



## Research Article

# Microclimatic drivers of winter bat activity in coast redwood forests

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### Abstract

Bats are among the least well-known mammals, particularly in terms of their behavior and activity patterns during the winter. Here, we use passive acoustic monitoring to overcome some of the challenges inherent in surveying cryptic forest bats during the wet season to quantify overwintering behavior for 11 species in California coast redwood forests under varying microclimates. Because different species are active at different forest heights, we also examined the effect of acoustic detector placement (treetop or ground level). Generalized linear mixed models were used to relate acoustic detection probability for 8 species to daytime and nighttime temperature, relative humidity, water vapor pressure, and detector placement. The results indicate that daytime maximum temperature best explained variation in nightly probability of detection, and temperature threshold at which bats were predicted to be detected varied considerably across species. By using more precise species detection methods, we were able to resolve significant differences in activity patterns between *Myotis yumanensis* and *M. californicus*, 2 species with similar acoustic signatures that are often lumped together. *Myotis californicus* was predicted to have a 50% probability of detection at maximum daytime temperature as low as 12.5 °C, whereas *M. yumanensis* was not predicted to have 50% detection probability until maximum daytime temperature was at least 22 °C, suggesting that *M. californicus* spends less time in torpor. Also, monitoring at the top of the canopy revealed 4 migratory species to be present in the ecosystem on significantly more monitoring nights than could be observed using conventional ground-based monitoring methods. Improving winter bat survey methods provides evidence that diverse bat species are more active in redwood forests during the winter than previously documented. This finding suggests that coastal forests could provide important winter bat habitat for both resident and migratory species.

**Key words:** acoustic monitoring, canopy research, Chiroptera, climate, hibernation, insectivorous bats, winter ecology.

Globally, the International Union for the Conservation of Nature (IUCN) is unable to determine population trends for over half of the 1,236 bat species assessed, and 18% of assessed bat species are classified as data deficient on the IUCN red list (Frick et al. 2020). This dearth of ecological information is especially troubling given that many bat populations are experiencing unprecedented mortality from novel threats such as white-nose syndrome (WNS) and wind turbine development (O’Shea et al. 2016; Frick et al. 2017; Cheng et al. 2021). It can be especially challenging to study bat populations in regions such as the western United States where bats do not aggregate in large groups during the winter because these populations elude conventional hibernacula counts (Weller et al. 2018). However, acoustic monitoring provides a useful tool for detecting evidence of species presence and activity levels essential for determining habitat use and the potential need for protection (Ford et al. 2011; Rodhouse et al. 2019; Perea et al. 2022).

Climatic factors are known to influence activity patterns, energetics, and population dynamics of temperate bats (Seidman and Zabel 2001; Fukui et al. 2006). There is some evidence from North Carolina, Washington State, and islands in the northeastern United States that bats are more active during the winter closer to the

coast than inland populations of the same species suggesting that coastal areas with mild and stable climates may provide important habitat for North American bat populations (Falxa 2007; Grider et al. 2016; Parker et al. 2020; Hoff 2023). Some migratory species, such as *Lasiurus cinereus* (Hoary Bat), migrate longitudinally to coastal forest regions, but it is unknown to what extent they stay active in winter habitat after migration (Cryan et al. 2014). For example, there is evidence that at least some individuals of this foliage-roosting species hibernate more than previously believed (Weller et al. 2016; Marín et al. 2021).

Coast redwood forests are restricted to a narrow coastal band in Northern California and are considered invaluable in terms of carbon sequestration and storage (Van Pelt et al. 2016). There is no evidence to date of WNS infection within the ecosystem. However, of the 13 bat species that occur in the coast redwood ecosystem, 6 have been impacted by WNS in other regions, and 3 additional species are carriers of the disease (White-Nose Syndrome Response Team 2023; Table 1). There are limited data on the winter behavior of bats in the coast redwood ecosystem. Prior acoustic monitoring studies have detected 6 species active during February, but these studies were only conducted at 2 old-growth forest properties and

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**Table 1.** Summary of key attributes of bat species present in the study area, including evidence of WNS elsewhere caused by *Pseudogymnoascus destructans* (Pd), migratory status, whether previous studies have documented species activity and/or roosting in the coast redwood ecosystem during winter (December–February), and total nights detected at ground level and at treetop during our study.

Species	Common name	Species code	WNS	Migratory	Previous activity detected	Previous roost detected	Ground nights detected	Treetop nights detected
<i>Antrozous pallidus</i>	Pallid Bat	Anpa	—	—	—	Yes <sup>5</sup>	4	0
<i>Corynorhinus townsendii</i>	Townsend's Big-eared Bat	Coto	Pd	—	—	Yes <sup>5</sup>	0	0
<i>Eptesicus fuscus</i>	Big Brown Bat	Epfu	S	—	—	—	16	12
<i>Lasiurus blossevillei</i>	Western Red Bat	Labl	—	Yes	Yes <sup>1</sup>	—	6	19
<i>Lasiurus cinereus</i>	Hoary Bat	Laci	—	Yes	Yes <sup>1,2</sup>	—	12	57
<i>Lasionycteris noctivagans</i>	Silver-haired Bat	Lano	Pd	Yes	Yes <sup>1,2,4</sup>	—	12	38
<i>Myotis californicus</i>	California Myotis	Myca	—	—	Yes <sup>1,3</sup>	Yes <sup>5</sup>	67	50
<i>Myotis evotis</i>	Long-eared Myotis	Myev	S*	—	—	Possibly <sup>5</sup>	7	0
<i>Myotis lucifugus</i>	Little Brown Bat	Mylu	S*	—	—	—	0	4
<i>Myotis thysanodes</i>	Fringed Myotis	Myth	S*	—	—	Possibly <sup>5</sup>	24	5
<i>Myotis volans</i>	Long-legged Myotis	Myvo	S*	—	—	December only <sup>5</sup>	0	0
<i>Myotis yumanensis</i>	Yuma Myotis	Myyu	S*	—	Yes <sup>1,3</sup>	—	25	21
<i>Tadarida brasiliensis</i>	Mexican Free-tailed Bat	Tabr	Pd	Yes	Yes <sup>1,2</sup>	—	19	78

Pd = nonsymptomatic to WNS but known to carry Pd; S = symptomatic to WNS; S\* = symptomatic to WNS and predicted to be highly susceptible based on Haase et al. (2021). References: <sup>1</sup>Heady and Frick (2001); <sup>2</sup>Kennedy et al. (2014); <sup>3</sup>Kennedy (2011); <sup>4</sup>Weller and Stricker (2012); <sup>5</sup>Armstrong et al. (2022). *Myotis evotis* and *M. thysanodes* were grouped during genetic analyses.

no data were taken earlier in the winter (December and January; Heady and Frick 2001; Kennedy et al. 2014). Four of these species are known to be migratory, and it is unknown to what extent these species remain resident in the redwood ecosystem during the winter (Kennedy et al. 2014). Furthermore, previous research on winter bat activity has primarily focused on mature forest habitat, but 93% of the redwood ecosystem is second-growth forest that has been disturbed by logging and mostly composed of younger trees (Burns et al. 2018). It is therefore unclear how these findings apply across most of the ecosystem.

The primary objective of this study was to evaluate microclimatic conditions that are associated with detecting winter bat activity in coastal forests. Bats in coast redwood forests primarily roost in trees including in hollows, bark crevices, and foliage (Zielinski and Gellman 1999; Mazurek and Zielinski 2004; Armstrong et al. 2022). Tree-roosting bats experience less stable environmental conditions than bats that hibernate in deep caves, and passive rewarming on warm winter days can lower the energetic costs of arousing from torpor (Boyles et al. 2006; Turbill and Geiser 2008). We predicted that nightly detection probability would be positively associated with temperature and negatively associated with relative humidity and water vapor pressure because bats would be more active under warmer and drier conditions when both arousal and flight are less energetically costly and insect prey are more likely to be available (Burles et al., 2009; Bender and Hartman 2015; Brooks et al. 2017). Because different species are adapted to foraging at different levels of forest habitat and conventional ground-based acoustic monitoring may fail to detect high-flying bat activity (Kalcounis et al. 1999; Plank et al. 2012; Agranat 2014; Kennedy et al. 2014), we surveyed bat activity at each study site at both ground level and treetop. This field research using acoustic monitoring technologies provides the first comprehensive baseline data on winter bat presence and activity patterns in California coast redwood forests.

## Materials and methods.

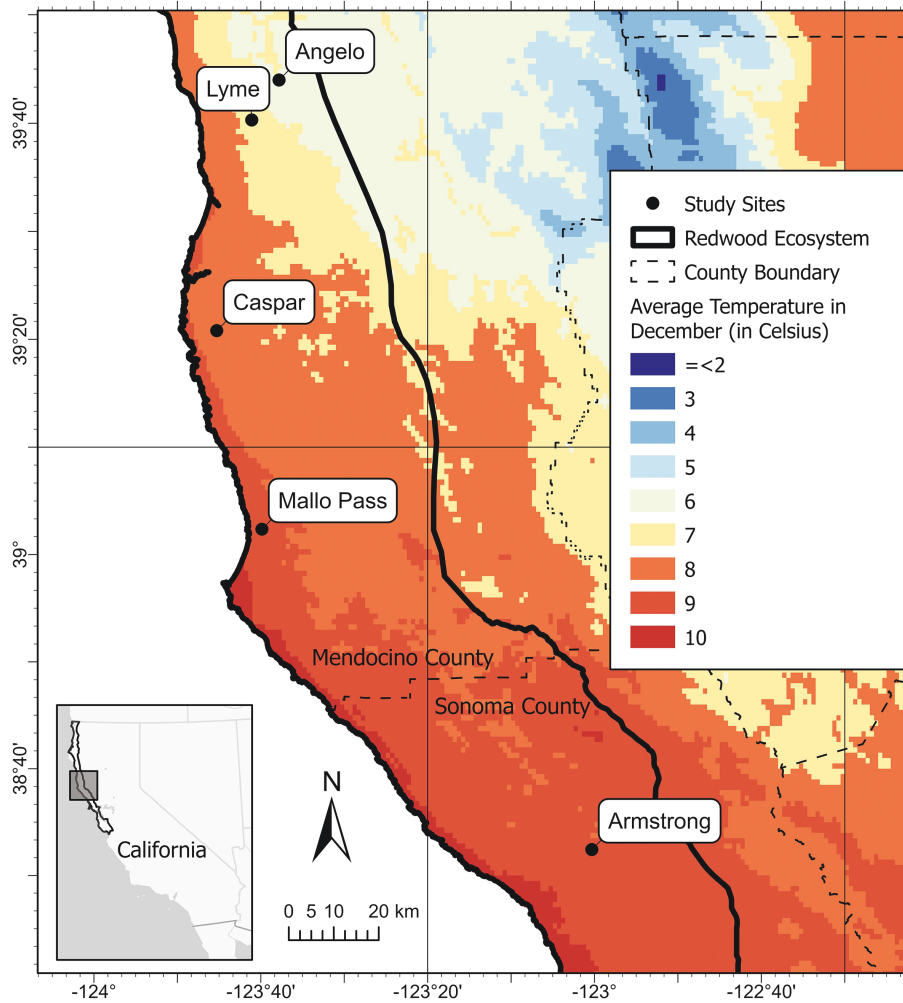
### Study sites.

We studied winter bat activity at 5 coast redwood forest sites in Mendocino and Sonoma Counties of Northern California (Fig. 1). This ecosystem is characterized as having Mediterranean climate with a dry season lasting up to 6 months followed by high levels of rainfall during the winter. Based on 30-year average climate data from the weather station closest to the study sites, located near the city of Fort Bragg (39.51°N, 123.76°W), December is normally the coldest and wettest month of the year, with a minimum temperature of 4.3 °C, maximum temperature of 10.8 °C, and monthly total precipitation of 220 mm (Palecki et al. 2021).

Study sites were selected to be representative of the mosaic of diverse forest management types of the redwood ecosystem, including 2 commercial timber properties (“Lyme” and “Mallo Pass”), Jackson Demonstration State Forest (“Caspar”), 1 state park (“Armstrong”), and a University of California natural reserve (“Angelo”). The most coastal study site (Mallo Pass) was located approximately 2 km from the coast, and the most inland study site (Angelo) was located approximately 15 km from the coast (Fig. 1). Each study site was located next to a stream channel to standardize detector placement across sites and to maximize the probability of detecting bat activity because insectivorous bats use stream corridors to drink, forage, and travel through forest habitat (Seidman and Zabel 2001; Fukui et al. 2006).

### Field data collection.

We monitored winter bat activity at fixed locations from 1 December 2019 to 29 February 2020 using Wildlife Acoustics Song Meter SM2BAT 384 kHz (SM2) with SMX-U1 omnidirectional microphones and SM4BAT (SM4) full-spectrum bat detectors with SMM-U2 omnidirectional microphones (Wildlife Acoustics Inc., Maynard, Massachusetts). One detector was placed at ground level at the



**Fig. 1.** Historical average temperature ( $^{\circ}\text{C}$ ) for December based on the WorldClim version 2.1 climate data for 1970 to 2000 at 30 second ( $\sim 1\text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017) with study sites located from 2 to 15 km of the coast.

edge of the riparian corridor and another detector was placed at the top of the highest nearby tree (within 50 m of the riparian corridor detector). The same model of detector (SM2 or SM4) was used at paired ground and treetop placements at each site. The microphones of ground-level detectors were elevated 3 to 4 m above the ground on telescopic poles. The microphones of treetop detectors were attached to telescopic poles and extended horizontally from the tree trunk along a branch to sample open-air fly space. Treetop microphone height was measured by dropping the weighted end of a tape measurer to an observer at ground level and ranged from 33 to 78 m (Table 2).

Each model of detector was deployed using the recommended settings for that model in California forest habitat and set to record from sunset to sunrise every other night. To record a sequence of bat calls as an individual bat pass, SM2 detectors were set to have a trigger window of 2 s and maximum trigger length of 5 s. SM4 detectors were set to have a minimum duration of 1.5 ms, trigger window of 3 s, and maximum trigger length of 15 s. During each monthly site visit, we recharged batteries, collected acoustic data, and reviewed the data to check equipment functionality. There were some issues with microphones ceasing to function or losing sensitivity, which seemed to be due to moisture entering the microphones. Monitoring nights when a detector malfunctioned were omitted from the analysis which led to differences in the number of detector nights per site (Table 2).

To relate bat activity to weather and microclimate, we monitored ambient temperature and relative humidity at each study site using iButton Hygrochron DS1923 sensors (Maxim Integrated Products Inc., San Jose, California). One sensor at each site was hung from vegetation near each ground-based detector and shielded from precipitation and sunlight by a plastic hood. The sensors sampled temperature ( $0.0625\text{ }^{\circ}\text{C}$  resolution) and relative humidity ( $0.04\%$  RH resolution) every 30 min.

### Species presence identification.

To determine bat species presence for each detector night, we used SonoBat bat call analysis software (“SonoBat,” Arcata, California) to identify recorded bat passes to species. We auto-classified bat passes to species using SonoBat version 4.2 with the Northwest California regional classifier. One researcher trained in bat call analysis (CLA) manually vetted the data by visually reviewing auto-classified call files for each detector night and confirming that there was at least 1 manually verified bat pass for each species that SonoBat had identified. If at least 1 bat pass was confidently verified, then we counted the species as “present” on that monitoring night at that detector location. We considered acoustic detection of species presence to be evidence that the species was active on that monitoring night.

After determining whether each species was detected as “present” or “not detected” on each detector night, we calculated the proportion of nights that each species was present at each of the 10

**Table 2.** Summary of detector nights and total bat passes confidently identified to species by study site and detector placement.

Site	Treetop mic height (m)	Detector model	Detector placement	Detector nights	Confident ID bat passes	Mean bat passes/night
Angelo	60.5	SM4	Ground	13	69	5.3
			Treetop	43	491	11.4
Armstrong	78	SM2	Ground	45	296	6.6
			Treetop	10	1,174	117.4
Caspar	49.5	SM2	Ground	38	52	1.4
			Treetop	26	206	7.9
Lyme	38	SM4	Ground	31	11	0.4
			Treetop	45	724	16.1
Mallo Pass	33	SM2	Ground	28	438	15.6
			Treetop	36	1,301	36.1

detector locations, as well as the proportion of nights it was detected out of all ground-detector nights and out of all treetop-detector nights. We examined proportions of total nights and ranges across study sites to compare winter bat activity by species, as well as to examine how much this varied across sites and detector heights.

### Weather and climate data analysis.

We analyzed iButton data recorded in the field at ground level to characterize daily and nightly temperature and relative humidity for each study site. We used R statistical analysis software (R Core Team 2023) with package `sunalc` (Theiurmel and Elmarhraoui 2022) to calculate sunset and sunrise times for each detector night based on the latitudinal and longitudinal coordinates of the field site. If iButton data were logged at or after sunrise and before sunset, then it was considered “daytime.” If data were logged at or after sunset and before sunrise, then it was considered “nighttime.” Even though the iButton sensors were shielded beneath a plastic hood, some logged relative humidity values were above 100%, which were erroneous values that result from the sensor being exposed to a wet environment. To correct this error, we adjusted these relative humidity values to be 100. Because relative humidity is dependent on temperature and not an absolute measure of ambient moisture, we derived a measure of actual water vapor pressure from field measurements of temperature and relative humidity, including the corrected values when relative humidity exceeded 100%. We performed calculations using the R package “humidity,” which provides functions for calculating water vapor measures from temperature and dewpoint (Cai 2019). The function “SVP” was used to first calculate saturation vapor pressure based on the Clausius–Clapeyron equation, and then the function “WVP2” was used to calculate partial water vapor pressure (Cai 2019). Finally, we calculated minimum, maximum, and mean values for both “nighttime” (referring to the monitoring night) and “daytime” (referring to the day preceding the monitoring night) for temperature, relative humidity, and water vapor pressure at each study site for each monitoring night date.

### Species presence models.

We developed species-specific generalized linear mixed models (GLMMs) for 8 species to relate microclimate explanatory variables to nightly detection of bat species presence. We used binomial distribution models with a logit-link function because this is appropriate for a binary outcome of nightly presence or nondetection. All statistical and model analyses were conducted using R version 4.3.2 (R Core Team 2023). We did not model 3 out of the 11 species observed due to a limited number of detections for *Antrozous*

*pallidus* (Pallid Bat), *Myotis evotis* (Long-eared Myotis), and *M. lucifugus* (Little Brown Bat).

Prior to running our initial models, we ran correlation tests of all microclimate variables (nighttime minimum humidity; nighttime minimum water vapor pressure; nighttime maximum, minimum, and mean temperature; daytime maximum, minimum, mean temperature) using the “`cor()`” function in R. A table of resulting correlation coefficients can be found in [Supplementary Data SD1](#). We found that temperature variables were strongly correlated with each other, which could distort model estimation (Dormann et al. 2013). We examined nighttime maximum temperature (“Night.Max.Temp”) to test the prediction that bats are more likely to be active at warmer temperatures when thermoregulatory costs of arousal and flight are lower and prey is more likely to be available. We also examined daytime maximum temperature (“Day.Max.Temp”) because it may be daytime environmental conditions that indirectly trigger arousal, and this variable represents the ambient temperature that bats experienced during the day preceding the monitoring night more accurately than daytime minimum temperature which may have occurred at sunrise. Because these 2 temperature variables were also highly correlated (correlation coefficient  $\rho = 0.84$ ; [Supplementary Data SD1](#)), we included these variables in separate models. To test the prediction that bats were more likely to be active on nights when relative humidity was lower, indicating drier weather that is more conducive to flight and foraging, we included the explanatory variable nighttime minimum relative humidity (“Night.Min.Humid”). Minimum relative humidity provides a measure of ambient moisture that is less sensitive to measurement errors that can occur when sensors become wet than mean or maximum humidity, and this variable had acceptable correlation coefficients to be able to include it with the temperature information ( $\rho = 0.091$  with nighttime maximum temperature and  $\rho = -0.31$  with daytime maximum temperature; Dormann et al. 2013). Because using relative humidity may confound ecological relationships between hibernating bats and ambient moisture (Kurta 2014), we also ran candidate models that included nighttime minimum water vapor pressure (“Night.Min.Vapor”) instead of nighttime minimum relative humidity as the humidity variable of interest. Detector placement (“Placement” factor with 2 levels: “ground” and “treetop”) was included as a fixed effect and study site (“Site” factor with 5 levels) was included as a random effect in all models (denoted as (1 | Site)). We examined 14 candidate models for each species ([Table 3](#)).

The “`glmer`” function was used from package `lme4` (Bates et al. 2021) and continuous variables were first standardized to a mean of 0 and standard deviation of 1. To test model fit, we first ran the full models that included the interaction of the relative humidity

variable with the daytime or nighttime temperature variable. Seven species models were fit without convergence issues using the default glmer() settings. The model for *L. blossevillii* (Western Red Bat) initially had model convergence issues, but this was resolved by setting the optimizer to “bobyqa” (Powell 2009). We tested fitted models for dispersion and residual diagnostics by using the DHARMA package (Hartig and Lohse 2021).

After confirming that there were no convergence issues with the full fitted models, we used function “model.sel” from package MuMIN (Bartoń 2022) to perform model selection. We ranked models by AIC corrected for small sample size (AICc) to assess which models best

explained nightly variation in bat presence and reported all models with  $\Delta AICc \leq 2$  as top models (Table 4). We examined the results of all top models to determine which variables had significant effects on species detection probability.

To predict when these species are most likely to be active during the winter, we used the “predict.merMod” function from package lme4 (Bates et al. 2021) to examine the effect of daytime maximum temperature (strongest explanatory variable from the GLMM analysis) on probability of species detection for both ground and tree-top detector placements. To generate new data values, we used the range of daytime maximum temperatures observed (4.1 °C to 21.8

**Table 3.** Set of candidate models developed to relate microclimate explanatory variables to nightly detection of bat species presence. Unless otherwise noted, all models include study site as a random effect “(1 | Site)” and detector placement “Placement” as a fixed effect.

Model	Microclimate variables
Null	Only includes (1   Site)
Placement	Only includes Placement + (1   Site)
RH	Night.Min.Humid
Vapor	Night.Min.Vapor
Day	Day.Max.Temp
Night	Night.Max.Temp
Day + RH	Day.Max.Temp + Night.Min.Humid
Night + RH	Night.Max.Temp + Night.Min.Humid
Day × RH	Day.Max.Temp + Night.Min.Humid + Day.Max.Temp × Night.Min.Humid
Night × RH	Night.Max.Temp + Night.Min.Humid + Night.Max.Temp × Night.Min.Humid
Day + Vapor	Day.Max.Temp + Night.Min.Vapor
Night + Vapor	Night.Max.Temp + Night.Min.Vapor
Day × Vapor	Day.Max.Temp + Night.Min.Vapor + Day.Max.Temp × Night.Min.Vapor
Night × Vapor	Night.Max.Temp + Night.Min.Vapor + Night.Max.Temp × Night.Min.Vapor

**Table 4.** Generalized linear mixed models with the lowest AICc for each species modeled.

Species	Model	K	LogLik	AICc	Delta	Weight
<i>E. fuscus</i> (Epfu)	Day + RH	5	-78.83	167.85	0	0.330
	Day × RH	6	-78.73	169.73	1.88	0.129
	Night	4	-80.81	169.75	1.902	0.128
<i>L. blossevillii</i> (Labl)	Day × Vapor	6	-70.01	152.28	0	0.635
<i>L. cinereus</i> (Laci)	Day	4	-117.8	243.73	0	0.361
	Day + RH	5	-117.21	244.61	0.883	0.232
	Day + Vapor	5	-117.42	245.04	1.309	0.187
<i>L. noctivagans</i> (Lano)	Day	4	-109.82	227.77	0	0.408
	Day + Vapor	5	-109.35	228.89	1.118	0.233
	Day + RH	5	-109.77	229.73	1.958	0.153
<i>M. californicus</i> (Myca)	Day	4	-182.99	374.11	0	0.388
	Day + RH	5	-182.91	376.02	1.916	0.149
<i>M. thysanodes</i> (Myth)	Night × Vapor	6	-66.80	145.87	0	0.435
<i>M. yumanensis</i> (Myyu)	Day × RH	6	-102.27	216.81	0	0.694
<i>T. brasiliensis</i> (Tabr)	Day + Vapor	5	-133.25	276.7	0	0.349
	Day	4	-134.44	277.02	0.319	0.298
	Day × Vapor	6	-133.14	278.56	1.86	0.138

Day + RH: Presence ~ Night.Min.Humid + Day.Max.Temp + Placement + (1 | Site); Day × RH: Presence ~ Night.Min.Humid + Day.Max.Temp + Night.Min.Humid × Day.Max.Temp + Placement + (1 | Site); Night: Presence ~ Night.Max.Temp + Placement + (1 | Site); Day × Vapor: Presence ~ Night.Min.Vapor + Day.Max.Temp + Night.Min.Vapor × Day.Max.Temp + Placement + (1 | Site); Day: Presence ~ Day.Max.Temp + Placement + (1 | Site); Day + Vapor: Presence ~ Night.Min.Vapor + Day.Max.Temp + Placement + (1 | Site); Night × Vapor: Presence ~ Night.Min.Vapor + Night.Max.Temp + Night.Min.Vapor × Night.Max.Temp + Placement + (1 | Site).

°C) and also included the mean observed daytime maximum temperature (10.2 °C). For the fitted model object, we used the model  $\text{Presence} \sim \text{Day.Max.Temp} + \text{Placement} + (1 | \text{Site})$ . Because the predict function is unable to return the standard error for the predicted values of models including random effects, we used function “bootMER” from package lme4 (Bates et al. 2021) to apply a bootstrapping approach and derive a 95% confidence interval from simulated predictions.

### Temperature thresholds for detection.

As a final step, we identified the range of daytime maximum temperatures at which species were predicted to have at least 0.50 probability of detection at either ground level or treetop and examined how often these temperatures normally occur across the study area. Daily maximum temperature values from the GridMET data set (Abatzoglou 2013) were retrieved to provide historical meteorological data. Specifically, we used the period from 1 January 2010 until 31 December 2020 for each of the 5 study site coordinates and filtered the data to only include winter months (January, February, and December). These data were filtered and combined for all 5 sites (4,965 total winter days) to calculate the average number of days per winter that maximum temperature was greater than or equal to temperature values from 11 °C to 22 °C, the range of maximum daytime temperature at which bats were detected during our study.

## Results

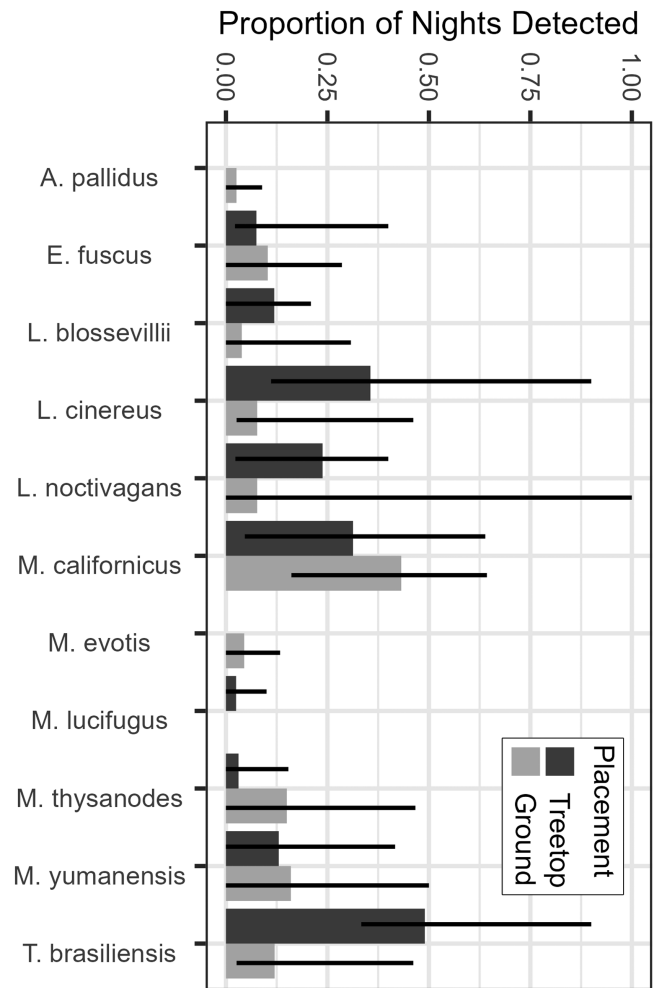
### Species presence results.

Data were collected over 315 detector nights at 10 locations. Total functional detector nights at each location ranged from 10 to 45 nights, with a mean of 32 nights (Table 2). The number of detector nights at a site did not correlate with the total number of bat passes detected or the mean number of bat passes detected per night. Total bat passes (4,762) were classified to the following 11 species: *A. pallidus*, *Eptesicus fuscus* (Big Brown Bat), *L. blossevillii*, *L. cinereus*, *Lasionycteris noctivagans* (Silver-haired Bat), *M. californicus* (California Myotis), *M. evotis*, *M. lucifugus*, *M. thysanodes* (Fringed Myotis), *M. yumanensis* (Yuma Myotis), and *Tadarida brasiliensis* (Mexican Free-tailed Bat). The only species known to occur in this study area during other seasons that were not detected during this winter study were *Corynorhinus townsendii* (Townsend’s Big-eared Bat) and *M. volans* (Long-legged Myotis; Andreozzi et al. 2024).

The proportion of nights for which bat activity was detected varied by species, study site, and detector placement (Fig. 2). Five species were detected more frequently at treetop and 6 were detected more frequently at ground level. The species detected most frequently by ground-level detectors was *M. californicus* (43% of total ground-detector nights averaged across all study sites; 31% of total treetop-detector nights). The species detected most frequently at treetop was *T. brasiliensis* (49% of total treetop-detector nights; 17% of total ground-detector nights). The most rarely detected species included *A. pallidus* (4 detector nights), *M. evotis* (7 detector nights), and *M. lucifugus* (4 detector nights). *Myotis lucifugus* was detected only at treetop at 4 study sites, and *A. pallidus* and *M. evotis* were detected only at ground level.

### Weather and climate data.

During the study, maximum daytime temperature ranged from 2.6 °C to 21.8 °C, with a mean of 10.2 °C across the 5 study sites. Maximum nighttime temperature ranged from 2.6 °C to 14.1 °C, with a mean of 8.6 °C. Minimum nighttime relative humidity ranged from 69.4% to 100%, with a mean of 98.5% relative humidity. January was the wettest month, with minimum nighttime relative



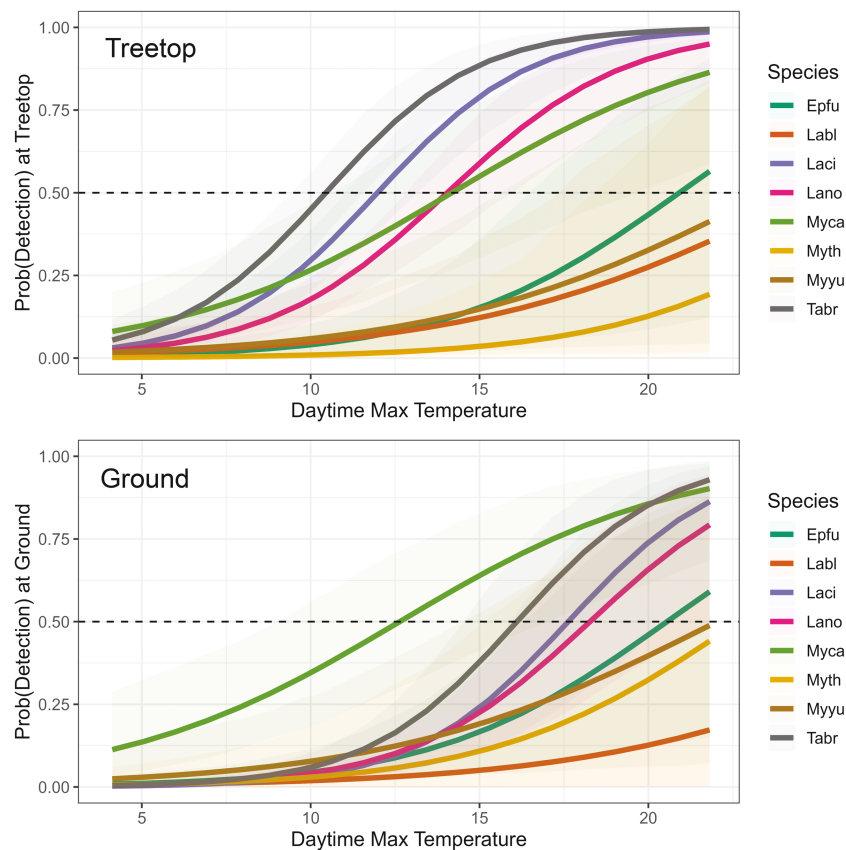
**Fig. 2.** Bars show the proportion of treetop-detector nights and the proportion of ground-detector nights that the species was detected (black lines are the range observed for proportion of nights detected across the 5 study sites).

humidity at 100% on all nights across the 5 study sites. Similar temporal trends in microclimate were observed across the 5 study sites, though greater variation between sites in relative humidity and maximum daytime temperature statistics was observed in February (see Supplementary Data SD2 for microclimate statistics data).

### Species presence model results.

Model selection results showed daytime maximum temperature was a better predictor of nightly variation in bat presence than nighttime maximum temperature (Table 4). Daytime maximum temperature was included in top-performing models for 7 species, and this variable had a significant positive effect ( $\text{Pr}(>|z|) < 0.05$ ) on probability of detecting presence for 6 of these species (Table 4; Fig. 3). The exception was *L. blossevillii*, for which the interaction between daytime maximum temperature and nighttime minimum water vapor pressure had a significant negative effect. Nighttime maximum temperature was included as an explanatory variable in a top-performing model for 2 species, *M. thysanodes* and *E. fuscus*, and this variable had a significant positive effect for both species (Table 4).

Relative humidity was included as an explanatory variable in top-performing models for 5 species (Table 4). Relative humidity had a significant positive effect on the probability of detecting *E. fuscus*, and the interaction between relative humidity and daytime



**Fig. 3.** Predicted probability of species detection is positively associated with daytime maximum temperature for all species when detector is at treetop (top) and at ground level (bottom) with 95% confidence intervals. Dashed line indicates temperature thresholds at which species have at least 0.50 predicted probability of being detected.

maximum temperature had a significant positive effect for *M. yumanensis* (Table 5). Actual water vapor pressure was included as an explanatory variable in top-performing models for 5 species (Table 5). This variable did not directly have a significant effect on the probability of detecting these species; however, the interaction of water vapor pressure and daytime maximum temperature had a significant negative effect on *L. blossevillii* (Table 5).

Placement of the monitoring equipment also had a significant effect on the probability of nightly detection for 5 species. *Lasiurus blossevillii*, *L. cinereus*, *L. noctivagans*, and *T. brasiliensis* were detected significantly more frequently at treetop, whereas *M. thysanodes* was detected significantly more frequently at ground level (Fig. 4; see Table 5 for significance values).

Modeling results showed that the probability of detecting a species at the mean winter daytime maximum temperature observed across the study sites (10.2 °C) varied from 0.01 to 0.47 depending on the species and detector placement (Fig. 5). For example, *T. brasiliensis* was predicted to have a probability of presence of 0.06 (95% confidence interval [CI] = 0.03 to 0.11) at ground level and 0.47 (95% CI = 0.34 to 0.58) at treetop.

The maximum daytime temperature at which species were predicted to have 50% probability of detection ranged from approximately 11 °C (*T. brasiliensis* at treetop) to approximately 22 °C (*M. yumanensis* at ground level), and most species had a low probability of being detected at ground level unless the temperature was at least 16 °C (Fig. 3). Based on historical meteorological data (2010 to 2020), maximum daytime temperature has reached or exceeded 16 °C on an average of 24 days per winter, and maximum daytime temperature has reached or exceeded 22 °C on an average of 2 days per winter (Fig. 6). The probability of detecting *M. thysanodes* or *L.*

*blossevillii* even following the highest daytime maximum temperature that we observed (22 °C) is estimated to be less than 50%.

## Discussion

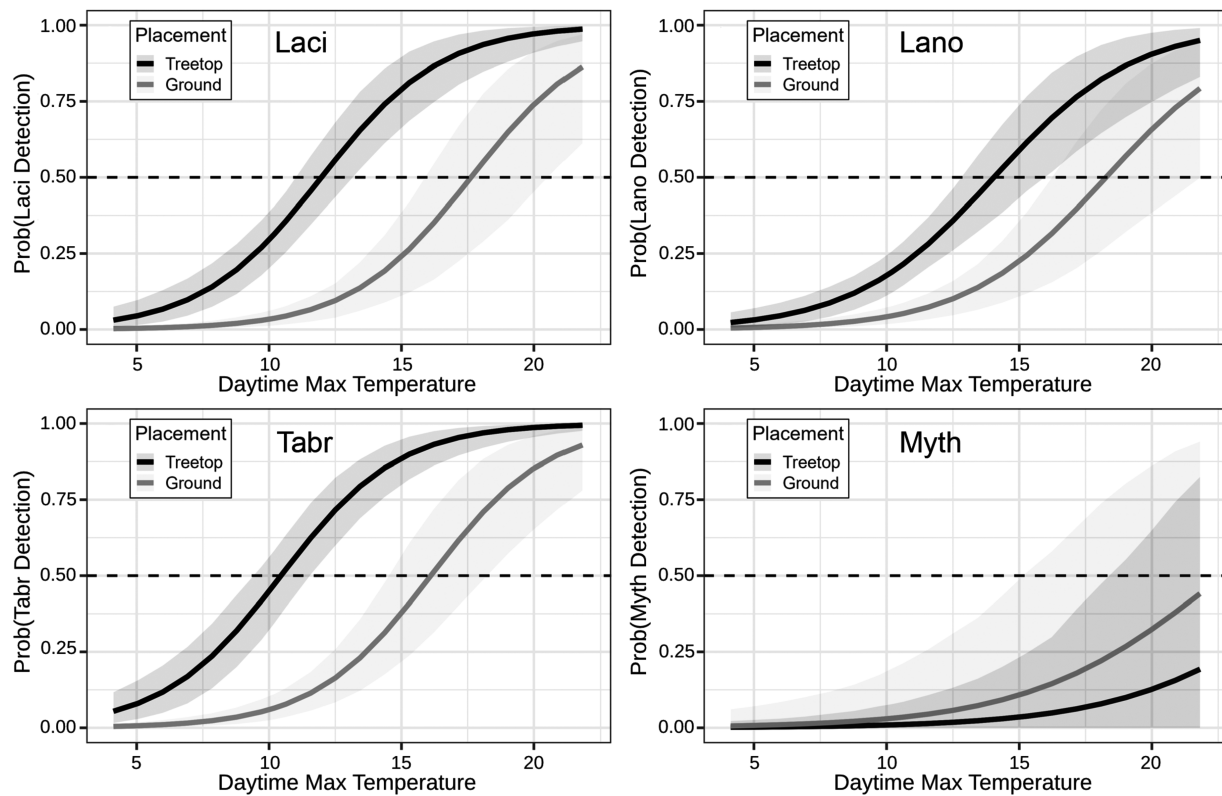
Acoustic monitoring confirmed that 11 of the 13 bat species known to occur in the coast redwood ecosystem are present during the winter season. The 2 species that were not detected, *C. townsendii* and *M. volans*, may also be present but hibernating or too rare to detect because other researchers have observed their winter roosts in the redwood ecosystem (Armstrong et al. 2022). *Corynorhinus townsendii* emits quiet calls that are difficult to detect with acoustic recorders, so it is also possible that this species was active but not detected (O'Farrell and Gannon 1999). We frequently detected 3 species (*L. cinereus*, *L. noctivagans*, and *T. brasiliensis*) known to migrate through the redwood ecosystem during the spring and fall (Kennedy et al. 2014), suggesting that at least some individuals of these species may overwinter in coast redwood forests. Identifying this winter presence in coastal California can inform conservation efforts because these are species that experience significant mortality across North America from collisions with wind turbines during migration (Arnett et al. 2016; American Wind Wildlife Institute 2020). We also detected 5 species (*E. fuscus*, *M. evotis*, *M. lucifugus*, *M. thysanodes*, and *M. yumanensis*) that have been impacted by WNS in other parts of their range (Table 1; White-Nose Syndrome Response Team 2023). By investigating the winter presence and activity patterns of these susceptible species prior to evidence of WNS infection in the ecosystem, our study provides information on overwintering behaviors and activity levels that can be referenced as a baseline for future impacts to these populations.

**Table 5.** Best GLMM model for nightly presence as shown in Table 4, only including fixed effects which had a significant effect ( $P < 0.05$ ) on species presence.

Species	Fixed effect	Estimate	SE	z-value	P-value
<i>E. fuscus</i> (Epfu)	Day	1.27	0.35	3.67	<0.001
	RH	1.03	0.51	2.00	0.045
<i>E. fuscus</i> (Epfu) <sup>a</sup>	Night	0.88	0.25	3.52	0.004
<i>L. blossevillii</i> (Labl)	Day × Vapor	-0.91	0.42	-2.17	0.030
	Placement	-0.59	0.27	-2.14	0.032
<i>L. cinereus</i> (Laci)	Day	1.26	0.21	5.98	<0.001
	Placement	-1.24	0.21	-5.91	<0.001
<i>L. noctivagans</i> (Lano)	Day	1.08	0.20	5.49	<0.001
	Placement	-0.80	0.20	-4.10	<0.001
<i>M. californicus</i> (Myca)	Day	0.69	0.16	4.39	<0.001
<i>M. thysanodes</i> (Myth)	Night	1.04	0.39	2.67	0.008
	Placement	0.62	0.30	2.04	0.041
<i>M. yumanensis</i> (Myyu)	Day	0.63	0.27	2.32	0.020
	Day × RH	0.96	0.41	2.35	0.019
<i>T. brasiliensis</i> (Tabr)	Day	1.22	0.20	5.96	<0.001
	Placement	-1.26	0.18	-6.96	<0.001

Day = maximum daytime temperature; RH = minimum nighttime relative humidity; Night = maximum nighttime temperature; Day × Vapor = the interaction of maximum daytime temperature and minimum nighttime water vapor pressure; Placement = detector placement (ground or treetop); Day × RH = the interaction of maximum daytime temperature and minimum nighttime relative humidity.

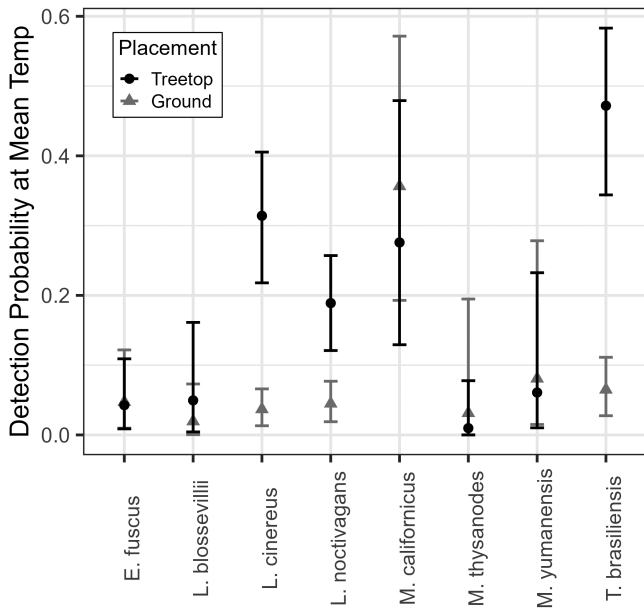
<sup>a</sup>The results of a second model ("Night") are included for *E. fuscus* because one of the top-performing models for this species had a unique variable with a significant effect that would not be reported if only results for the best-performing model were displayed.

**Fig. 4.** Predicted probability of presence for treetop detectors and ground-level detectors with 95% confidence intervals for 4 species for which detector placement had a significant effect: *Lasiurus cinereus* (Laci), *L. noctivagans* (Lano), *Tadarida brasiliensis* (Tabr), and *Myotis thysanodes* (Myth).

All species had a significantly greater probability of detection at higher temperatures. This observation corroborates other studies that have found ambient temperature to be positively associated

with winter bat activity outside of a hibernaculum (Klüg-Baerwald et al. 2016; Parker et al. 2020). Models including maximum daytime temperature were a better predictor of winter bat activity than

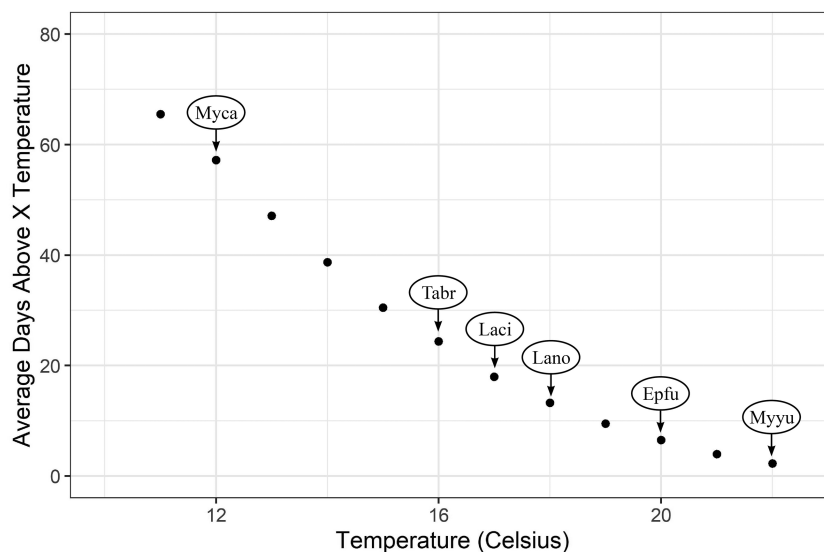
models including maximum nighttime temperature. This result may suggest that the mechanism driving winter bat activity is warm daytime environmental conditions indirectly triggering arousal from torpor. However, temperature variables were highly correlated and maximum daytime temperature influences the early evening temperature when bats are initially active. Despite over 50 years of research on why hibernating mammals show periodic arousals (e.g., Ransome 1971; Speakman and Racey 1989), the precise trigger for bat arousals is not clear. The contribution of environmental contributors to this trigger and the arousal mechanism also remains poorly known, including the extent to which passive rewarming is enabling tree-roosting bats to arouse and rehydrate or forage (Turbill and Geiser 2008).



**Fig. 5.** Predicted probability of detection with 95% confidence interval at treetop and ground level for each species at mean observed winter daytime maximum temperature (10.2 °C).

One application of our findings is that scientists and natural resource managers can optimize winter bat surveys to detect species presence by conducting acoustic monitoring on nights following warmer daytime temperatures. More precisely, most species are not predicted to be detected by conventional ground-level monitoring until maximum daytime temperature is at least 16 °C (Fig. 3). This temperature threshold is typically reached or exceeded for 18 days, on average, during the winter in the California North Coast redwood region (Fig. 6). Several species (*E. fuscus*, *L. blossevillii*, *M. thysanodes*, and *M. yumanensis*) are not likely to be detected by conventional ground-level monitoring until maximum daytime temperature is at least 20 °C, which has historically occurred at these sites on fewer than 10 days per winter. This means that these bat species have a very low probability of being detected during the winter unless acoustic monitoring is conducted on multiple nights during the warmest periods. Recognizing that species might be present but unobserved in winter habitat due to challenges of detecting rare, quiet, or less active species is also important for bat conservation.

Model results revealed that relative humidity had a significant positive effect on *E. fuscus*, and the interaction of relative humidity and maximum daytime temperature had a significant positive effect on *M. yumanensis*. The direction of this effect was contrary to our hypothesis that bats would be less active under wetter conditions because the thermoregulatory costs of flight are higher when wet, flying insects are less likely to be available, and fog and rain droplets can interfere with bat perception of echolocation calls (Burlles et al. 2009; Voigt et al. 2011; Geipel et al. 2019). One explanation for this is that these species are selecting to hibernate in habitat with higher relative humidity to reduce evaporative water loss during torpor (Thomas and Cloutier 1992; Perry 2013). However, when we included actual water vapor pressure in models as an absolute measure of moisture in the environment, this variable did not have a significant effect on species detection. On the other hand, the interaction between water vapor pressure and maximum daytime temperature did have a significant negative effect for 1 species, *L. blossevillii*. This finding suggests that this species is less active following warmer daytime temperatures on nights when there is more moisture in the air, which does corroborate our initial hypothesis.



**Fig. 6.** Average number of days per winter at which daytime maximum temperature historically reached or exceeded each integer value ranging from 11 °C to 22 °C across the 5 study site locations from 2010 to 2020. Species labels correspond to the approximate temperature threshold at which each species has a 0.50 predicted probability of detection at ground level. For species not shown (*Lasiurus blossevillii* and *Myotis thysanodes*), there are on average 0 days per winter at which these species have at least 0.50 predicted probability of detection (see Table 1 for species codes).

An alternative explanation for the positive association observed for *E. fuscus* and *M. yumanensis* is that relative humidity is higher closer to the coast where the influence of marine fog is more intense (Torregrosa et al. 2016). In addition to fog increasing ambient humidity closer to the coast, other coastal effects on air temperature also contribute to a milder and more stable environment, and this in turn allows for increased winter bat activity. Future research to explore the influence of relative humidity and water vapor pressure on bat activity would be good to conduct in interior forest types along a gradient of varying levels of valley fog. It is important to note that relative humidity was observed to be at or near saturation in our ecosystem on many monitoring nights. Future research should also explore the relationship between relative humidity and bat activity in drier environments, as well as collect data on localized nightly rainfall pattern and intensity to improve our understanding of the influence of precipitation on winter bat activity.

Detector placement had a significant effect in 5 of the 8 species models, with 4 species having a higher probability of detection at treetop and 1 species having a higher probability of detection at ground level. The species detected more frequently at treetop (*L. blossevillii*, *L. cinereus*, *L. noctivagans*, and *T. brasiliensis*) migrate through the redwood forest ecosystem during the spring and fall (Kennedy et al. 2014). Bat migration is generally poorly understood (McGuire et al. 2012). However, the high frequency of detection that we observed suggests that at least some individuals of these migratory populations may overwinter in the California North Coast redwood forests. Earlier studies (Gellman and Zielinski 1996; Weller and Stricker 2012; but see Kennedy et al. 2014) that relied on standard ground-level acoustic surveys, guano sampling of tree cavities, or mist netting from the forest floor may have underestimated the winter activity patterns that we were able to detect above the canopy. Also, *M. lucifugus* was exclusively detected at treetop, though it was too rarely detected to be modeled for detection probabilities. Our findings of higher detections at treetop for certain species is a pertinent reminder that standard ground-based monitoring may particularly underrepresent species that are adapted to flying and foraging in open, uncluttered environments (Menzel et al. 2005; Froidevaux et al. 2014; Andreozzi 2022).

Another key finding of our study was that the most frequently detected species was *M. californicus* with detections recorded for 43% of total ground-detector nights, whereas the similarly sized *M. yumanensis* was only detected on 16% of ground-detector nights. During the summer, both species are ubiquitous in the study area and approximately equal detection rates have been observed for the 2 species (Andreozzi et al. 2024). Modeling probability of detection suggests that the difference between these species is even more pronounced at colder temperatures (Fig. 3). At mean observed daytime maximum temperature (10.2 °C), *M. californicus* is predicted to have 0.36 probability of detected presence, whereas *M. yumanensis* is predicted to have 0.08 probability (Fig. 5). Because *M. californicus* and *M. yumanensis* emit similar high-frequency echolocation calls, these 2 species are often combined into 1 species group in acoustic studies that rely on autoclassification software to reduce the probability of misidentification (Schwab and Mabee 2014; Johnson et al. 2017). Our results suggest that this grouping obscures critical differences in species ecology. We document here that *M. californicus* continues to be active in the coast redwood ecosystem during the winter, suggesting that this may be a species that uses shallow torpor while roosting in trees in order to take advantage of warmer temperatures to rewarm passively and forage (Turbill and Geiser 2008). In contrast, *M. yumanensis* may either be present but less active during the winter or much of the summer population of this species may have migrated from the study area to hibernate elsewhere (e.g., in habitat with mines and caves).

In general, we discovered that bats were more active in coast redwood forests during the winter than previously documented, and all 8 species modeled had a higher probability of detection with increasing daytime maximum temperature. Future research should investigate whether bats in this ecosystem are able to successfully forage during these active periods, including sampling insect abundance to determine resource availability. Protecting coastal forest habitat in areas where bats are able to forage during the winter may be an effective conservation strategy to not only support local bat populations but also have wider implications for the conservation of species that are severely declining across North America.

## Supplementary data

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

**Supplementary Data SD1.**—Spearman's rank correlation results between microclimate variables.

**Supplementary Data SD2.**—Microclimate data results. Included plots show daily temperature and relative humidity statistics calculated from iButton data logged from December 2019 through February 2020 at the 5 study sites for (a) maximum daytime temperature, (b) maximum nighttime temperature, and (c) minimum nighttime relative humidity.

**Supplementary Data SD3.**—GLMM species presence model summary results for daytime temperature model. To predict the probability of species presence in relation to only daytime maximum temperature, we used the model: Presence ~ scale(Day.MaxTemp) + Placement + (1 | Site). Included are the model summary results for each of the 8 species modeled.

**Supplementary Data SD4.**—Predicted probability of detection for daytime temperature model results. Included plots show the predicted probability of detecting each species in relation to maximum daytime temperature based on the GLMM models used in Supplementary Data SD3.

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## Author contributions

CLA and AMM conceived and designed the study. CLA led the field investigation, data curation, and analysis. AMM contributed supervision throughout the study. CLA wrote the manuscript with editing by AMM.

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## Conflict of interest

None declared.

## Data availability

All associated data and code are currently provided as private-for-peer review at <https://figshare.com/s/0416666aba6458e43583>.

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