in wind-energy complexes in Brazil and implications for environmental assessment. *Zoologia* 39: e21041. <https://doi.org/10.1590/s1984-4689.v39.e21041>
- Pliscoff P, Fuentes-Castillo T (2011) Representativeness of terrestrial ecosystems in Chile's protected area system. *Environmental Conservation* 38(3): 303–311. <https://doi.org/10.1017/S0376892911000208>

- R Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>
- Ramírez-Fráncel LA, García-Herrera LV, Losada-Prado S, Reinoso-Flórez G, Sánchez-Hernández A, Estrada-Villegas S, Lim BK, Guevara G (2022) Bats and their vital ecosystem services: A global review. *Integrative Zoology* 17(1): 2–23. <https://doi.org/10.1111/1749-4877.12552>
- Ransome RD (1971) The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. *Journal of Zoology (London, England)* 164(3): 353–371. <https://doi.org/10.1111/j.1469-7998.1971.tb01323.x>
- Reichard JD, Fellows SR, Frank AJ, Kunz TH (2010) Thermoregulation during flight: Body temperature and sensible heat transfer in free-ranging Brazilian Free-tailed Bats. *Physiological and Biochemical Zoology* 83(6): 885–897. <https://doi.org/10.1086/657253>
- Rodríguez-San Pedro A, Simonetti JA (2013) Foraging activity by bats in a fragmented landscape dominated by exotic pine plantations in central Chile. *Acta Chiropterologica* 15(2): 393–398. <https://doi.org/10.3161/150811013X679017>
- Rodríguez-San Pedro A, Simonetti JA (2014) Variation in search-phase calls of *Lasiurus varius* (Chiroptera: Vespertilionidae) in response to different foraging habitats. *Journal of Mammalogy* 95(5): 1004–1010. <https://doi.org/10.1644/13-MAMM-A-327>
- Rodríguez-San Pedro A, Allendes JL, Ossa G (2016) Lista actualizada de los murciélagos de Chile con comentarios sobre taxonomía, ecología, y distribución. *Biodiversity and Natural History* 2(1): 18–41.
- Rodríguez-San Pedro A, Chaperon PN, Beltrán CA, Allendes JL, Ávila FI, Grez AA (2018) Influence of agricultural management on bat activity and species richness in vineyards of central Chile. *Journal of Mammalogy* 99: 1495–1502. <https://doi.org/10.1093/jmammal/gyy121>
- Rodríguez-San Pedro A, Allendes JL, Beltrán CA, Chaperon PN, Saldarriaga-Córdoba MM, Silva AX, Grez AA (2020) Quantifying ecological and economic value of pest control services provided by bats in a vineyard landscape of central Chile. *Agriculture, Ecosystems & Environment* 302: 107063. <https://doi.org/10.1016/j.agee.2020.107063>
- Rodríguez-San Pedro A, Ávila FI, Chaperon PN, Beltrán CA, Allendes JL, Grez AA (2021) The Role of the Adjacent Habitat on Promoting Bat Activity in Vineyards: A Case Study from Central Chile. *Acta Chiropterologica* 23(1): 177–187. <https://doi.org/10.3161/15081109ACC2021.23.1.014>
- Rodríguez-San Pedro A, Allendes JL, Bruna T, Grez AA (2024) Species-specific responses of insectivorous bats to weather conditions in central Chile. *Animals (Basel)* 14(6): 860. <https://doi.org/10.3390/ani14060860>
- Ruczynski I, Barton KA (2020) Seasonal changes and the influence of tree species and ambient temperature on the fission-fusion dynamics of tree-roosting bats. *Behavioral Ecology and Sociobiology* 74(63): 1–8. <https://doi.org/10.1007/s00265-020-02840-1>
- Ruf T, Geiser F (2015) Daily torpor and hibernation in birds and mammals. *Biological Reviews of the Cambridge Philosophical Society* 90(3): 891–926. <https://doi.org/10.1111/brv.12137>
- Saldaña-Vázquez RA, Munguía-Rosas MA (2013) Lunar phobia in bats and its ecological correlates: A meta-analysis. *Mammalian Biology* 78(3): 216–219. <https://doi.org/10.1016/j.mambio.2012.08.004>

- Shapiro JT, Monadjem A, Röder T, McCleery RA (2020) Response of bat activity to land cover and land use in savannas is scale-season and guild-specific. *Biological Conservation* 241: 108245. <https://doi.org/10.1016/j.biocon.2019.108245>
- Speakman J, Thomas MD (2005) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (Eds) *Bat Biology*. University of Chicago Press, Chicago, 430–461.
- Swift SM (1980) Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology (London, England)* 190(3): 285–295. <https://doi.org/10.1111/j.1469-7998.1980.tb01428.x>
- van den Driessche R, Chatwin T, Mather M (2000) Habitat Selection by Bats in Temperate Old-Growth Forests. Clayoquot Sound. British Columbia. In: Darling LM (Ed.) *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk*. Volume One.
- Vásquez DA, Grez AA, Rodríguez-San Pedro A (2020) Species-specific effects of moonlight on insectivorous bat activity in central Chile. *Journal of Mammalogy* 101(5): 1356–1363. <https://doi.org/10.1093/jmammal/gyaa095>
- Vaughan N, Jones G, Harris S (1997) Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology* 34(3): 716–730. <https://doi.org/10.2307/2404918>
- Venegas-González A, Muñoz AA, Carpintero-Gibson S, González-Reyes A, Schneider I, Gipolou-Zúñiga T, Aguilera-Betti I, Roig FA (2023) Sclerophyllous forest tree growth under the influence of a historic megadrought in the Mediterranean ecoregion of Chile. *Ecosystems (New York, N.Y.)* 26(2): 344–361. <https://doi.org/10.1007/s10021-022-00760-x>
- Verboom B, Huitema H (1997) The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12(2): 117–125. <https://doi.org/10.1007/BF02698211>
- Voigt CC, Lewanzik D (2011) Trapped in the darkness of the night: Thermal and energetic constraints of daylight flight in bats. *Proceedings of the Royal Society of London: Biological Sciences* 278: 2311–2317. <https://doi.org/10.1098/rspb.2010.2290>
- Walsh A, Barclay R, McCracken G (2004) Designing bat activity surveys for inventory and monitoring studies at local and regional scales. In: Brigham R, Kalko E, Jones G, Parsons S, Lumpens H (Eds) *Bat Echolocation Research: tools, techniques and analysis*, Bat Conservation International, Austin, Texas.
- Webala PW, Craig MD, Law BS, Armstrong KN, Wayne AF, Bradley JS (2011) Bat habitat use in logged jarrah eucalypt forests of south-western Australia. *Journal of Applied Ecology* 48(2): 398–406. <https://doi.org/10.1111/j.1365-2664.2010.01934.x>
- Weinzettel J, Vačkář D, Medková H (2018) Human footprint in biodiversity hotspots. *Frontiers in Ecology and the Environment* 16(8): 447–452. <https://doi.org/10.1002/fee.1825>
- Weller TJ, Zabel CJ (2002) Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin* 30: 922–930.
- Zukal J, Berková H, Řehák Z (2005) Activity and shelter selection by *Myotis myotis* in the Kateřinská cave (Czech Republic). *Mammalian Biology* 70: 271–281. <https://doi.org/10.1016/j.mambio.2005.03.003>

Appendix 1

Table A1. Results of model selection on Generalized Linear Mixed Models predicting the activity of bats species according to predictor variables. Best models had the lowest AICc value and p-values are shown: * < 0.05; (.) ≤ 0.1.

Species	Intercept	Predictor variable coefficient			AICc	Delta	Weight
		Woody cover (%) at 100 m radius	Canopy cover (%) at 12 m transects	Distance to water (m)			
<i>T. brasiliensis</i>	1.98	–	–	-0.01*	63.6	0,00	0.49
	1.86	–	-0.03**	–	63.8	0.13	0.45
	2.27	-0.03	–	–	67.8	4.15	0.06
<i>M. arescens</i>	2.20	–	–	0.001	99.1	0.00	0.34
	2.24	–	0.002	–	99.2	0.08	0.33
	2.18	0.003	–	–	99.2	0.09	0.33
<i>L. varius</i>	2.1	–	-0.02 .	–	75.5	0.00	0.48
	2.6	–	–	-0.004	75.6	1.06	0.28
	1.9	-0.02	–	–	75.8	1.31	0.25
<i>L. villosissimus</i>	1.24	–	–	-0.006 .	60.1	0.00	0.51
	1.15	–	-0.01	–	61.0	0.98	0.31
	1.13	-0.01	–	–	62.1	2.07	0.18
<i>H. macrotus</i>	0.42	–	–	0.001	44.3	0.00	0.37
	0.68	–	-0.008	–	44.4	0.08	0.35
	0.05	-0.01	–	–	44.8	0.52	0.28
<i>H. montanus</i>	0.21	–	–	-0.003	38.5	0.00	0.4
	0.12	–	-0.006	–	39.0	0.51	0.3
	0.10	-0.004	–	–	39.2	0.73	0.3