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By

Chelsea Lynn Andreozzi

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Committee in charge:

Professor Adina M. Merenlender, Chair
Professor Todd Dawson
Professor Arthur Middleton

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Abstract

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Anthropogenic climate change poses an existential threat to biodiversity that is compounded by habitat conversion, disease, and other disturbances. Understanding the ecological needs of sensitive species and identifying priority habitat is vital for wildlife conservation. However, there is growing recognition that the traditional conservation emphasis on protected areas is not sufficient to sustain biodiversity. We also need to understand the habitat value of working lands and incorporate these areas in conservation planning. My dissertation explores these themes through the lens of bats in the California coast redwood ecosystem. Bats are extremely sensitive to climate and habitat disturbance, making them useful indicators of ecosystem health. Coast redwood forests may provide critical habitat for bats under climate change because coastal effects on temperature and fog patterns buffer the coast from the extreme temperatures and drought experienced inland. Although 13 species of bats are found in coast redwood forests, bats are an especially elusive taxon and much about their basic ecology remains unknown. In addition to climate change, hibernating bat populations in North America are threatened by an emerging disease called white-nose syndrome. The disease has newly spread to the west coast, heightening the urgency to understand the ecology of western bat populations.

I conducted research on the factors shaping habitat suitability for bats across the coast redwood ecosystem, the environmental drivers behind species activity, and how species activity patterns shift seasonally. In Chapter 1, a large landscape field study demonstrates that both working forests and protected areas provide valuable summer bat habitat, but species vary significantly in their sensitivity to microclimate and forest habitat conditions. In Chapter 2, I complement conventional, ground-level acoustic survey techniques with canopy-level monitoring. This comparison reveals that treetop deployment methods significantly increase the detection of tree-roosting and migratory species across all forest management types and all seasons, revealing new insights about niche partitioning and seasonal bat activity. In Chapter 3, the results of winter bat activity surveys were examined in relation to microclimate, and daytime maximum temperature was determined to be the variable that best explained variation in nightly probability of bat acoustic presence. The winter data also show that 11 bat species are detected in coast redwood forests during the winter, but species vary in their winter activity levels, which may have ramifications for population susceptibility to white-nose syndrome. In the final chapter, the implications for bat conservation of laws and policies regulating California

timberland are discussed, and ways to improve protections are recommended based on scientific understanding of species ecology.

Taken together, the findings from this dissertation highlight the value of coastal forests as habitat for bat species threatened by climate change and emerging diseases. Species of special concern are present and active in coast redwood forests year-round. However, the presence of high-flying species was found to be systematically underestimated by ground-level survey methods, especially during the winter. Standard survey protocols may thus bias assessment of forest use and management impacts by primarily detecting species that make frequent use of understory habitat. The results of this research that includes year-round, canopy-level monitoring and advanced approaches to statistical analysis can be used to improve bat monitoring efforts and identify priority habitat to conserve bat species under global change.

For Edwin and Gwendolyn --

Because in thirty years,

I hope you, too, can stand

calmly at dusk

at forest streams

and watch bats fly.

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Introduction

Anthropogenic climate change is expected to be a major driver of global biodiversity loss in the 21st century (Thomas et al., 2004), and there is mounting evidence that climate-related local extinctions and population losses are already widespread (Ceballos et al., 2017; Wiens, 2016). As scientists and natural resource managers collaborate to develop guidelines for climate change adaptation, one increasingly important conservation strategy is to identify and protect habitat that is predicted to be resilient to climate change (Anderson et al., 2014; Balantic et al., 2021; Carroll and Noss, 2021; Morelli et al., 2016; Schmitz et al., 2015; Thorne et al., 2020). Such areas, known as climate refugia, may support the persistence of vulnerable species by providing refuge from unfavorable regional climates (Dobrowski, 2011). Locations that may function as climate refugia are generally identified by several characteristics, including relatively low degree of projected climatic change, availability of diverse microclimates, and accessibility of favorable future climatic conditions (Michalak et al., 2020). One of the few regions of North America that are predicted to offer all of these refugial characteristics is the California Coastal Mountain region (Michalak et al., 2020), which includes the coast redwood ecosystem.

Coast redwood forests grow in a narrow range within approximately 50 km of the California coast, coinciding with the area known as the ‘fog belt’ (Johnstone and Dawson, 2010; Torregrosa et al., 2016). This current range is considered to be a relict of a more extensive historic distribution, which suggests that the areas where coast redwoods (*Sequoia sempervirens*) persist are already functioning as climate refugia (McLaughlin et al., 2017). Underlying this resilience is the vital freshwater subsidy provided by marine fog (Dawson, 1998). Coast redwood trees and many of the understory plants of this ecosystem are adapted to absorb fog water directly through leaf surfaces as well as roots, which enables the plants to withstand the dry summers typical of California’s Mediterranean climate (Burgess and Dawson, 2004; Limm et al., 2009). Fog moisture also reduces evapotranspiration and increases streamflow (Fischer et al., 2009; Hiatt et al., 2012; Sawaske and Freyberg, 2015). Additionally, coastal effects on air temperature can result in dramatically cooler summer temperatures and significant microclimate heterogeneity over short distances inland from the coast (Daly et al., 2008, 2002). Coastal habitat may thus buffer regional biodiversity from the impacts of the rising temperatures and longer dry periods that are projected for California (Williams et al., 2015). However, previous research on the relationship between fog and the redwood ecosystem has largely focused on the flora. Little is known about how fog affects terrestrial fauna species distribution and behavior.

In this dissertation, I investigate the potential value of coast redwood forests as refugia for a diverse mammal taxon of high conservation concern, bats. At least thirteen species of insectivorous bats, including three California Species of Special Concern and seven additional “species at risk” (California Natural Diversity Database, 2021), inhabit coast redwood forests. Bats provide a valuable indicator for monitoring climate change impacts on ecosystems because of their sensitivity to environmental stresses, including their susceptibility to temperature, humidity, and precipitation patterns (Jones et al. 2009; Adams 2010; Adams and Hayes 2008). There is evidence that global bat populations are already being impacted by climate change (Adams, 2018; Sherwin et al., 2013), and species in drought-prone regions may be especially vulnerable (Adams and Hayes, 2008; Piccioli Cappelli et al., 2021). Consequently, the extreme drought episodes that are forecast to occur more frequently across western North America, including California, may impact bat reproductive success and lead to significant regional population declines (Adams, 2010; Amorim et al., 2015; Williams et al., 2015).

Another imminent threat to western bat populations is white-nose syndrome (WNS), a disease that takes hold during hibernation and has decimated eastern North American bat populations (Frick et al., 2010). The disease is caused by a fungal pathogen, *Pseudogymnoascus destructans*, which was first detected in New York in 2006. The pathogen causes bats to arouse more frequently during hibernation, depleting essential energy reserves at a time that they cannot successfully forage (Verant et al., 2014). This can cause mortality to affected bats, and it can also indirectly result in population declines by affecting reproductive success (Maslo et al., 2015). Certain species are more susceptible to WNS than others. In particular, three *Myotis* species have experienced mean declines of over 90% at affected hibernacula (Cheng et al., 2021), which has triggered the U.S. Fish & Wildlife Service to do species status assessments to consider whether these species qualify for additional protections under the Endangered Species Act. One of the species being reviewed is the little brown bat (*Myotis lucifugus*), a species found in coast redwood forests.

In 2016, the first case of WNS was detected on the west coast in Washington, heightening the urgency to understand the susceptibility of western North American bat populations and the implications for bat conservation (Lorch et al., 2016). In 2019, the causative fungal pathogen was detected in California, and scientists and wildlife managers believe that it is only a matter of time before California bat populations also show symptoms of the disease. However, there is some hope that bats in the coast redwood ecosystem may be more resilient to WNS than inland populations. Studies in other coastal ecosystems that experience mild winters have found that bats are more active along the coast than elsewhere in their range (Falxa, 2007; Grider et al., 2016; Parker et al., 2020). This suggests that these populations are not hibernating and might therefore be less susceptible to WNS (Grider et al. 2016). If coast redwood forests function as climate refugia and the bat populations living there are less susceptible to WNS, then populations in this habitat could become critical source populations for species persistence.

However, when evaluating the potential value of coast redwood forests as refugia for bats and other species, it is important to consider how this ecosystem still bears the scars of intense anthropogenic disturbance (Thornburgh et al., 2000). Of the 1.6 million acres of remaining coast redwood forest, 93% has been logged at least once and remnant old-growth persists in small, discontiguous patches (Burns et al., 2018; Cowan et al., 2017). Moreover, 35% of redwood forest continues to be managed by commercial timber companies (Burns et al., 2018). Forest condition and management practices will likely influence the capacity of the habitat to sustain biodiversity (Morelli et al., 2016). We need to better understand the habitat value of working forests. Working lands can provide vital accessory habitat and resources to wildlife, as well as connect otherwise isolated protected areas (Kremen and Merenlender, 2018). Working lands conservation might be particularly important for a mammal such as a bat which forages over long distances and seasonally shifts roosting habitat to meet thermoregulatory requirements. Because prior research has tended to focus on protected areas, especially mature forests, the influence of forest condition and management practices on bats in this ecosystem has been largely unexplored. My dissertation aims to address this gap by studying bat ecology across sites that reflect the diverse mosaic of public and private management types that compose the coast redwood ecosystem. In doing so, I hope to ultimately inform conservation planning for bats threatened by global change.

Dissertation Overview

Chapter 1 uses a large landscape approach to study the factors shaping habitat suitability for bats in the coast redwood ecosystem during the summer. I surveyed bats at twenty study sites spanning diverse management contexts across Mendocino and Sonoma Counties to investigate how bat community composition and activity patterns relate to stand maturity and forest management. Because bats are highly sensitive to microclimate, field sites were chosen that represent the coastal gradient of fog-influenced climate. Conventional passive acoustic monitoring techniques were used to sample bat activity at riparian corridors and recorded bat passes were identified to species. I ultimately use generalized linear mixed models to relate species activity to key environmental variables, including forest canopy height, temperature, humidity, historical climatic moisture deficit, and stream channel area in order to understand the species-specific drivers of summer bat activity.

Chapter 2 explores bat seasonal ecology and vertical niche partitioning at a subset of five sites from Chapter 1. Because acoustic monitoring is limited by detection range, conventional ground-based monitoring may fail to detect high-flying bat activity. This is especially true in the coast redwood ecosystem, which includes the tallest forests in the world. An earlier study found significant differences in species composition between ground-level and treetop (Kennedy et al., 2014). However, this study included only two old-growth trees in one state park (Kennedy et al., 2014), and it was unknown how these findings applied to other forests with different stand structure. I investigate this by monitoring for a full year with paired ground and treetop detectors in sites ranging from old-growth groves to commercial timber properties. Generalized additive models are used to examine how species activity varied by both detector location and Julian day. This study sheds light on seasonal presence and activity patterns, and this approach also reveals significant differences in habitat use that elude conventional monitoring.

In Chapter 3, I expand on the work of Chapter 2 by examining the microclimatic conditions under which bats are detected during the winter. Understanding winter bat behavior in the coast redwoods can critically inform understanding of how susceptible coastal populations will be to the emerging threat of white-nose syndrome. I apply generalized linear mixed models to relate detected species presence to ambient temperature and humidity variables. I also explore how the predicted probability of detecting a species varies with daytime maximum temperature and detector placement. These results can help guide how winter bat surveys are conducted to optimize detection of target species presence.

Scientific understanding of species' ecological needs will not promote biodiversity conservation unless it is also translated into management actions and legal provisions. In the last chapter, I review the laws and policies that either directly or indirectly protect wildlife on public and privately owned timberland in California and point to shortcomings in the protection for forest bats and other species whose conservation status are not well understood. I also discuss ways in which regulations could be improved to support the conservation of sensitive bat populations while still being compatible with economic development and other public values.

References

Adams, R.A., 2018. Dark side of climate change: species-specific responses and first indications of disruption in spring altitudinal migration in myotis bats. Journal of Zoology 304, 268–275. https://doi.org/10.1111/jzo.12526

Adams, R.A., 2010. Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91, 2437–2445. https://doi.org/10.1890/09-0091.1

Adams, R.A., Hayes, M.A., 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. Journal of Animal Ecology 77, 1115–1121. https://doi.org/10.1111/j.1365-2656.2008.01447.x

Amorim, F., Mata, V.A., Beja, P., Rebelo, H., 2015. Effects of a drought episode on the reproductive success of European free-tailed bats (Tadarida teniotis). Mamm Biol 80, 228–236. https://doi.org/10.1016/j.mambio.2015.01.005

Anderson, M.G., Clark, M., Sheldon, A.O., 2014. Estimating Climate Resilience for Conservation across Geophysical Settings. Conservation Biology 28, 959–970. https://doi.org/10.1111/cobi.12272

Balantic, C., Adams, A., Gross, S., Mazur, R., Sawyer, S., Tucker, J., Vernon, M., Mengelt, C., Morales, J., Thorne, J.H., Brown, T.M., Athearn, N., Morelli, T.L., 2021. Toward climate change refugia conservation at an ecoregion scale. Conservation Science and Practice 3, e497. https://doi.org/10.1111/csp2.497

Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): foliar uptake and prevention of dehydration. Plant, Cell & Environment 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burns, E.E., Campbell, R., Cowan, P.D., 2018. State of Redwoods Conservation Report. Save the Redwoods League.

Carroll, C., Noss, R.F., 2021. Rewilding in the face of climate change. Conservation Biology 35, 155–167. https://doi.org/10.1111/cobi.13531

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114, E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Cheng, T.L., Reichard, J.D., Coleman, J.T.H., Weller, T.J., Thogmartin, W.E., Reichert, B.E., Bennett, A.B., Broders, H.G., Campbell, J., Etchison, K., Feller, D.J., Geboy, R., Hemberger, T., Herzog, C., Hicks, A.C., Houghton, S., Humber, J., Kath, J.A., King, R.A., Loeb, S.C., Massé, A., Morris, K.M., Niederriter, H., Nordquist, G., Perry, R.W., Reynolds, R.J., Sasse, D.B., Scafini, M.R., Stark, R.C., Stihler, C.W., Thomas, S.C., Turner, G.G., Webb, S., Westrich, B.J., Frick, W.F., 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35, 1586–1597. https://doi.org/10.1111/cobi.13739

Cowan, P., Burns, E.E., Campbell, R., 2017. A GIS approach to identifying the distribution and structure of coast redwood across its range.

Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L., Pasteris, P., 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22, 99–113. https://doi.org/10.3354/cr022099

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28, 2031–2064. https://doi.org/10.1002/joc.1688

Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476–485. https://doi.org/10.1007/s004420050683

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Falxa, G., 2007. WINTER FORAGING OF SILVER-HAIRED AND CALIFORNIA MYOTIS BATS IN WESTERN WASHINGTON. nwnt 88, 98–100. https://doi.org/10.1898/1051-1733(2007)88[98:WFOSAC]2.0.CO;2

Fischer, D.T., Still, C.J., Williams, A.P., 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. Journal of Biogeography 36, 783–799. https://doi.org/10.1111/j.1365-2699.2008.02025.x

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M., Kunz, T.H., 2010. An Emerging Disease Causes Regional Population Collapse of a Common North American Bat Species. Science 329, 679–682.

Grider, J.F., Larsen, A.L., Homyack, J.A., Kalcounis-Rueppell, M.C., 2016. Winter Activity of Coastal Plain Populations of Bat Species Affected by White-Nose Syndrome and Wind Energy Facilities. PLOS ONE 11, e0166512. https://doi.org/10.1371/journal.pone.0166512

Hiatt, C., Fernandez, D., Potter, C., 2012. Measurements of Fog Water Deposition on the California Central Coast. Atmospheric and Climate Sciences 02, 525–531. https://doi.org/10.4236/acs.2012.24047

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. PNAS 107, 4533–4538. https://doi.org/10.1073/pnas.0915062107

Kennedy, J.-P., Sillett, S.C., Szewczak, J.M., 2014. Bat Activity Across the Vertical Gradient of an Old-Growth Sequoia sempervirens Forest. Acta Chiropterologica 16, 53–63. https://doi.org/10.3161/150811014X683264

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science. https://doi.org/10.1126/science.aau6020

Limm, E.B., Simonin, K.A., Bothman, A.G., Dawson, T.E., 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Lorch, J.M., Palmer, J.M., Lindner, D.L., Ballmann, A.E., George, K.G., Griffin, K., Knowles, S., Huckabee, J.R., Haman, K.H., Anderson, C.D., Becker, P.A., Buchanan, J.B., Foster, J.T., Blehert, D.S., 2016. First Detection of Bat White-Nose Syndrome in Western North America. mSphere 1, e00148-16. https://doi.org/10.1128/mSphere.00148-16

Maslo, B., Valent, M., Gumbs, J.F., Frick, W.F., 2015. Conservation implications of ameliorating survival of little brown bats with white-nose syndrome. Ecological Applications 25, 1832–1840. https://doi.org/10.1890/14-2472.1

McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. Glob Change Biol 23, 2941–2961. https://doi.org/10.1111/gcb.13629

Michalak, J.L., Stralberg, D., Cartwright, J.M., Lawler, J.J., 2020. Combining physical and species-based approaches improves refugia identification. Frontiers in Ecology and the Environment 18, 254–260. https://doi.org/10.1002/fee.2207

Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., Beissinger, S.R., 2016. Managing Climate Change Refugia for Climate Adaptation. PLOS ONE 11, e0159909. https://doi.org/10.1371/journal.pone.0159909

Parker, K.A., Jr., Li, H., Kalcounis-Rueppell, M.C., 2020. Species-specific environmental conditions for winter bat acoustic activity in North Carolina, United States. Journal of Mammalogy 101, 1502–1512. https://doi.org/10.1093/jmammal/gyaa133

Piccioli Cappelli, M., Blakey, R.V., Taylor, D., Flanders, J., Badeen, T., Butts, S., Frick, W.F., Rebelo, H., 2021. Limited refugia and high velocity range-shifts predicted for bat communities in drought-risk areas of the Northern Hemisphere. Global Ecology and Conservation 28, e01608. https://doi.org/10.1016/j.gecco.2021.e01608

Sawaske, S.R., Freyberg, D.L., 2015. Fog, fog drip, and streamflow in the Santa Cruz Mountains of the California Coast Range. Ecohydrol. 8, 695–713. https://doi.org/10.1002/eco.1537

Schmitz, O.J., Lawler, J.J., Beier, P., Groves, C., Knight, G., Boyce, D.A., Bulluck, J., Johnston, K.M., Klein, M.L., Muller, K., Pierce, D.J., Singleton, W.R., Strittholt, J.R., Theobald, D.M., Trombulak, S.C., Trainor, A., 2015. Conserving Biodiversity: Practical Guidance about Climate Change Adaptation Approaches in Support of Land-use Planning. Natural Areas Journal 35, 190–203. https://doi.org/10.3375/043.035.0120

Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2013. The impact and implications of climate change for bats. Mammal Review 43, 171–182. https://doi.org/10.1111/j.1365-2907.2012.00214.x

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. https://doi.org/10.1038/nature02121

Thornburgh, D.A., Noss, R.F., Angelides, D.P., Olson, C.M., Euphrat, F., Welsh, H.H., 2000. Managing redwoods. Pages 229-261 in R.F. Noss, ed., The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Covelo, California.

Thorne, J.H., Gogol-Prokurat, M., Hill, S., Walsh, D., Boynton, R.M., Choe, H., 2020. Vegetation refugia can inform climate-adaptive land management under global warming. Frontiers in Ecology and the Environment 18, 281–287. https://doi.org/10.1002/fee.2208

Torregrosa, A., Combs, C., Peters, J., 2016. GOES-derived fog and low cloud indices for coastal north and central California ecological analyses. Earth and Space Science 3, 2015EA000119. https://doi.org/10.1002/2015EA000119

Verant, M.L., Meteyer, C.U., Speakman, J.R., Cryan, P.M., Lorch, J.M., Blehert, D.S., 2014. White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. BMC Physiology 14, 10. https://doi.org/10.1186/s12899-014-0010-4

Wiens, J.J., 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLOS Biology 14, e2001104. https://doi.org/10.1371/journal.pbio.2001104

Williams, A.P., Seager, R., Abatzoglou, J.T., Cook, B.I., Smerdon, J.E., Cook, E.R., 2015. Contribution of anthropogenic warming to California drought during 2012-2014: GLOBAL WARMING AND CALIFORNIA DROUGHT. Geophysical Research Letters 42, 6819–6828. https://doi.org/10.1002/2015GL064924

Chapter 1:

Influence of climate and forest management on summer bat activity in coastal forests

Abstract

As biodiversity is increasingly threatened by climate change, it is critical to understand the factors shaping habitat suitability for sensitive species. Forest bats are a taxon of high conservation concern, and their sensitivity to climate and habitat disturbance makes them a useful bioindicator of ecosystem health. At least 13 species of insectivorous bats inhabit coast redwood forests, an ecosystem containing some of the world's tallest and oldest trees that has also experienced widespread anthropogenic disturbance. However, the mechanisms behind bat distribution patterns in this ecosystem are largely unknown. I used passive acoustic monitors to investigate how microclimate and forest structure influence bat species activity across a large landscape. My 20 study sites span a coastal gradient of fog-influenced climate and forest management types, including working forests and protected areas. I predicted that bat activity would be higher closer to the coast, where temperatures are more stable and more moisture is available. I also predicted that bat activity would be higher in mature forests where roosting habitat is more available. Generalized linear mixed models were used to relate species activity to climate and forest habitat variables. Contrary to my hypotheses, summer bat activity for six species was positively associated with warmer nighttime temperature, and two species had lower rates of activity with higher humidity. This suggests that habitat suitability within the coast redwood ecosystem may be driven more by selection for optimal foraging conditions than refuge from warming temperatures and drought. Only three of the species examined were positively associated with canopy height, though that is likely because I studied bat activity based on echolocation calls and not roosting behavior. Twelve of the thirteen regionally present bat species were regularly detected in young, commercial timberland stands, signifying the importance of integrating working forests into conservation planning for bats.

1. Introduction

As climate change existentially threatens global biodiversity, scientists and natural resource managers are striving to understand how species will be affected and how impacts might be mitigated (Cross et al., 2013; Schmitz et al., 2015; Thurman et al., 2021). Many species are already shifting their distributional ranges or phenological behaviors in response to climate change (Adams, 2018; Chen et al., 2011; Hitch and Leberg, 2007; Moreno-Rueda et al., 2012; Moritz et al., 2008; Stepanian and Wainwright, 2018). However, the ability of a species to remain within its climatic niche is highly dependent on its dispersal abilities, the velocity of climate change, and habitat connectivity (Keeley et al., 2018; Loarie et al., 2009; Robillard et al., 2015). Populations that are unable to disperse to suitable habitat or otherwise adapt to tolerate changed conditions may face significant range contractions or extirpation (Freeman et al., 2018; Piccioli Cappelli et al., 2021; Román-Palacios and Wiens, 2020).

One emerging conservation strategy is to identify and protect habitat with high natural resilience to climate change (Anderson et al., 2014; Balantic et al., 2021; Carroll and Noss, 2021; Morelli et al., 2016; Schmitz et al., 2015). Such areas, known as climate refugia, facilitate the persistence of species, including both flora and fauna, by providing favorable local climate conditions that buffer against unfavorable regional climates and extreme weather events (Dobrowski, 2011). The capacity of an area to function as a refugium is associated with certain factors, including environmental stability, microclimate heterogeneity, size, and accessibility (Keppel et al., 2015). Additionally, human activities that modify habitat or ecosystem processes can affect refugial capacity (Rojas et al., 2021).

Coast redwood forests may serve as important refugia for California biodiversity threatened by rising temperatures and longer dry periods. Coastal effects on air temperature buffer the coast redwood range against extreme weather events and contribute to a high degree of environmental stability year-round, while also creating microclimate heterogeneity over short distances from the coast (Daly et al., 2008). Fog drip also provides a vital freshwater resource for biota and reduces both evapotranspiration and streamflow decline (Hiatt et al., 2012; Fischer et al., 2009; Sawaske & Freyberg, 2015). Fog will likely play a key role in the resilience of California’s landscape to climate change; however, little is known about how fog affects terrestrial fauna species distribution and behavior.

I investigated the habitat value of the coast redwood ecosystem for bats, a diverse mammal taxon that is recognized as a useful bioindicator (Jones et al., 2009; Russo et al., 2021). Global bat populations are increasingly impacted by climate change (Adams, 2018; Sherwin et al., 2013). Species in high-drought regions, including Western North America, may be especially at risk (Adams and Hayes, 2008; Piccioli Cappelli et al., 2021). In part this is because bats experience high rates of evaporative water loss even when roosting (Studier et al., 1970), and their reproductive success can decline dramatically when water sources drop below a critical threshold (Adams, 2010). Severe drought events may also affect the reproductive success of insectivorous bats by reducing prey resources (Amorim et al., 2015). There is evidence from other ecosystems that climate refugia may effectively protect bats from the impacts of climate change (Law et al., 2018; Loeb and Winters, 2013). However, even within sympatric bat communities, responses to climate change are expected to be highly species-specific (Linton and Macdonald, 2018), and it is imperative that we understand the factors driving habitat suitability for individual species.

Forest structure and silviculture treatment are also known to affect bat activity in species-specific ways (Dodd et al., 2012; Erasmy et al., 2021; Morris et al., 2010; Wright et al., 2021). Of the 1.6 million acres of remaining coast redwood forest, 93% has been logged at least once (Burns et al., 2018; Cowan et al., 2017). The relict old-growth is scattered across 20,000 patches, with half of the patches less than 30 acres in size (Burns et al., 2018). Furthermore, 35% of redwood forest continues to be managed by commercial timber companies, while an additional 37% is owned by small private landowners and also considered unprotected (Burns et al., 2018). Most bat research in the coast redwood forests has focused on protected areas, especially mature forests, so the influence of forest condition and management practices on bats in this ecosystem is largely unknown.

To address this gap, I used a large landscape study approach to investigate how forest structure and microclimate influence bat activity across the North Coast redwood forest ecosystem. I specifically examined how species presence and activity levels vary with: (i) temperature and humidity patterns influenced by coastal fog, and (ii) stand maturity associated with forest management. I predicted that during the summer when regional temperatures are highest, bat activity would be higher in high-fog, coastal study sites because habitat with cooler temperatures and high humidity reduces evaporative water loss. I also hypothesized that bat activity would be higher in more mature forests because these areas offer more roosting habitat (Zielinski and Gellman, 1999a). Because bat activity has been found to be higher at larger streams in the redwood ecosystem (Seidman and Zabel, 2001), I also account for differences in stream area in my analysis. By elucidating the species-specific drivers of bat activity, I ultimately aim to inform conservation planning for bat populations threatened by global change.

2. Methods

2.1 Study Species

At least thirteen species of bats, including three California Species of Special Concern and seven additional "species at risk" (California Natural Diversity Database, 2021), inhabit coast redwood ecosystems. All species present are insectivorous, though their ecology varies significantly, and species are differently adapted to foraging in cluttered, edge or open space habitat depending on their morphology (Denzinger and Schnitzler, 2013). At least ten of these species are known to roost in redwood basal hollows, which form over centuries of fire scarring and thus are only found in old growth trees (Armstrong, 2021; Fellers and Pierson, 2002; Mazurek and Zielinski, 2004; Zielinski and Gellman, 1999a). Bats also roost in other tree cavities and bark crevices, and at least two species roost in foliage (Kunz and Fenton, 2005).

2.2 Study Area

To investigate across the two key environmental variables: fog-influenced climate and forest management type, I paired available spatially explicit data with ground-truthing to select twenty study sites in the North Coast redwood forest ecosystem. I first used ArcGIS to examine fog and low cloud cover (FLCC) digital maps derived from decadal satellite data for the California coast (Torregrosa et al., 2016). Fog intensity was calculated as mean FLCC hours per day averaged over nine summer seasons (Torregrosa et al., 2016). This layer was overlaid on a statewide vegetation data map ("Vegetation (fveg) - CAL FIRE FRAP [ds1327] GIS Dataset," n.d.) that I masked for redwood habitat. I also added to the map property boundaries for California protected areas (CPAD 2016a, Green Info Network 2016) and the property boundaries of major forest landowners in the region. From this map, I identified both protected properties and working forest properties in high fog and low fog zones. I then added a stream layer that I used to identify specific riparian corridor locations as potential study sites for selected properties.

After identifying potential study sites, I reached out to the landowners or appropriate land managers to discuss my interest in conducting research on their property and request access permissions. For public landowners, there was typically an established application process for requesting research permits. For private landowners, there was often little precedent of independent conservation research on their land, and it was important to take steps to not only obtain entry permissions but to ensure a successful partnership throughout the study (Hilty and Merenlender, 2003). I provided all landowners with an overview of the study objectives and study design. I asked for their feedback on the proposed monitoring locations and for advice on additional locations to consider. Both public and private land managers were interested in receiving research results, so I offered to share with each property manager species monitoring reports for their property, as well as ultimate study findings. In some cases, these species presence reports were especially valuable because no previous bat acoustic monitoring had been conducted on the property. All contacted landowners were receptive of my interest in researching bats on their properties. For those who had liability concerns, I sent documentation from my university providing proof of liability insurance coverage. Once contracts were signed or permits otherwise issued, I visited each study site to assess whether the quality of both the redwood habitat and the riparian corridor were in fact suitable for my study design.

I ultimately selected five study sites in Mendocino and Sonoma Counties that best spanned High Fog and Low Fog and Mature/Protected Forest and Young/Working Forest. These twenty sites represent different ownership types, ranging from public and private reserves to commercial timberland and one small family ownership (see Figure 1). It should be noted that I regarded three sites at the Jackson Demonstration State Forest as mature forest study sites because even though parts of the 48,652-acre property are actively managed for timber production, my study sites were located in areas with remnant old-growth trees. Each study site was located at least 5 km apart from its nearest neighbor and on an independent stream to ensure independent sampling of bat activity.

While the entire region is characterized by a Mediterranean climate, this study design enabled me to capture the significant microclimate heterogeneity that occurs within short distances of the coast. The climate of the highest-fog, coastal study sites is best represented by the thirty-year (1991-2020) normal weather data from the Fort Bragg 5 N weather station (39.51ºN, 123.76ºW), whereas the climate of the lowest-fog, inland study sites is represented by the Ukiah municipal airport weather station (39.13ºN, 123.20ºW) (National Centers for Environmental Information, U.S. Climate Normals). At Fort Bragg station, thirty-year normal maximum and minimum temperatures for June were 63.0ºF and 47.3ºF, respectively; for July, 65.0ºF and 49ºF; and for August, 65.2ºF and 49.7ºF. In contrast, in Ukiah, thirty-year normal maximum and minimum temperatures for June were 85.5ºF and 52.4ºF, respectively; for July, 94.0ºF and 56.1ºF; and for August, 93.5ºF and 54.8ºF.

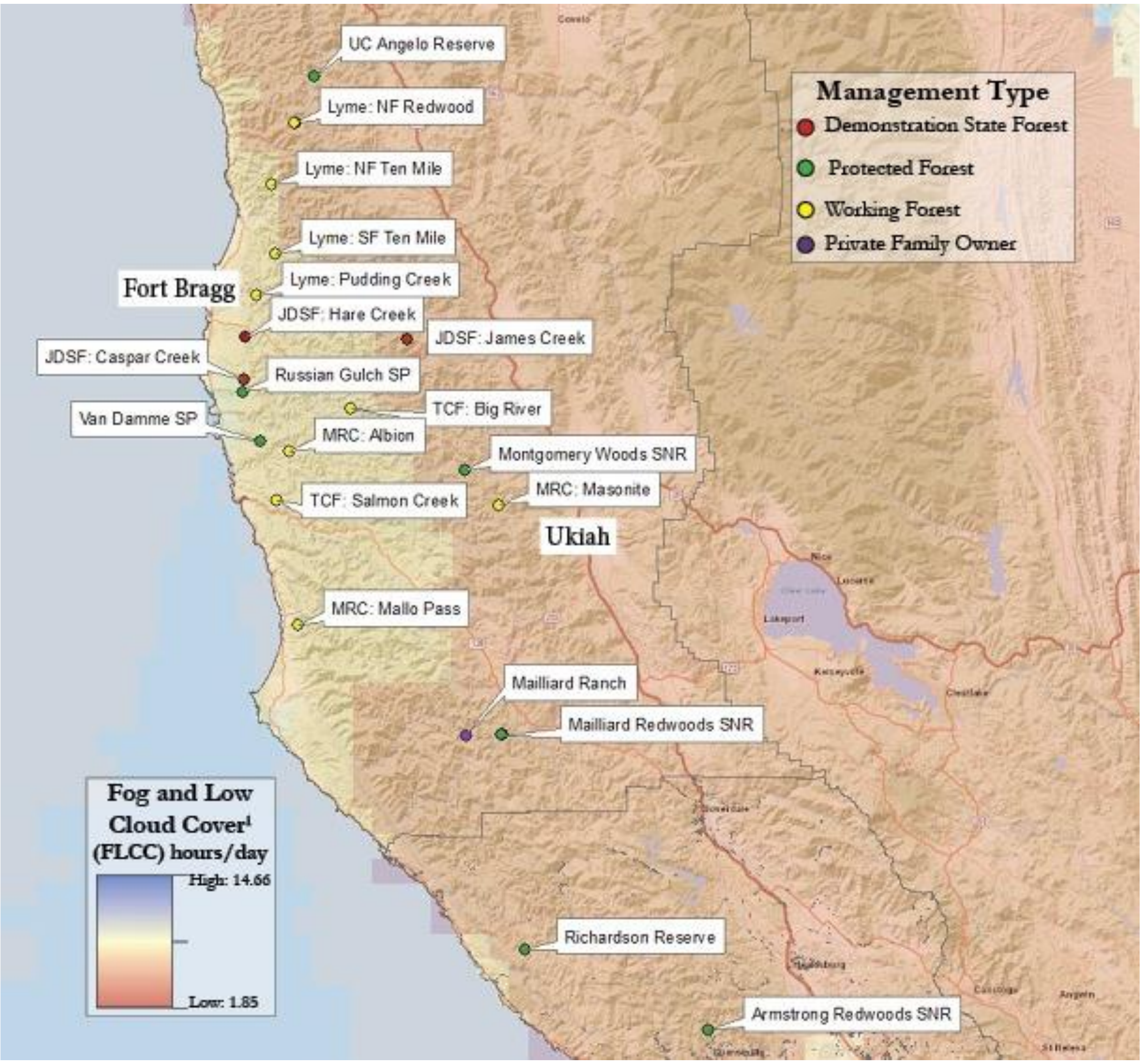


Figure 1: Study area in northern California representing a gradient of fog-related climate and different forest management types, including mature, protected forests and young, working forests in both public and private ownership.

2.3 Acoustic Sampling

I conducted acoustic surveys of bat activity during summer 2019 (June 24 – August 20) and summer 2020 (June 18 – August 14). I recorded bat calls using Song Meter SM2BAT 384kHz (SM2) and SM4BAT (SM4) full-spectrum bat detectors with omnidirectional microphones (Wildlife Acoustics Inc., Maynard, MA). At each site, I deployed one passive acoustic monitor in the riparian corridor because, based on the results of my summer 2018 pilot season, I found that location to be optimal for detecting bats as they foraged and moved through the landscape. Placing the detectors at the riparian corridor of a perennial stream also helped me to standardize detector placement across study sites. In most cases, detector location was held constant between site visits. In the few cases when location needed to be shifted, the field coordinates of each monitoring round were noted and used in later analyses of canopy height, THP area and stream area.

During each field season, I conducted an early and a late summer monitoring round at each site. I programmed detectors to record from 30 minutes before sunset until 30 minutes after sunrise. I rotated detectors between sites after a minimum of four nights, the survey length recommended by North American Bat Monitoring Protocol (Loeb et al., 2015). I visited each site for the early monitoring round then immediately started the late summer monitoring round. I ultimately recorded a total of 424 monitoring nights across the twenty sites.

I deployed detectors according to the recommended settings for surveying for bat activity in a forest habitat. However, recommended settings varied slightly for each model of detector. SM2 detectors were set to have a gain of 10 dB, trigger window of 2 s, and maximum trigger length of 5 s. SM4 detectors were set to have a gain of 12 dB, minimum duration of 1.5 ms, minimum trigger frequency of 16 kHz, trigger window of 3 s, and maximum trigger length of 15 s. Both detectors had a sample rate of 384 kHz, trigger level of 12 SNR, and division ratio of 8.

Omnidirectional ultrasonic microphones were deployed near the stream channel, away from vegetation clutter and elevated at least 2 m above the ground using telescopic poles. For the SM2 detectors, an SMX-U1 microphone was positioned parallel to the stream. For the SM4 detectors, an SMM-U2 microphone was positioned facing upward. Over the course of the study, I had a total of six SM2 detectors and six SM4 detectors, and I randomly assigned detectors to each site during each monitoring round to ameliorate any biases that may have occurred from the two different detector setups or individual detector functionality (Eric R. Britzke et al., 2013). I personally positioned and deployed all detectors to further minimize bias in acoustic sampling between sites.

2.4 Acoustic Call Classification

I used SonoBat bat call analysis software (Arcata, CA) to classify bat passes recorded as individual wav files in the field to species. First, I used the SonoBat Batch Attributer 6.5 to scrub non-bat files. I then used SonoBat version 30 with the Northwest California regional classifier to auto-classify calls to species. SonoBat parameterizes call sequences and uses an ensemble consensus of redundant hierarchical decision algorithms to classify calls to species (Szewczak et al., 2011). An accepted species decision is only determined when a result meets or exceeds specific acceptance thresholds and other classification checks (Szewczak et al., 2011). Only call files which received an accepted species identification by the software were included in my analysis. Once bat calls were auto-classified to species, I used knowledge from my training in bat call analysis to manually vet these classified calls. Auto-classified identifications were either accepted or overruled with a manual species identification. For each species, I ultimately calculated the total number of confidently identified bat passes on each monitoring night at each site, and I used this as the measure of bat activity.

2.5 Climate Data Analysis

To understand the effect of microclimate on bat activity, I actively recorded the ambient temperature and humidity at each acoustic sampling site. I programmed Hygrochron iButton sensors to log temperature and relative humidity every 15 minutes. Sensors were hung from vegetation nearby each detector and shielded from sunlight by a plastic hood. I later analyzed daytime and nighttime trends in temperature and humidity at each site by calculating mean, maximum, minimum, standard deviation and coefficient of variation for each monitoring night. Nighttime was defined as the period from sunset to sunrise for each monitoring night.

I also considered the influence of historical climate on bat species presence and activity. I downloaded climate data from ClimateNA Version 7.01 (Wang et al., 2016). ClimateNA is a software application that extracts and downscales gridded (4 x 4km) monthly climate data from PRISM, and the software also calculates and derives climate variables (Daly et al., 2008; Wang et al., 2016). I used decadal normal data for 2011-2020, and I extracted Hargreave's climatic moisture deficit (CMD) at each monitoring location coordinate. CMD is derived from monthly precipitation and monthly reference evaporation, and the annual CMD value is the sum of the monthly moisture deficits (Wang et al., 2016). The gradient of CMD values across my study area well-represented the regional climate differences between coastal and inland sites.

2.6 Forest Maturity Analysis

I analyzed spatially explicit data in ArcGIS Pro 2.8.3 (ESRI, 2021) to assess forest maturity of each study site in terms of both canopy height and disturbance history. To calculate canopy height metrics, I used publicly available Lidar Point Cloud data downloaded from the USGS National Map 3D Elevation Program. LAS data was added to a map and clipped to a 500 m buffer area around each monitoring field coordinates. I created a canopy height raster by first converting the LAS dataset filtered by first return and by ground return to rasters and then subtracting the ground return raster from first return raster. I used the "Con (Spatial Analyst)" tool to check the presence of large canopy height values (e.g., > 80 m) and identify outliers that indicated erroneous LiDAR points that needed to be filtered out. I then filtered for canopy height values in the actual range of trees at the study site by setting to null values that were < 2 m. This created the final canopy height raster from which I obtained statistics of mean, maximum and standard deviation in canopy height within 100m and 250m buffer distances of each monitoring location.

As an additional metric of forest maturity and of disturbance, I used spatially explicit Timber Harvesting Plan (THP) data to assess forest management history at each monitoring site. In California, before a private landowner can legally harvest timber on their property, they must submit a detailed THP prepared by a Registered Professional Forester to the California Department of Forestry and Fire Protection (CAL FIRE) (Duggan and Mueller, 2005). All THP records since 1997 are publicly available from CAL FIRE as spatially explicit data. I downloaded the data and filtered it to only include records of timber harvests completed as of 12/31/2020. I used "Dissolve boundaries" to merge THP polygons so that areas which experienced repeated harvest would not be counted more than once. I clipped the THP layer to a 500 m buffer around each monitoring field coordinate. From the attribute table of the resulting polygon layer, I was able to obtain the total area within each buffer covered by THP record, from which I calculated the proportion of the buffer area covered by THP record.

2.7 Stream Area Analysis

To account for differences in stream channel size that might influence bat activity or call detection, I calculated the stream surface area within a 50 m radius of each monitoring site. For each study site, I added one-meter resolution digital elevation model data (USGS, 2020) to a map in ArcGIS Pro. I created a new point layer for 'monitoring point' at the point in the stream closest to where the detector was deployed. I also created a point layer upstream for where the stream would start. Using the DEM and point layers, I applied a flow accumulation model to produce a raster that represented the relative height and width from the defined stream. I evaluated the resulting raster to identify the appropriate height cutoff for the stream channel based on the stream topography modeled in ArcGIS Pro and my knowledge from being on the ground at the study site. Height cutoffs ranged from 0.5 to 1.0 m. I then re-ran the model with the final height cutoff and a buffer distance of 50 m from the monitoring point. This created a raster layer representing the shape of the stream channel where monitoring took place. I then used the area of the raster as my measurement for surface area of the overall spatial extent of the stream channel at each study site.

2.8 Species Activity Models

I developed generalized linear mixed models for each species to examine the influence of all of the environmental variables (climate, forest maturity and stream area) on nightly bat activity. Bat activity for each species was measured as total confidently identified calls on a monitoring night (see 2.4 above). I developed negative binomial models with a log-link function because this distribution is appropriate for overdispersed count data (Zurr et al., 2013). All statistical and model analyses were conducted using R version 4.1.2 (R Core Team, 2021), and employed various packages detailed below.

Before running my initial model, I used 'cor( )' function in R to check the Spearman correlation coefficients of all variables. A table of resulting correlation coefficients can be found in Supporting Information. I found THP record to be significantly collinear with all canopy height variables, with correlation coefficients ranging from -.69 to -.78. I therefore excluded THP disturbance from my GLMM analysis and retained canopy height. The various metrics for canopy height were all strongly correlated with each other as well, with correlation coefficients ranging from .68 to .93. I therefore decided to only include mean canopy height within a 100 m radius of the monitoring location in my models because this variable best represented the differences in forest maturity and management history across all sites.

Daytime and nighttime microclimate data statistics were significantly correlated (see Supporting Information). After examining the correlation coefficients, I decided to only include minimum nighttime relative humidity and minimum nighttime temperature in my models. These two variables best represented the microclimate effects of interest while having an acceptable correlation coefficient of -.33.

I included study site (factor with 20 levels) and monitoring night as Julian day (factor with 62 levels) as random effects in all models. For fixed effects, I included year (factor with 2 levels: 2019 and 2020), detector model (factor with 2 levels: SM2 and SM4), mean canopy height (continuous), minimum nighttime relative humidity (continuous), minimum nighttime temperature (continuous), climatic moisture deficit (continuous), and stream area (continuous). All continuous variables were standardized to a mean of 0 and standard deviation of 1. After observing trends in the residuals of my initial models, I transformed the stream area term by taking the square-root and found that this effectively corrected my model fit. I considered a variable to have a significant effect on bat species activity when the range of the 95% confidence interval did not contain 0 (Elsen et al., 2017; Muñoz-Sáez et al., 2021).

I performed the negative binomial GLMM analysis using function glmer.nb( ) from package 'lme4' (Bates et al., 2021). I used 'sum contrasts' to specify the model matrix for the 2-level categorical variables of detector model and year, so that the effect of the first level is obtained by adding the model estimate, and the effect of the second level is obtained by subtracting the estimate. If there were any convergence warnings when I used glmer.nb( ) to run the initial model, then I used function lme4::allFit( ) with additional packages 'dfoptim' (Varadhan et al., 2020) and 'optimx' (Nash et al., 2021) to fit the initial model with alternative optimizers. With the exception of three species, I was able to select an optimizer for each species model so that the full model converged. All models and summary results can be found in Supporting Information. I omitted species model for Towsend's big-eared bat (*Corynorhinus townsendii*), California myotis (*Myotis californicus*) and little brown bat (*Myotis lucifugus*) because I could not trust model estimates given the unresolved convergence warnings.

I used the 'DHARMa' package (Hartig and Lohse, 2021) to confirm that all fitted models passed the checks for dispersion and residual diagnostics (see Supporting Information for residuals diagnostics plots). I also evaluated the variance inflation factor using the function vif( ) (Naimi et al., 2014) to confirm that there was low correlation between predictor variables. I am interested in the biological significance of all the independent environmental variables included on bat activity and therefore report the full model for each species rather than removing variables and testing for optimal model selection.

3. Results

3.1 Acoustic Data Across Species

I identified a total of 121,379 bat calls to 13 species across 20 study sites and 407 monitoring nights (Table 1). Of the total identified calls, 84.29% were classified as coming from two species with 42.37% (51,427 calls) identified as California myotis (*Myotis californicus*) and 40.72% (49,430 calls) as Yuma myotis (*Myotis yumanensis*). Other species that were regularly detected included: little brown bat (*Myotis lucifugus*; 6,968 calls, 5.74%), long-legged myotis (*Myotis volans*; 4,366, 3.60%), big brown bat (*Eptesicus fuscus*; 3,406, 2.81%), silver-haired bat (*Lasionycteris noctivagans*; 2,267, 1.87%), fringed myotis (*Myotis thysanodes*; 1,259, 1.04%), and long-eared myotis (*Myotis evotis*; 992, 0.82%). Species detected more rarely included: Mexican free-tailed bat (*Tadarida brasiliensis*; 381, 0.31%), pallid bat (*Antrozous pallidus;* 187, 0.15%), and hoary bat (*Lasiurus cinereus*; 172, 0.14%). Only 11 calls (0.01%) were identified as Townsend's big-eared bat (*Corynorhinus townsendii*).

Table 1: Summary of total species detections over the entire study, including total calls identified, total nights detected, and the number of sites at which species was detected as present which were in protected forest and working forest sites.

Species	**Species Code**	**Calls Identified**	**% of Total Calls**	**Nights Detected**	**% of Total Nights**	**Protected Sites**	**Working Sites**
Pallid	Anpa	187	0.15%	58	14%	5	3
Townsend's big-eared	Coto	11	0.01%	8	2%	3	0
Big brown	Epfu	3406	2.81%	274	67%	10	10
Western red	Labl	513	0.42%	110	27%	7	8
Hoary	Laci	172	0.14%	59	14%	5	5
Silver-haired	Lano	2267	1.87%	216	53%	10	10
California myotis	Myca	51427	42.37%	400	98%	10	10
Long-eared myotis	Myev	992	0.82%	233	57%	10	10
Little brown	Mylu	6968	5.74%	210	52%	10	9
Fringed myotis	Myth	1259	1.04%	192	47%	9	9
Long-legged myotis	Myvo	4366	3.60%	236	58%	10	10
Yuma myotis	Myyu	49430	40.72%	372	91%	10	10
Mexican free-tailed	Tabr	381	0.31%	112	28%	7	10

3.2 Site Characteristics

I analyzed the habitat conditions at each monitoring point, including canopy height, THP record, climatic moisture deficit, and stream channel. The mean canopy height of protected forests ranged from 24.4 – 51.2 m, with a mean of 36.9 m. The maximum canopy height of protected forests within the 100 m buffer ranged from 63.8 – 94.1 m, with a mean of 77.6 m. The mean canopy height of working forests ranged from 20.8 – 36.0 m, with a mean of 26.0 m; and the maximum canopy height ranged from 49.9 – 74.5 m, with a mean of 59.8 m.

My analysis of forest management history based on Timber Harvesting Plan (THP) area calculations confirmed that there were differences in disturbance history at protected forest compared to working forest sites. Within the 500 m radius buffer of each monitoring location, the proportion of area covered by historical THP record at protected forests ranged from 0 – 56.5%, with a mean of 10.2%. However, 8 out of 10 sites had a THP record of ≤ 7.7%, and 5 of those sites had a THP record of ≤ 1.1%. The two sites with a higher THP record were both part of the Jackson Demonstration State Forest: JDSF Caspar (21.0%) and JDSF Hare (56.5%). Working forests had a THP area record ranging from 35.0% - 88.4% of the buffer area, with a mean of 60.6%. 6 out of 10 sites had a THP record ≥ 50.0%. Although this variable was ultimately omitted from the statistical models, this analysis served as a helpful validation of the study design.

Although climatic moisture deficit varied significantly between coastal and inland sites, the distribution was similar between protected forest and working forest treatment groups. At protected forests, climatic moisture deficit ranged from 434 – 704 mm, with a mean of 557 mm. At working forests, climatic moisture deficit ranged from 419 – 683 mm, with a mean of 522 mm. Minimum nighttime humidity and minimum nighttime temperature also varied considerably between sites, as well as between monitoring rounds and even unique monitoring nights at each site, and comparisons of these statistical results and example plots of the raw data can be found in Supporting Information.

Stream channel area also varied significantly between sites, with a range of 449 – 2590 m^2. Although site variation was significant, the distribution of sizes was similar between protected forest and working forest treatment groups. In protected forests, the stream area ranged from 272 – 1336 m^2, with a mean of 994 m^2. In working forests, the stream area ranged from 674 – 1814 m^2, with a mean of 1110 m^2.

3.3. Species Activity Model Results

I used the habitat covariates for each field coordinates and each monitoring round in the GLMM analysis. After developing models relating species activity to the selected environmental covariates (mean canopy height, minimum nighttime relative humidity, minimum nighttime temperature, climatic moisture deficit, and stream area), I identified which variables had a significant effect ($Pr(>|z|) < 0.05$) on bat activity for each species (see table 2 and fig. 2). I found that the variable which had a significant effect on bat activity for the highest number of species was temperature. Six species were positively associated with temperature: big brown bat, western red bat, hoary bat, silver-haired bat, long-legged bat, and Mexican free-tailed bat. Conversely, two of these species were negatively associated with humidity: big brown bat, and western red bat. Three species were positively associated with climatic moisture deficit: pallid bat, fringed myotis, and Mexican free-tailed bat.

Canopy height had a significant positive effect on three species: pallid bat, long-eared myotis, and fringed myotis. Three species were positively associated with stream area: silver-haired bat, long-legged bat, and Mexican free-tailed bat.

Species also responded differently to fixed effects associated with the study design. I detected significantly higher activity in year 2 (2020) for four species: western red bat, hoary bat, silver-haired bat, and Mexican free-tailed bat. Using the SM4 model of detector revealed higher activity for three species: pallid bat, western red bat, long-legged bat; and lower activity for one species: silver-haired bat.

Table 2: GLMM species model results including estimates and standard error only for fixed effects which had a significant effect (Pr(>|z|) < 0.05) on species activity.

Species	Species Code	Covariate	Estimate	Std. Error	Lower CI	Upper CI	Pr(>|z|)
Pallid bat	Anpa	Canopy	1.112	0.539	0.056	2.168	0.03909
		CMD	1.467	0.610	0.271	2.662	0.01619
		Detector	-0.646	0.246	-1.128	-0.164	0.00868
Big brown bat	Epfu	Humidity	-0.629	0.124	-0.872	-0.386	3.92E-07
		Temperature	0.549	0.101	0.352	0.747	4.99E-08
Western red bat	Labl	Humidity	-0.666	0.181	-1.020	-0.312	0.00023
		Temperature	0.635	0.130	0.380	0.891	1.13E-06
		Year	-0.459	0.137	-0.726	-0.191	0.00078
		Detector	-0.340	0.142	-0.619	-0.061	0.01679
Hoary bat	Laci	Temperature	0.681	0.176	0.336	1.025	0.00011
		Year	-0.577	0.215	-0.999	-0.155	0.00732
Silver-haired bat	Lano	Stream	0.883	0.321	0.254	1.512	0.00590
		Temperature	0.374	0.113	0.154	0.595	0.00089
		Year	-0.236	0.106	-0.444	-0.028	0.02640
Long-eared myotis	Myev	Canopy	0.722	0.334	0.067	1.376	0.03060
Fringed myotis	Myth	Canopy	0.898	0.326	0.259	1.536	0.00585
		CMD	0.961	0.329	0.316	1.606	0.00349
Long-legged myotis	Myvo	Stream	1.114	0.352	0.423	1.804	0.00157
		Temperature	0.250	0.081	0.092	0.408	0.00194
		Detector	-0.744	0.103	-0.945	-0.542	4.36E-13
Mexican free-tailed bat	Tabr	Stream	1.124	0.286	0.563	1.685	0.00009
		CMD	0.629	0.303	0.034	1.223	0.03811
		Temperature	0.347	0.129	0.094	0.600	0.00725
		Year	-0.437	0.134	-0.699	-0.174	0.00111

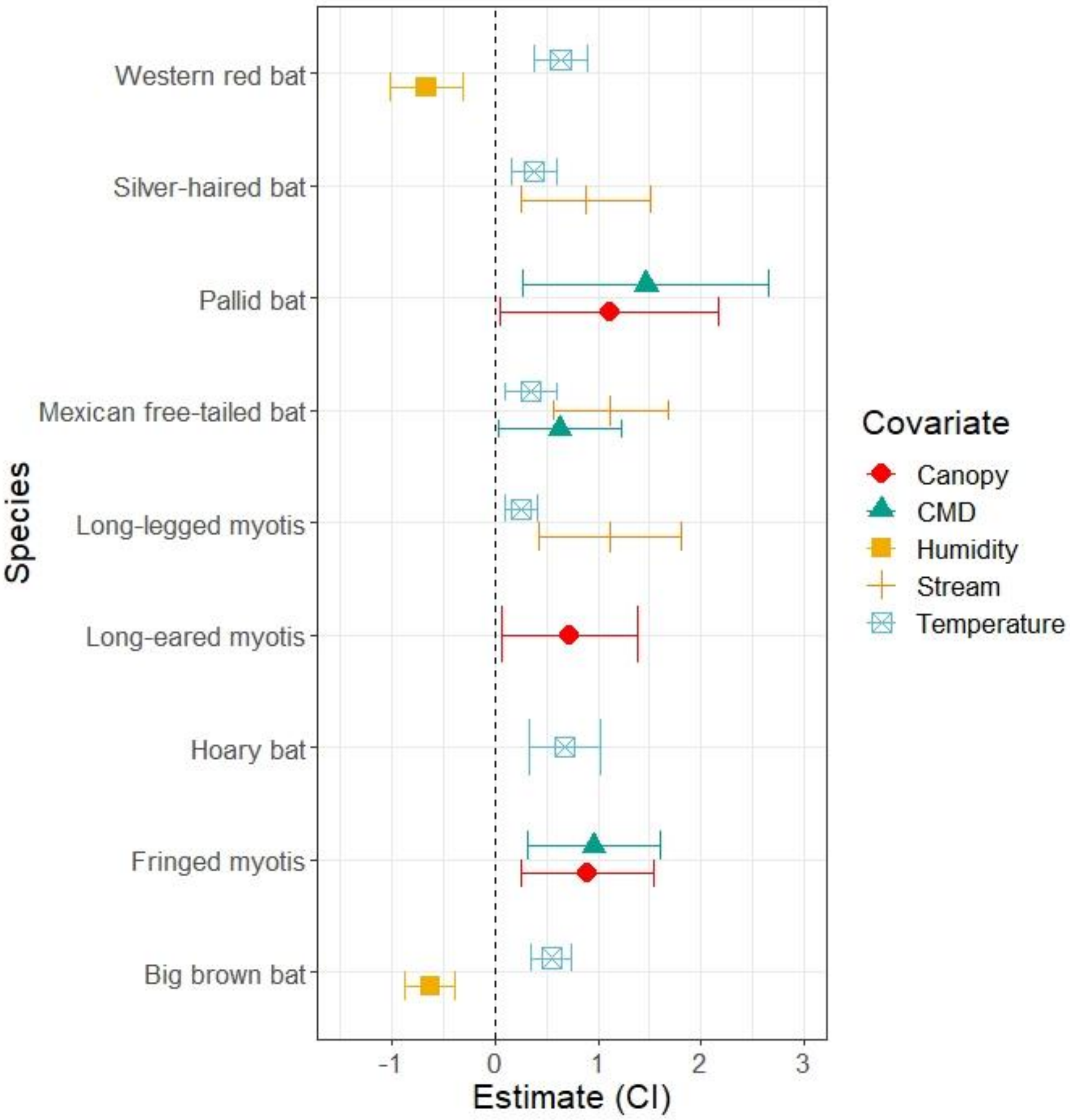


Figure 2: Generalized linear mixed model results for the influence of climate and forest management variables on bat activity, with error bars representing 95% confidence intervals for model estimates and only significant effects (Pr(>|z|) < 0.05) shown for each species model.

3.4 Species Activity Across Habitat Type

Species presence varied between sites (see Table 1). Six species were found at all twenty study sites on at least one monitoring night, including big brown bat, silver-haired bat, California myotis, long-eared myotis, long-legged myotis, and Yuma myotis. For most species, there was no difference in detected species presence between mature/protected forest sites and young/working forest sites. The important exception was Townsend’s big-eared bat, which was detected at three mature/protected forest sites and not detected at any of the young/working forest sites.

To visualize differences in species activity between habitat groups, I calculated mean species activity across all monitoring nights for each study site, and I used boxplots to visualize differences between mature/protected and young/working forests (fig. 3).

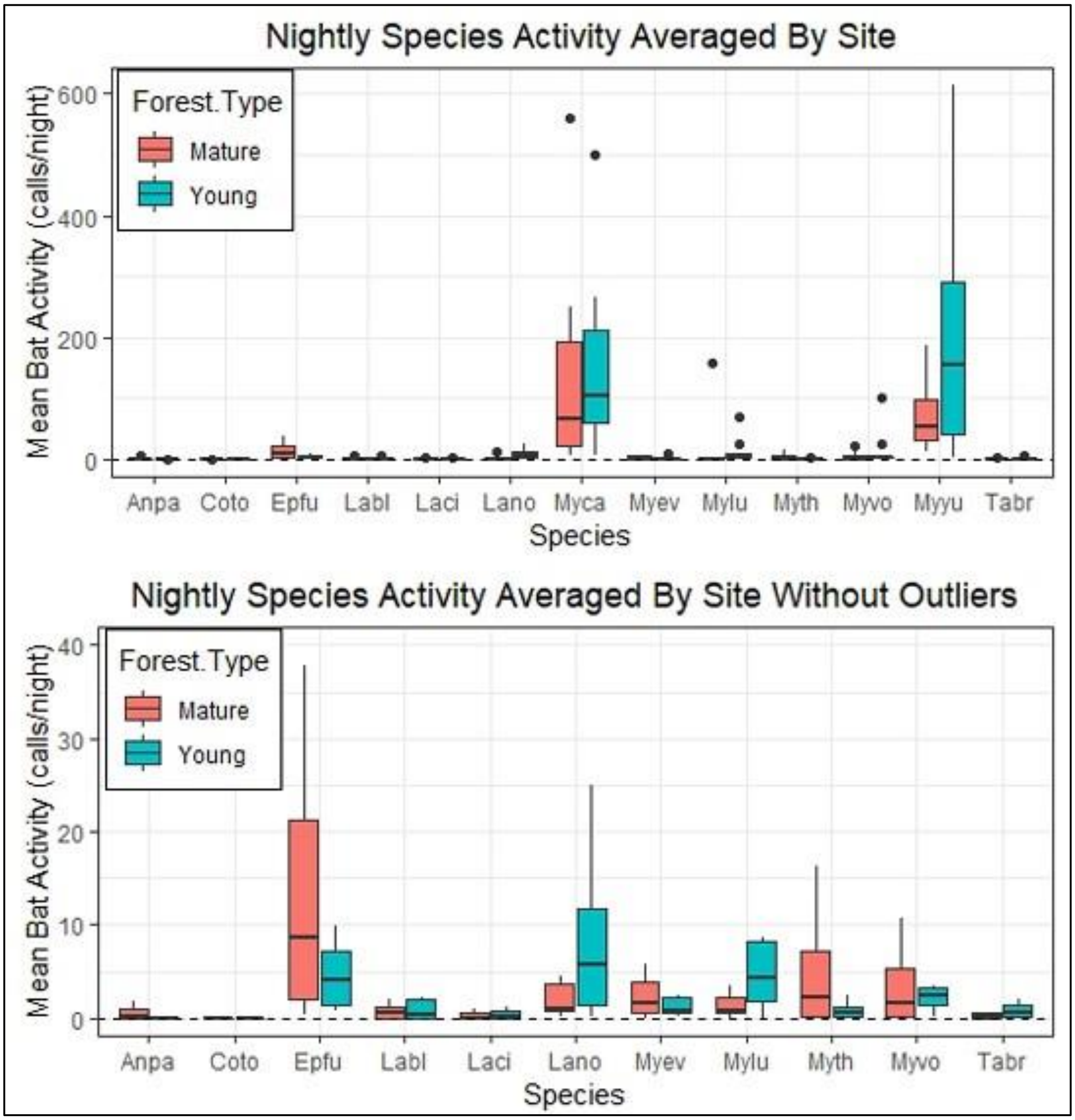


Figure 3: I averaged nightly species activity for each site across all monitoring nights and used boxplots to visualize how these results compared between mature and young forest sites.

4. Discussion

My findings illustrate that bats respond in species-specific ways to climate and forest habitat variables. Earlier bat studies in the redwood ecosystem often focused on total bat activity because it was not possible to classify acoustic calls or guano sampling to species (Seidman and Zabel, 2001; Zielinski and Gellman, 1999a). This aggregation obscures critical differences in species sensitivity to climate change and habitat disturbance. Advancements in acoustic monitoring technology have enabled me and other researchers to better investigate the ecology of individual species and assess the drivers of habitat suitability to inform conservation planning.

Contrary to my prediction that summer bat activity would be higher at high-fog coastal sites, GLMM results revealed that bat activity was generally higher under drier and warmer microclimate conditions associated with inland sites. Six species were positively associated with warmer nighttime temperature and two of these species were also negatively associated with higher relative humidity. This finding coincides with studies in other habitats that show that insectivorous bat activity increases with increasing temperature (Bender and Hartman, 2015; Brooks et al., 2017) and that bats spend more time in nightly torpor when humidity increases (Fjelldal et al., 2021). It may be that activity is driven more by selection for optimal foraging conditions with greater prey availability or when thermoregulation costs are lower (Brooks et al., 2017).

I also modeled the influence of historical climate in terms of climatic moisture deficit derived from downscaled climate data (Wang et al., 2016). Three species: pallid bat, fringed-bat, and Mexican free-tailed bat, were found to be associated with higher climatic moisture deficit. This was surprising given my hypothesis that bats would select for more coastal habitat as a refuge from the high temperatures and drought stress that is present inland. However, it is important to note that I restricted my study area to the coast redwood ecosystem. Redwood forest only persists in a narrow range within 50 km of the California coast that meets a small climatic envelope, characterized by cool and humid marine conditions (Dawson, 1998; Johnstone and Dawson, 2010). Therefore, this lack of association between climatic moisture deficit and bat activity for most species may suggest that even the most inland edge offers sufficient freshwater resources and may function as an important climate refuge compared with other habitat types. Further study of the influence of climatic moisture deficit on California bats should examine this in different forest types.

Another surprising finding was that the majority of species did not show a significant relationship with canopy height. The species which did (pallid bat, long-eared myotis, and fringed myotis) are all known to roost in basal hollows in the redwood ecosystem (Armstrong, 2021). However, at least seven other species are also known to use basal hollows as roosts (Armstrong, 2021), and all of these species, except for Townsend’s big-eared bat, were also detected in younger forest stands. Although basal hollows and other high quality roosting habitat are strongly associated with more mature forests, it can also be found in remnant old growth and legacy trees in younger forest stands (Mazurek and Zielinski, 2004; Zielinski and Gellman, 1999a). The lack of an association that I found between these tree-roosting species and canopy height may suggest bats are finding suitable roosting sites in a few remaining legacy trees, second-growth trees (Evelyn et al., 2004), or human structures.

However, it is important to note that I studied bat activity based on echolocation behavior, not roosting ecology. Bats have been observed to forage long distances only to return elsewhere to roost (Fellers and Pierson, 2002). Consequently, although my study demonstrates that working lands provide important foraging habitat, more mature tree stands may be vital for roosting habitat (Gellman and Zielinski, 1996; Mazurek and Zielinski, 2004; Zielinski and Gellman, 1999). Also, this study only investigated summer bat activity, and there might be additional seasonal differences in bat habitat use. Furthermore, at least one sensitive species did show a significant dependence on protected forest habitat. Townsend's big-eared bat was the most rarely detected species in my study, and all detections were on three protected forest properties, suggesting that protected forest habitat might be particularly essential for conserving this species in the redwood ecosystem.

Although the influence of stream was not a primary focus of my study, I found that my results agreed with other research findings that higher bat activity is detected at larger streams (Seidman and Zabel, 2001). However, this relationship was only significant for three species (silver-haired bat, long-legged bat, and Mexican free-tailed bat). This relationship might be driven by greater insect prey availability at larger streams or greater bat movement through larger stream corridors, or it might reflect differences in detection range because acoustic technology can detect ultrasonic calls at greater distances in more open habitat (Parsons, 1996; Patriquin et al., 2003). This could particularly explain the effect of stream area on Mexican free-tailed bat because canopy tends to be more open overhead of larger stream areas, and this species is known to fly above the redwood forest canopy (Kennedy et al., 2014). The lack of a significant relationship between stream area and the activity level of other species might be because the width of stream channels included in my study were all above the threshold used to classify 'small' streams by a previous study of stream size effect on redwood forest bat activity (Seidman and Zabel, 2001). If I had included smaller streams, than I might have found that stream area had a more significant effect on bat activity.

Differences in ultrasonic detector model did not have a significant effect on activity for most species. The species which were detected significantly more frequently by the newer detector model, SM4, included pallid bat, western red bat, and long-legged bat. Interestingly, silver-haired bat was detected more frequently by the older detector model. The SM2 detector model's microphone was deployed parallel to the stream channel. It is possible that this orientation was more effective at detecting identifiable calls of this species, which is known to use the riparian corridors for both migration and other movement through the redwood ecosystem (Weller and Stricker, 2012a). However, other species (hoary bat and western red bat) are known to have similar movement patterns, and I found no significant relationship between detector model and activity for these species.

Year also had an effect on a subset of species. The species for which I detected significantly higher activity in my summer 2020 field season (western red bat, hoary bat, silver-haired bat, and Mexican free-tailed bat) are all known to migrate through the redwood ecosystem during the spring and fall. The start and finish of the summer 2020 field season was shifted one week earlier than summer 2019 and did not overlap with known migration periods, so it is unlikely that detection differences were an artifact of changes in monitoring schedule between the two field seasons. Rather, this suggests that there might be interannual variation in migratory species activity in this ecosystem.

Ten species were detected as present on at least 8 out of 10 of my working forest study sites, and seven of these species were present at every working forest study site. This finding signifies the importance of integrating working forests into conservation planning for bats. These working forest lands may offer considerable conservation value by providing vital accessory habitat and resources to wildlife, as well as connecting otherwise isolated protected areas (Kremen and Merenlender, 2018). Working lands might be particularly important for a mammal such as a bat which forages over long distances and seasonally shifts roosting habitat to meet thermoregulatory requirements (Evelyn et al., 2004; Weller and Stricker, 2012b). My findings demonstrate that bats are present and highly active throughout this forest ecosystem. Consequently, bat conservation cannot only focus on remnant protected areas. Protecting legacy old growth trees and cultivating mature characteristics in second-growth forest will be indispensable for ensuring that suitable roosts remain available across working forest landscapes.

In summary, my research elucidated some of the species-specific drivers influencing bat activity patterns across a large forest ecosystem. Although my study demonstrates that both protected forests and working forests provide important habitat to bats, certain species are more sensitive to different management types and more reliant on mature habitat for species conservation. Also, I found that while both inland and coastal sites functioned as important bat habitat, higher bat activity in the redwood ecosystem was associated with higher temperature. Additional research is necessary to investigate how that finding might relate to prey availability or thermoregulatory costs. Moreover, the temperature metric used in this study was minimum nighttime temperature. Further research should examine the influence of other microclimate variables, such as maximum daytime temperature. Finally, this study provides a baseline understanding of the influence of climate and forest management on bat activity, and future research should evaluate whether these relationships hold as climate change increasingly stresses the redwood ecosystem.

References

Adams, R. A. (2010). Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology*, *91*(8), 2437–2445. https://doi.org/10.1890/09-0091.1

Adams, R. A. (2018). Dark side of climate change: Species-specific responses and first indications of disruption in spring altitudinal migration in myotis bats. *Journal of Zoology*, *304*(4), 268–275. https://doi.org/10.1111/jzo.12526

Adams, R. A., & Hayes, M. A. (2008). Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, *77*(6), 1115–1121. https://doi.org/10.1111/j.1365-2656.2008.01447.x

Amorim, F., Mata, V. A., Beja, P., & Rebelo, H. (2015). Effects of a drought episode on the reproductive success of European free-tailed bats (Tadarida teniotis). *Mammalian Biology - Zeitschrift Für Säugetierkunde*, *80*(3), 228–236. https://doi.org/10.1016/j.mambio.2015.01.005

Anderson, M. G., Clark, M., & Sheldon, A. O. (2014). Estimating Climate Resilience for Conservation across Geophysical Settings. *Conservation Biology*, *28*(4), 959–970. https://doi.org/10.1111/cobi.12272

Armstrong, A. (2021). Use of redwood basal hollows by bats: A focus on the Townsend's big-eared bat on the North Coast of California. *HSU Theses and Projects*. https://digitalcommons.humboldt.edu/etd/491

Balantic, C., Adams, A., Gross, S., Mazur, R., Sawyer, S., Tucker, J., Vernon, M., Mengelt, C., Morales, J., Thorne, J. H., Brown, T. M., Athearn, N., & Morelli, T. L. (2021). Toward climate change refugia conservation at an ecoregion scale. *Conservation Science and Practice*, *3*(9), e497. https://doi.org/10.1111/csp2.497

Bates, D., Maechler, M., Bolker [aut, B., cre, Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., & simulate.formula), P. N. K. (shared copyright on. (2021). *lme4: Linear Mixed-Effects Models using "Eigen" and S4* (1.1-27.1) [Computer software]. https://CRAN.R-project.org/package=lme4

Bender, M. J., & Hartman, G. D. (2015). Bat Activity Increases with Barometric Pressure and Temperature during Autumn in Central Georgia. *Southeastern Naturalist*, *14*(2), 231–242. https://doi.org/10.1656/058.014.0203

Britzke, E. R., Gillam, E. H., & Murray, K. L. (2013). Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, *58*(2), 109–117.

Brooks, J. D., Loeb, S. C., & Gerard, P. D. (2017). Effect of forest opening characteristics, prey abundance, and environmental factors on bat activity in the Southern Appalachians. *Forest Ecology and Management*, *400*, 19–27. https://doi.org/10.1016/j.foreco.2017.05.045

Burns, E. E., Campbell, R., & Cowan, P. D. (2018). *State of Redwoods Conservation Report*. Save the Redwoods League. https://www.savetheredwoods.org/about-us/publications/state-of-redwoods-conservation-report-2018/

Carroll, C., & Noss, R. F. (2021). Rewilding in the face of climate change. *Conservation Biology*, *35*(1), 155–167. https://doi.org/10.1111/cobi.13531

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*. https://doi.org/10.1126/science.1206432

Cowan, P., Burns, E. E., & Campbell, R. (2017). *A GIS approach to identifying the distribution and structure of coast redwood across its range*. https://www.fs.fed.us/psw/pubs/55453

CPAD 2016a (2016th ed.). (n.d.). [Map]. GreenInfo Network.

Cross, M. S., McCarthy, P. D., Garfin, G., Gori, D., & Enquist, C. A. F. (2013). Accelerating Adaptation of Natural Resource Management to Address Climate Change. *Conservation Biology*, *27*(1), 4–13. https://doi.org/10.1111/j.1523-1739.2012.01954.x

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*(15), 2031–2064. https://doi.org/10.1002/joc.1688

Dawson, T. E. (1998). Fog in the California redwood forest: Ecosystem inputs and use by plants. *Oecologia*, *117*(4), 476–485. https://doi.org/10.1007/s004420050683

Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, *4*, 164. https://doi.org/10.3389/fphys.2013.00164

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Dodd, L. E., Lacki, M. J., Britzke, E. R., Buehler, D. A., Keyser, P. D., Larkin, J. L., Rodewald, A. D., Wigley, T. B., Wood, P. B., & Rieske, L. K. (2012). Forest structure affects trophic linkages: How silvicultural disturbance impacts bats and their insect prey. *Forest Ecology and Management*, *267*, 262–270. https://doi.org/10.1016/j.foreco.2011.12.016

Duggan, S. E., & Mueller, T. (2005). *Guide to the California Forest Practice Act and Related Laws:* (first edition). Solano Press Books.

Elsen, P. R., Tingley, M. W., Kalyanaraman, R., Ramesh, K., & Wilcove, D. S. (2017). The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. *Ecology*, *98*(2), 337–348. https://doi.org/10.1002/ecy.1669

Erasmy, M., Leuschner, C., Balkenhol, N., & Dietz, M. (2021). Shed light in the dark – How do natural canopy gaps influence temperate bat diversity and activity? *Forest Ecology and Management*, *497*, 119509. https://doi.org/10.1016/j.foreco.2021.119509

Evelyn, M. J., Stiles, D. A., & Young, R. A. (2004). Conservation of bats in suburban landscapes: Roost selection by Myotis yumanensis in a residential area in California. *Biological Conservation*, *115*(3), 463–473. https://doi.org/10.1016/S0006-3207(03)00163-0

Fellers, G. M., & Pierson, E. D. (2002). Habitat Use and Foraging Behavior of Townsend's Big-Eared Bat (Corynorhinus Townsendii) in Coastal California. *Journal of Mammalogy*, *83*(1), 167–177. https://doi.org/10.1644/1545-1542(2002)083<0167:HUAFBO>2.0.CO;2

Fischer, D. T., Still, C. J., & Williams, A. P. (2009). Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. *Journal of Biogeography*, *36*(4), 783–799. https://doi.org/10.1111/j.1365-2699.2008.02025.x

Fjelldal, M. A., 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

Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences*, *115*(47), 11982–11987. https://doi.org/10.1073/pnas.1804224115

Gellman, S. T., & Zielinski, W. J. (1996). Use by Bats of Old-Growth Redwood Hollows on the North Coast of California. *Journal of Mammalogy*, *77*(1), 255–265. https://doi.org/10.2307/1382726

Hartig, F., & Lohse, L. (2021). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (0.4.4) [Computer software]. https://CRAN.R-project.org/package=DHARMa

Hiatt, C., Fernandez, D., & Potter, C. (2012). Measurements of Fog Water Deposition on the California Central Coast. *Atmospheric and Climate Sciences*, *02*(04), 525–531. https://doi.org/10.4236/acs.2012.24047

Hilty, J., & Merenlender, A. M. (2003). Studying Biodiversity on Private Lands. *Conservation Biology*, *17*(1), 132–137. https://doi.org/10.1046/j.1523-1739.2003.01361.x

Hitch, A. T., & Leberg, P. L. (2007). Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. *Conservation Biology*, *21*(2), 534–539. https://doi.org/10.1111/j.1523-1739.2006.00609.x

Johnstone, J. A., & Dawson, T. E. (2010). Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences*, *107*(10), 4533–4538. https://doi.org/10.1073/pnas.0915062107

Jones, G., Jacobs, D., Kunz, T., Willig, M., & Racey, P. (2009). Carpe noctem: The importance of bats as bioindicators. *Endangered Species Research*, *8*, 93–115. https://doi.org/10.3354/esr00182

Keeley, A. T. H., Ackerly, D. D., Cameron, D. R., Heller, N. E., Huber, P. R., Schloss, C. A., Thorne, J. H., & Merenlender, A. M. (2018). New concepts, models, and assessments of climate-wise connectivity. *Environmental Research Letters*, *13*(7), 073002. https://doi.org/10.1088/1748-9326/aacb85

Kennedy, J.-P., Sillett, S. C., & Szewczak, J. M. (2014). Bat Activity Across the Vertical Gradient of an Old-Growth Sequoia sempervirens Forest. *Acta Chiropterologica*, *16*(1), 53–63. https://doi.org/10.3161/150811014X683264

Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., & Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*, *13*(2), 106–112. https://doi.org/10.1890/140055

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*. https://doi.org/10.1126/science.aau6020

Kunz, T. H., & Fenton, M. B. (2005). *Bat Ecology*. University of Chicago Press.

Law, B. S., Chidel, M., & Law, P. R. (2018). Forest bat population dynamics over 14 years at a climate refuge: Effects of timber harvesting and weather extremes. *PLOS ONE*, *13*(2), e0191471. https://doi.org/10.1371/journal.pone.0191471

Linton, D. M., & Macdonald, D. W. (2018). Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations. *The Journal of Animal Ecology*, *87*(4), 1080–1090. https://doi.org/10.1111/1365-2656.12832

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Loeb, S. C., Rodhouse, T. J., Ellison, L. E., Lausen, C. L., Reichard, J. D., Irvine, K. M., Ingersoll, T. E., Coleman, J. T. H., Thogmartin, W. E., Sauer, J. R., Francis, C. M., Bayless, M. L., Stanley, T. R., & Johnson, D. H. (n.d.). *A Plan for the North American Bat Monitoring Program (NABat)*. 112.

Loeb, S. C., & Winters, E. A. (2013). Indiana bat summer maternity distribution: Effects of current and future climates. *Ecology and Evolution*, *3*(1), 103–114. https://doi.org/10.1002/ece3.440

Mazurek, M. J., & Zielinski, W. J. (2004). Individual legacy trees influence vertebrate wildlife diversity in commercial forests. *Forest Ecology and Management*, *193*(3), 321–334. https://doi.org/10.1016/j.foreco.2004.01.013

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

Moreno-Rueda, G., Pleguezuelos, J. M., Pizarro, M., & Montori, A. (2012). Northward Shifts of the Distributions of Spanish Reptiles in Association with Climate Change. *Conservation Biology*, *26*(2), 278–283. https://doi.org/10.1111/j.1523-1739.2011.01793.x

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. *Science*. https://doi.org/10.1126/science.1163428

Morris, A. D., Miller, D. A., & Kalcounis-Rueppell, M. C. (2010). Use of Forest Edges by Bats in a Managed Pine Forest Landscape. *The Journal of Wildlife Management*, *74*(1), 26–34.

Muñoz-Sáez, A., Kitzes, J., & Merenlender, A. M. (2021). Bird-friendly wine country through diversified vineyards. *Conservation Biology*, *35*(1), 274–284. https://doi.org/10.1111/cobi.13567

Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, *37*(2), 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Nash, J. C., Varadhan, R., & Grothendieck, G. (2021). *optimx: Expanded Replacement and Extension of the "optim" Function* (Version 2021-10.12) [Computer software]. https://CRAN.R-project.org/package=optimx

Parsons, S. (1996). A Comparison of the Performance of a Brand of Broad-Band and Several Brands of Narrow-Band Bat Detectors in Two Different Habitat Types. *Bioacoustics*, *7*(1), 33–43. https://doi.org/10.1080/09524622.1996.9753313

Patriquin, K. J., Hogberg, L. K., Chruszcz, B. J., & Barclay, R. M. R. (2003). The Influence of Habitat Structure on the Ability to Detect Ultrasound Using bat Detectors. *Wildlife Society Bulletin (1973-2006)*, *31*(2), 475–481.

Piccioli Cappelli, M., Blakey, R. V., Taylor, D., Flanders, J., Badeen, T., Butts, S., Frick, W. F., & Rebelo, H. (2021). Limited refugia and high velocity range-shifts predicted for bat communities in drought-risk areas of the Northern Hemisphere. *Global Ecology and Conservation*, *28*, e01608. https://doi.org/10.1016/j.gecco.2021.e01608

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, *29*(6), 1586–1595. https://doi.org/10.1111/cobi.12556

Rojas, I. M., Jennings, M. K., Conlisk, E., Syphard, A. D., Mikesell, J., Kinoshita, A. M., West, K., Stow, D., Storey, E., De Guzman, M. E., Foote, D., Warneke, A., Pairis, A., Ryan, S., Flint, L. E., Flint, A. L., & Lewison, R. L. (2021). A landscape-scale framework to identify refugia from multiple stressors. *Conservation Biology*, *n/a*(n/a). https://doi.org/10.1111/cobi.13834

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, *117*(8), 4211–4217. https://doi.org/10.1073/pnas.1913007117

Russo, D., Salinas-Ramos, V. B., Cistrone, L., Smeraldo, S., Bosso, L., & Ancillotto, L. (2021). Do We Need to Use Bats as Bioindicators? *Biology*, *10*(8), 693. https://doi.org/10.3390/biology10080693

Sawaske, S. R., & Freyberg, D. L. (2015). Fog, fog drip, and streamflow in the Santa Cruz Mountains of the California Coast Range. *Ecohydrology*, *8*(4), 695–713. https://doi.org/10.1002/eco.1537

Schmitz, O. J., Lawler, J. J., Beier, P., Groves, C., Knight, G., Boyce, D. A., Bulluck, J., Johnston, K. M., Klein, M. L., Muller, K., Pierce, D. J., Singleton, W. R., Strittholt, J. R., Theobald, D. M., Trombulak, S. C., & Trainor, A. (2015). Conserving Biodiversity:

Practical Guidance about Climate Change Adaptation Approaches in Support of Land-use Planning. *Natural Areas Journal*, *35*(1), 190–203. https://doi.org/10.3375/043.035.0120

Seidman, V. M., & Zabel, C. J. (2001). Bat activity along intermittent streams in northwestern california. *Journal of Mammalogy*, *82*(3), 738–747. https://doi.org/10.1644/1545-1542(2001)082<0738:BAAISI>2.0.CO;2

Sherwin, H. A., Montgomery, W. I., & Lundy, M. G. (2013). The impact and implications of climate change for bats. *Mammal Review*, *43*(3), 171–182. https://doi.org/10.1111/j.1365-2907.2012.00214.x

Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Global Change Biology*, *24*(7), 3266–3275. https://doi.org/10.1111/gcb.14051

Studier, E. H., Procter, J. W., & Howell, D. J. (1970). Diurnal Body Weight Loss and Tolerance of Weight Loss in Five Species of Myotis. *Journal of Mammalogy*, *51*(2), 302–309. https://doi.org/10.2307/1378480

Szewczak, J. M., Parsons, S., & Morrison, M. L. (2011). *Automated Acoustic Identification of Bats*. HUMBOLDT STATE UNIV ARCATA CA. https://apps.dtic.mil/sti/citations/ADA600404

Thurman, L. L., Gross, J. E., Mengelt, C., Beever, E. A., Thompson, L. M., Schuurman, G. W., Hoving, C. L., & Olden, J. D. (2021). Applying assessments of adaptive capacity to inform natural-resource management in a changing climate. *Conservation Biology*, *n/a*(n/a). https://doi.org/10.1111/cobi.13838

Torregrosa, A., Combs, C., & Peters, J. (2016). GOES-derived fog and low cloud indices for coastal north and central California ecological analyses. *Earth and Space Science*, *3*(2), 2015EA000119. https://doi.org/10.1002/2015EA000119

USGS one meter x47y437 CA NoCAL Wildfires B3 2018—ScienceBase-Catalog. (n.d.). Retrieved January 1, 2022, from https://www.sciencebase.gov/catalog/item/5e291aa0e4b0a79317cd7979

Varadhan, R., University, J. H., Borchers, H. W., Research, A. C., Bechard, and V., & University), H. M. (Montreal. (2020). *dfoptim: Derivative-Free Optimization* (2020.10-1) [Computer software]. https://CRAN.R-project.org/package=dfoptim

Vegetation (fveg)—CAL FIRE FRAP [ds1327] GIS Dataset. (n.d.). Retrieved December 30, 2021, from https://map.dfg.ca.gov/metadata/ds1327.html

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Weller, T. J., & Stricker, C. A. (2012a). Northern California redwood forests provide important seasonal habitat for migrant bats. *In: Standiford, Richard B.; Weller, Theodore J.; Piirto, Douglas D.; Stuart, John D., Tech. Coords. Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. Pp. 447-457*, *238*, 447–457.

Weller, T. J., & Stricker, C. A. ; (2012b). *Northern California redwood forests provide important seasonal habitat for migrant bats* (pp. 447–457). http://www.treesearch.fs.fed.us/pubs/41178

Wright, D. W., Rittenhouse, C. D., Moran, K., Worthley, T. E., & Rittenhouse, T. A. G. (2021). Bat responses to silviculture treatments: Activity over 13 years of regeneration. *Forest Ecology and Management*, *494*, 119359. https://doi.org/10.1016/j.foreco.2021.119359

Zielinski, W. J., & Gellman, S. T. (1999a). Bat Use of Remnant Old-Growth Redwood Stands. *Conservation Biology*, *13*(1), 160–167. https://doi.org/10.1046/j.1523-1739.1999.97424.x

Zielinski, W. J., & Gellman, S. T. (1999b). Bat Use of Remnant Old-Growth Redwood Stands. *Conservation Biology*, *13*(1), 160–167. https://doi.org/10.1046/j.1523-1739.1999.97424.x

Zurr, A. F., Hilbe, J. M., & Ieno, E. N. (2013). *A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists* (0 edition). Highland Statistics Ltd.

Chapter 2:

Forest canopy acoustic surveys reveal year-round bat activity

Abstract

Biodiversity conservation requires innovative ways to study the ecology of forest species that are often elusive and their response to forest management and environmental change. Forest bats are one taxon of high conservation concern that is especially cryptic. This holds true in the tall redwood forests of coastal California, where much about bat populations' seasonal movements and activity patterns is unknown. Remaining active in the winter may help these populations stave off white-nose syndrome, a wildlife disease threatening bats elsewhere. To detect bat activity, I installed year-round passive acoustic monitoring stations at five forest properties, including old-growth groves and working forests. Acoustic monitoring is limited by detection range, so I installed monitors simultaneously at the top of redwood trees and nearby at ground-level to investigate differences in vertical habitat use and seasonal activity patterns that may be missed by conventional survey methods. I used generalized additive models to examine how species activity at each detector location varied by Julian day. Treetop deployment methods significantly increased detection of tree-roosting and migratory species across all forest management types and all seasons. Furthermore, standard ground-based surveys primarily detected clutter-adapted *Myotis* species, which may limit understanding of how forest management practices differentially impact bat species. Applying innovative year-round canopy-level survey and advanced statistical modeling approaches revealed new insights about niche partitioning and seasonal bat activity in this ecosystem. These approaches could be applied to other monitoring studies to better understand how elusive species use forest habitat.

1 Introduction

Effective conservation planning requires an understanding of species ecology and how populations respond to management actions and environmental change (Hulme, 2005). Large-scale population monitoring is increasingly important as species ranges shift and populations collapse as a result of climate change and other global threats (Jetz et al., 2019; Newbold et al., 2018; Pimm et al., 2014). By understanding when and where sensitive species are present, measures can be taken to promote their conservation (Kunz et al., 2007). Conversely, failure to detect species or accurately assess population vulnerability may result in inappropriate management actions and missed conservation opportunities. Efforts have been made to standardize monitoring approaches and create shared repositories for species abundance and distribution data so that local findings can also contribute to regional understanding of species conservation status ("Global Biodiversity Information Facility (GBIF)"; Loeb et al., 2015; Sauer et al., 2013; Walters et al., 2012).

Bats are one taxon of high conservation concern that has historically eluded ecological monitoring. Much about the basic ecology and species-specific habitat needs of bats remains poorly understood because of their cryptic nature as volant, nocturnal mammals (O'Shea and Bogan, 2003). Obtaining accurate assessments of bat species distribution and abundance has recently become a high conservation priority in North America, where many bat populations have been devastated by a fungal disease called white-nose syndrome (WNS) (Bombaci et al., 2021; Frick et al., 2015). WNS has decimated eastern North American hibernating bat populations since 2006 and continues to spread across the continent (Cheng et al., 2021; Foley et al., 2011). As evidence of the severity of this threat, one of the species that was commonly found throughout the United States until the emergence of WNS, the little brown bat (*Myotis lucifugus*), is now at high risk of regional extinction in affected areas (Frick et al., 2010). At hibernacula with WNS establishment, little brown bat colonies have experienced mean declines of 98%, and other species, such as the big brown bat (*Eptesicus fuscus*), were also recently found to be more impacted by WNS than previously realized (Cheng et al., 2021). In order to understand the impacts of WNS on bat populations, we need to accurately assess population trends both before and after infections occur (Deeley et al., 2021).

Forest bats are especially elusive in part because they do not form large hibernacula colonies or maternity roosts, so their populations cannot be monitored by traditional colony surveys (Loeb et al., 2015). Instead, species roost in foliage or under tree bark or form inconspicuous colonies in tree cavities (Fellers and Pierson, 2002; Kunz and Fenton, 2005; Zielinski and Gellman, 1999a). Additionally, many forest bat species regularly switch roosts or seasonally migrate (Kühnert et al., 2016; Russo et al., 2005; Weller and Stricker, 2012). Forest bat populations might be less susceptible to the spread of WNS than in other habitat types precisely because they do not roost in large winter colonies where the fungal pathogen rapidly spreads between individual bats (Flory et al., 2012; Langwig et al., 2012). However, the challenges of locating and systematically monitoring dispersed populations have hampered efforts to determine range distributions, migration patterns and baseline population estimates (Bogan et al., 2003; Carter et al., 2003).

Passive acoustic monitoring has emerged as an important non-invasive tool for investigating temporal and spatial patterns in bat species presence and activity in relation to environmental variables (Bombaci et al., 2021; Frey-Ehrenbold et al., 2013; Froidevaux et al., 2018). Acoustic files are recorded in the field and software can later be used to classify calls to species. Passive acoustic monitoring has proven to be invaluable for studying habitat selection and impacts of forest management on bats (Bender et al., 2015; Jung et al., 2012; Klingbeil and Willig, 2009; Patriquin and Barclay, 2003). However, the effectiveness of passive acoustic monitoring is contingent on the focal species and survey methods (Adams et al., 2012; E. R. Britzke et al., 2013; Duff and Morrell, 2007; Loeb et al., 2019; Meyer et al., 2011). Rarer species generally require more sampling nights before they are detected as present in a habitat (Meyer et al., 2011). During the summer, the precise timing and duration of a survey period can significantly affect which species are detected in a habitat due to species-specific changes in activity during the maternity season (Loeb et al., 2019). Also, some acoustic detector models are able to detect bat calls at greater distances and higher quality than others (Adams et al., 2012).

Differences in species call structure and foraging ecology can also bias understanding of bat community assemblage and habitat use. For example, high-intensity, low frequency echolocation calls have greater range than low-intensity, broadband calls, and thus can be detected at further distances (Neuweiler, 1983). Similarly, species which emit more distinctive echolocation calls are more likely to be accurately identified, whereas species whose call characteristics overlap with sympatric species, such as the *Myotis* genus, might be misclassified or only studied as part of an acoustic guild (Jones et al., 2000; Walters et al., 2012). This grouping may be necessary in some regions due to classification limitations, but such approaches mask important nuances in species ecology, including how syntopic species partition resources by foraging in different habitat (Denzinger and Schnitzler, 2013; Saunders and Barclay, 1992).

Bat species occupy landscapes very differently depending on their morphology and foraging style. Smaller, agile species are generally adapted to foraging in cluttered vegetation, whereas larger, less maneuverable species are restricted to open space or edge habitat (Fenton, 1990). Survey efforts therefore need to be strategized to sample different habitat depending on the species of interest (Duff and Morrell, 2007). Research has revealed that bat communities also partition vertical space, with different species selecting for different strata of forest habitat (Jung et al., 2012; Kalcounis et al., 1999; Müller et al., 2013; Plank et al., 2012). However, because acoustic detectors have limited range, conventional ground-based survey methods are biased toward detecting species that occupy lower habitat (Menzel et al., 2005).

Understanding how species activity varies across vertical habitat might be especially important in a forest as tall the coast redwoods (*Sequoia sempervirens*), where much about bat populations' seasonal movements and activity patterns is unknown. California's coast redwoods are the world's tallest forests, and old-growth trees regularly exceed heights of 90 m (Sillett et al., 2015). The only prior study to investigate how bat activity varied from ground to treetop in a redwood forest detected two migratory bat species (western red bat, *Lasiurus blossevillii;* and Mexican free-tailed bat, *Tadarida brasiliensis*) at one site, which were not previously documented to occur in redwood forests (Kennedy et al., 2014). However, these species have since been detected in this ecosystem using ground-based monitoring methods. It is possible that technological advancements in acoustic monitoring equipment have increased capacity to detect these species and thus mitigated this species detection bias. Additionally, this earlier study was conducted only at one old-growth site (Kennedy et al., 2014). Old-growth habitat is not representative of the majority of the redwood ecosystem, 93% of which has been logged at least once (Burns et al., 2018; Cowan et al., 2017), so it is important to test how species detections and abundance in mature, protected habitat may differ from shorter and denser timberland stands.

Migratory bat species are believed to move through the coast redwood ecosystem during the spring and fall; however, their precise movements and activity patterns are unknown (Weller et al., 2016). Capture records suggest that male silver-haired bats might be resident in coast redwoods year-round, while females may migrate in the spring and fall (Weller and Stricker, 2012a). However, much of the evidence of tree-roosting species migration patterns is based on museum records (Cryan, 2003) or stable isotope analysis of bat hair (Cryan et al., 2014; Weller and Stricker, 2012). These are useful methods for inferring seasonal movements of long-distance migrants at a coarse scale, but different approaches are needed to understand finer scale activity patterns and behavior.

It has historically been assumed that tree bats that migrate to coastal ecosystems with warm winter temperatures remain active year-round (Lacki et al., 2007). Capture records show that silver-haired bats are indeed significantly more active than other resident species during the winter (Weller and Stricker, 2012). However, the first direct evidence of migration patterns from hoary bats tagged with GPS trackers and recaptured in the redwood ecosystem indicates that hoary bats may hibernate more than previously believed. Understanding winter activity patterns of coastal populations is important because hibernating bats are more susceptible to mortality from WNS, whereas bats that are normally active and foraging during the winter might be more resilient to disease (Grider et al., 2016).

Here I develop a novel approach to surveying bats across tall forest habitat that combines canopy-level and ground-level acoustic surveys with generalized additive models (GAMs) in order to explore seasonal bat activity and vertical niche partitioning for 13 forest bat species. Paired canopy-level and ground-level monitoring enables me to examine if vertical niche partitioning is observed in both mature forest stands which harbor taller trees as well as in young working forests. Also, canopy-level detectors may improve detection of bat activity during migration seasons, when migratory bats are believed to move rapidly through the ecosystem (Cryan, 2003; Weller and Stricker, 2012). Applying unconventional approaches to study bat activity can help identify the limitations of standard monitoring methods, as well as shed light on elusive species ecology.

2 Materials and Methods

2.1 Study species

Thirteen species of bats are found in coast redwood forests. This includes three migratory tree bats (hoary bat, *Lasiurus cinereus*; western red bat, *Lasiurus blossevillii*; and silver-haired bat, *Lasionycteris noctivagans*), as well as an additional migrant (Mexican free-tailed bat; *Tadarida brasiliensis*). There are also six species of the *Myotis* genus, as well as big-brown bats, pallid bats (*Antrozous pallidus*), and Townsend's big-eared bats. Ten of these species are known to roost in redwood basal hollows, and there is evidence that they continue to roost in this habitat during the winter (Armstrong, 2021; Mazurek and Zielinski, 2004; Zielinski and Gellman, 1999a). Six of the thirteen species present in the redwood ecosystem have been elsewhere identified with WNS symptoms, and three additional species have been found to carry the causative fungal pathogen ("White-Nose Syndrome," 2022). The fungal pathogen was first detected in northern California in 2019 (CDFW, 2019), heightening urgency to understand bat seasonal ecology before local populations become infected.

2.2 Study Area

Redwood forests grow in a narrow range within 50 km of the California coast, where climate is heavily influenced by frequent marine fog and other coastal effects (Johnstone and Dawson, 2010; Torregrosa et al., 2016). Consequently, summers are cool and moist, and winters are mild and wet. Temperature and precipitation of my study area is represented by the thirty-year (1991-2020) normal weather data from the Fort Bragg 5 N weather station (39.51ºN, 123.76ºW). Even during December, the coldest winter month, minimum temperature is normally above 4ºC and mean temperature is normally above 7ºC. The hottest month is August, when maximum temperature is normally still below 19ºC and mean temperature is normally 14ºC. The majority of rainfall occurs between October – April and averages 1100 mm annually (National Centers for Environmental Information, U.S. Climate Normals).

Study sites were selected in Mendocino and Sonoma Counties of Northern California. This is considered to be part of the central redwood region (Save-the-Redwoods League and

Noss, 2013). In these forests, redwoods generally co-occur with Douglas-fir (*Pseudotsuga menziesii),* tanoak (*Lithocarpus densiflorus),* madrone (*Arbutus menziesii*), bay laurel (*Umbellularia californica),* and other hardwood trees; and the shrub layer may be dense with huckleberry (*Vaccinium* spp.) and salal (*Gaultheria shallon)* (Save-the-Redwoods League and Noss, 2013). The ground is often carpeted with redwood oxalis (*Oxalis oregana)* and a variety of ferns. There is very little remaining old-growth redwood habitat (Burns et al., 2018). Therefore, it is critical to investigate species ecology in second-growth forests, including sites which continue to be actively logged (Mooney and Dawson, 2015).

2.3 Site selection

To survey across diverse management types, I selected five study sites under different ownerships including old-growth protected forests and young working forests. These sites represented a subset of the full landscape study sites included in Chapter 1 (see Fig. 1) (see Chapter 1 for more details on land access).

The northernmost site, Angelo Coast Range Reserve (hereafter “Angelo”), is managed by the University of California Natural Reserve System as an ecological reserve for research with some limited recreation. My study site was located in an old-growth redwood stand along the South Fork Eel River. Upslope from this site was a mixed conifer-deciduous forest, dominated by Douglas fir, canyon live oak (*Quercus chrysolepis*), and interior live oak (*Quercus wislizenii*) trees, along with tanoak, madrone, bay laurel, and black oak (*Quercus kelloggii*) (Polis et al., 2004). Downslope from the redwood stand, riparian tree species, dominated by white alder (*Alnus rhombifolia*), lined sections of the river. Meadow and chapparal habitat were also present on the property.

The other study properties were more homogeneous redwood dominant or co-dominant forest. The southernmost site, Armstrong Redwoods State Natural Reserve (“Armstrong”), is managed by the California State Parks. It is an old-growth redwood forest with many conservation protections in place, though it is also heavily used for public recreation, including hiking and camping. The monitoring location was along Fife Creek, which had substantial water flowing during the winter but was dry at the end of the summer. This is the only stream site that was not perennial during the survey period.

A third study site, “Caspar”, was selected near the western end of Jackson Demonstration State Forest (JDSF) along North Fork Caspar Creek. The United States Forest Service (USFS) and California Department of Forestry and Fire Protection (CAL FIRE) jointly manage JDSF. Although most of the 48,652 acre property has been previously logged, my study site is located in a second-growth stand that has mature characteristics (California Department of Forestry and Fire Protection, 2016). The property is primarily managed for research and forest management demonstration purposes, and fulfilling this mandate includes harvesting timber according to diverse silviculture treatments (California Department of Forestry and Fire Protection, 2016).

The final two study sites were both commercial timber properties. These were owned by two different companies: Lyme Redwood Forest Company (Lyme) and Mendocino Redwood Company (MRC). One property was located at Lyme’s Ten Mile River property at North Fork Redwood Creek (“Lyme”). The MRC property was located along Mallo Pass Creek (“Mallo

Pass”). Although the forest structure at both sites was dominated by dense, young redwood trees, the microclimate and habitat differed significantly between the two sites. Mallo Pass was significantly more coastal than Lyme and experienced much higher fog frequency. The habitat had noticeably more fog drip throughout the year, whereas the habitat at Lyme experienced relatively little fog input and vegetation was consequently much drier.

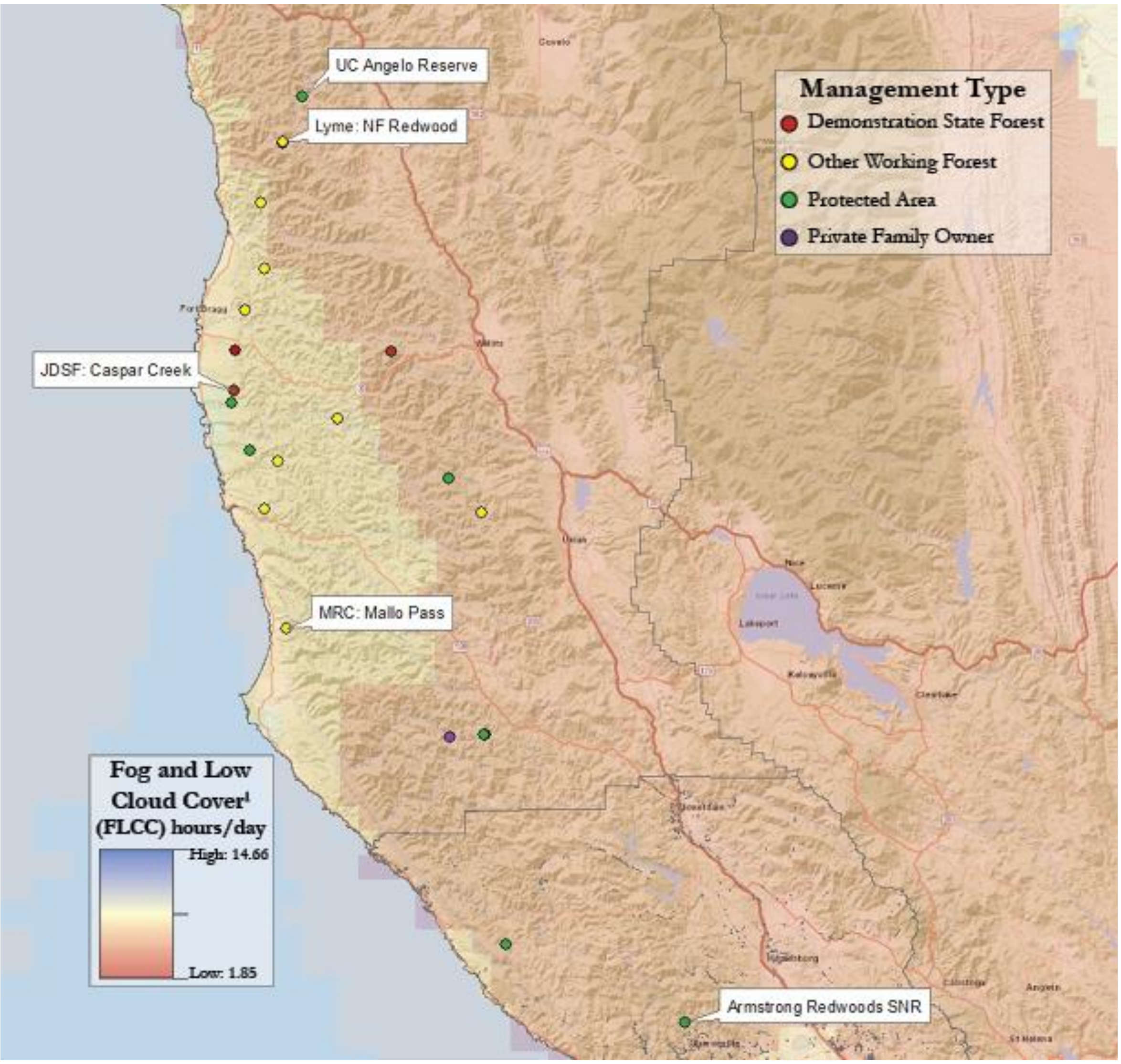


Figure 1: Northern California study sites represented diverse redwood forest management types, including old-growth protected areas and young working forests. Chapter 2 study sites represent a subset of the study sites surveyed across in Chapter 1.

2.4 Equipment setup

For my acoustic monitoring instruments, I used Song Meter SM2BAT 384 kHz (SM2) and SM4BAT (SM4) full-spectrum bat detectors (Wildlife Acoustics Inc., Maynard, MA). SM2 detectors used an SMX-U1 microphone, and SM4 detectors used an SMM-U2 microphone. Both microphone models are omnidirectional and weatherproof, and they were the recommended versions for the corresponding detector models. Although both detectors had a sample rate of 384 kHz, recommended acoustic settings varied slightly for each model of detector. SM2 detectors were deployed as follows: gain = 10 dB, trigger window = 2 s, maximum trigger length = 5 s, trigger level = 12 SNR, division ratio = 8. For SM4 detectors: gain = 12 dB, minimum duration = 1.5 ms, minimum trigger frequency = 16 kHz, trigger window = 3 s, maximum trigger length = 15 s., trigger level = 12 SNR, division ratio = 8.

Because detectors would need to run unattended between monthly site visits, I calculated power requirements for each detector model, and then I constructed external power setups that would also fit the physical specifications of my weatherproof cases. SM2 units each had three 6 V 12 Ah sealed lead acid batteries connected in parallel. The newer SM4 detector units were more power efficient and only needed two 6 V 12 Ah batteries. This design enabled me to record from sunset to sunrise at least every second night. Photos of acoustic detector set up and field deployment methods can be found in Supporting Information.

2.5 Acoustic sampling

Acoustic monitors were deployed at fixed locations in October 2019 and monitored bat activity until October 2020. At each site, I positioned one detector at ground-level and one detector at treetop. To minimize detection bias from using different monitoring equipment, the same model of detector (SM2 or SM4) was used at paired ground and treetop locations at each site. Furthermore, each model of detector was used at an old-growth site and at a commercial timber site.

Each ground-level detector was deployed at the edge of the riparian corridor. Riparian corridors are optimal habitat to survey for forest bats because bats access streams to drink and forage, and streams serve as important movement corridors. Also, because the interior of the forest is cluttered environment, the riparian corridor is the most open environment at ground-level. Siting the detector at the forest edge was thus the best option for sampling bats with different foraging styles (narrow-space, edge-space, and open-space) with only one detector. To reduce echoes that may affect call quality, microphones were sited at least 2 m from vegetation and elevated 3-4 m above the ground using telescopic poles. SMX-U1 microphones were positioned parallel to the stream and angled slightly below horizontal, and SMM-U2 microphone were positioned with the microphone surface facing upward.

Each treetop detector was installed at the top of the highest redwood tree in close vicinity of the riparian corridor. Project installation was accomplished with the aid of a professional canopy researcher who used advanced climbing techniques to rig each tree and securely hang the equipment at treetop using nylon webbing. Treetop microphones were attached to telescopic poles, and each of these poles was extended horizontally from the tree and tied parallel along a branch. This set up allowed me to sample open-air fly space and reduce call interference from vegetation clutter.

Although I positioned the equipment at treetop at each site, the actual height of the microphone varied between sites because the forest habitats were of different heights. Height was measured from treetop by dropping the weighted end of a tape measurer until an observer at ground level confirmed that the end had reached the forest floor. Microphone height ranged as follows: Armstrong, 78 m; Angelo, 60.5 m; Caspar, 49.5 m; Lyme, 38 m; and Mallo Pass, 33 m.

During project installation, a pulley was also attached to the tree with webbing, and a discreet cord was left running from the pulley to ground level. At each site visit, I used this narrow cord to pull my climbing rope into the tree and then anchored the rope at ground level. Then I used single-rope techniques with ascenders to climb the tree. These are recommended techniques for conducting canopy research without harming trees.

I made monthly site visits to recharge the batteries and retrieve SD cards with acoustic detector data (Fig. 2). These regular field visits were also necessary to ensure that equipment was functioning. There were a number of issues with both ground and treetop microphones ceasing to function or losing sensitivity, which seemed to be due to moisture entering the microphones. When this occurred, equipment needed to be replaced. Monitoring nights when a detector malfunctioned were omitted from the analysis.

From June 18 to August 16, 2020, I rotated the ground detectors to allow additional sites to be monitored during the summer season for another study. A wildfire burned my study site at Armstrong soon after my last field site visit in August 2020. As a result, data from August 16 until the study ended in early October was lost for this site.

Figure 2: Monthly maintenance of equipment included retrieving acoustic data and changing batteries.

2.6 Call classification

I processed acoustic data using SonoBat bat call analysis software (SonoBat; Arcata, CA). Non-bat files were first scrubbed using SonoBat Batch Attributer. I then applied SonoBat with the Northwest California regional classifier to auto-classify calls to species based on parameterized call sequences (Szewczak et al., 2011). SonoBat provides an accepted species decision when a result passes specific acceptance thresholds and other classification checks (Szewczak et al., 2011). Species autoclassification software is an extremely powerful tool that enables bat researchers to process large datasets such as this. However, this tool should be paired with manual vetting to check for misclassifications, and it is especially important to visually review call files that received an unexpected classification (Loeb et al., 2015).

I reviewed the data in SonoBat and placed particular emphasis on vetting migratory species (hoary bat, western red bat, silver-haired bat, and Mexican free-tailed bat) since they were the target species of interest for this study. For each monthly monitoring round, I also carefully vetted a sample of calls for every classified species to confirm species presence at each detector location. While reviewing call data, I doublechecked for evidence of monitoring nights when acoustic equipment malfunctioned so that these nights could be omitted from future analysis.

2.7 Comparison of paired detectors

After vetting acoustic data, I batched call classification results to csv files that I analyzed using R statistical analysis software (R Core Team, 2021). For each species, I calculated “bat activity” as the total number of confidently identified bat passes per monitoring night at each detector location. I used R to calculate basic site statistics and compare total species detections at paired detectors. For the paired comparison analysis, I filtered the full dataset to only include data from nights when both paired detectors were functional and recording. In some cases, one of the paired detectors did not detect bat activity, despite being functional and on the same monitoring schedule, so the total monitoring nights may still be different from its pair after filtering. For each detector location, I calculated ‘species presence,’ defined as the total number of monitoring nights during which at least one call was confidently identified, and ‘species activity’ results, defined in this case as the total number of identified calls. To better investigate how bat community assemblage shifted between ground and treetop and across sites, I standardized across total detections by computing the proportion of each species’ calls relative to total calls at that detector location, and I compared these proportions between detector locations and species.

2.8 Species activity models

I used generalized additive models (GAMs) to examine species activity in relation to study site and detector position over the 12-month study period. GAMs are more flexible than linear models because they can model nonlinear trends by applying a smoothing function in the form of a spline (Hastie, 1992). In this case, I needed to account for the non-independence of monitoring nights, as well as the nonlinear temporal trends that influence species presence and activity. An additional advantage of using GAMs over conventional paired analyses is that I was able to model the full study data, instead of only the nights when both paired detectors were functional.

I performed the analysis using function gam( ) from package ‘mgcv’ (Wood, 2021) in R version 4.1.2 (R core team, 2021). Model terms included the interaction of study site (“site”; 5-level factor) and detector position (“location”, 2-level factor: Ground and Treetop), and an additional smoothing function fit over monitoring night represented as Julian day. This smooth term was fit with a cyclic cubic regression spline (bs = “cc”) so that the ends of the spline were connected, as is appropriate for year-round monitoring data when the end of the year by Julian date (December 31 = ‘365’) is followed by the beginning of the new year (January 1 = ‘1’). All species models used a negative binomial distribution with a log-link function, and I set the basis dimension ‘k’ to 25. I used ‘sum contrasts’ to specify the model matrix for the 2-level categorical variables of detector position, so that the effect of the first level (‘Ground’) was obtained by adding the model estimate, and the effect of the second level (‘Treetop’) was obtained by subtracting the estimate. After running each species model, I used function gam.check( ) to produce residual plots, check model convergence and test adequacy of the basis model choices (“gam.check function - RDocumentation,” n.d.). The species activity models for the three least common species: Townsend’s big-eared bat, pallid bat, and long-legged myotis, did not produce model convergence and were omitted.

For models which converged, I applied analysis of variance (ANOVA) to fitted species activity models to test whether model terms (Site, Location, and Site:Location interaction) were significant. This was computed using function anova( ) from package ‘car’ (Fox et al., 2021). I determined whether a model term was significant based on whether the ANOVA result had a p-value < 0.05.

Finally, I used function predict.gam( ) to generate new model predictions for each fitted species model (Wood, 2021). I then applied function ggplot( ) from package ‘ggplot2’ (Wickham et al., 2021) with geom_smooth_ci( ) from package ‘tidymv’ (Coretta et al., 2022) to plot model predictions as fitted splines with 95-percent confidence intervals alongside actual detection activity indicated by point data. I visually compared the fitted splines for each study site to examine how species detections compared between ground and treetop. I also examined each spline to identify temporal trends in species activity, including significant peaks in species activity that might indicate migration activity or other notable seasonal patterns.

3 Results

3.1 Summary of acoustic data

1,413 monitoring nights were recorded across the ten detector locations, with total functional monitoring nights for each of the ten detector locations ranging from 93 to 206 nights. 104,596 calls were attributed to individual species by the combination of SonoBat software classification and manual vetting, with confidently identified calls per site ranging from 4,629 to 29,220 calls. Total number of confidently identified calls per detector location are shown in Table 1.

Table 1: Only calls confidently identified by SonoBat autoclassification and manual vetting were used in GAM analysis, and data was further filtered so that only nights when both paired detectors were functional and simultaneously recording were included in paired comparison analysis.

Site	Mic Hgt (m)	Location	Total Nights	Confident ID Calls	Filtered Nights	Filtered Calls
Angelo	60.5	Ground	128	11,575	102	10,501
		Treetop	192	11,534	104	5,324
Armstrong	78	Ground	133	4,629	83	4,054
		Treetop	93	5,342	83	3,940
Caspar	49.5	Ground	150	9,101	102	6,280
		Treetop	112	6,842	106	6,549
Lyme	38	Ground	130	6,799	128	6,763
		Treetop	206	5,765	136	3,777
MalloPass	33	Ground	114	29,220	99	27,159
		Treetop	155	13,789	99	11,784
		Total	**1,413**	**104,596**	**1,042**	**86,131**

3.2 Comparison of paired detector results

Species presence and species activity results reveal significant differences between paired canopy and ground-level detectors at all study sites. For example, in Fig. 3 and Fig. 4, migratory species, including hoary bats, silver-haired bats, and Mexican free-tailed bats, comprised the majority of calls at treetop, while *Myotis* species comprised the majority of detections at ground-level. This pattern held at the highest site, Armstrong (mic height = 78 m), and the lowest site, Mallo Pass (mic height = 33 m), as well as the other study sites. Comparison of proportion of each species' calls relative to all calls at the detection location further confirmed this trend. Hoary bats, silver-haired bats, and Mexican free-tailed bats comprised a much greater proportion of total detected calls at treetop than at ground-level at all sites (Table 2 and Fig. 5; see Supporting Info for full table and additional site and species plots).

Comparison of proportional calls also revealed differences in community assemblage between sites. At Armstrong, Mexican free-tailed bats comprised the majority of calls at treetop (74.9%). At Caspar, silver-haired bats comprised a higher proportion of treetop calls (48.0%) than at other sites (≤ 30.1%). Hoary bats were detected significantly more frequently at treetop than ground-level, but they composed a relatively low proportion of treetop calls at all study sites (≤ 10.8%). The California myotis comprised the vast majority of all ground-level calls at three sites (Caspar, 77.9%; Lyme, 82.1%; and Mallo Pass, 69.8%). No one species accounted for such a high proportion of calls at Angelo or Armstrong, though the little brown bat comprised 35.4% of calls at ground-level at Angelo, and the fringed myotis comprised 39.3% of the calls at ground-level at Armstrong (Table 2 and Fig. 5).

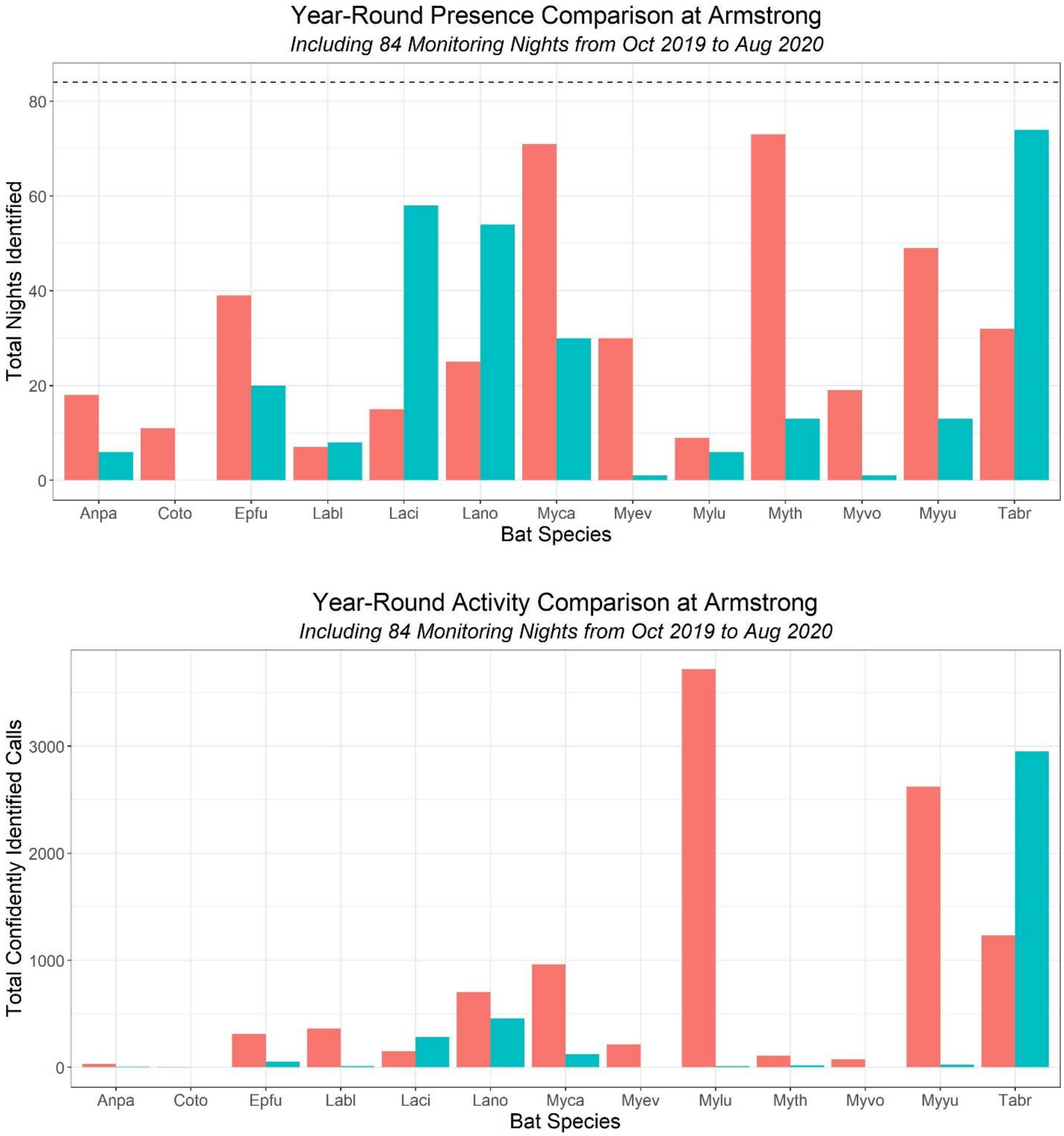
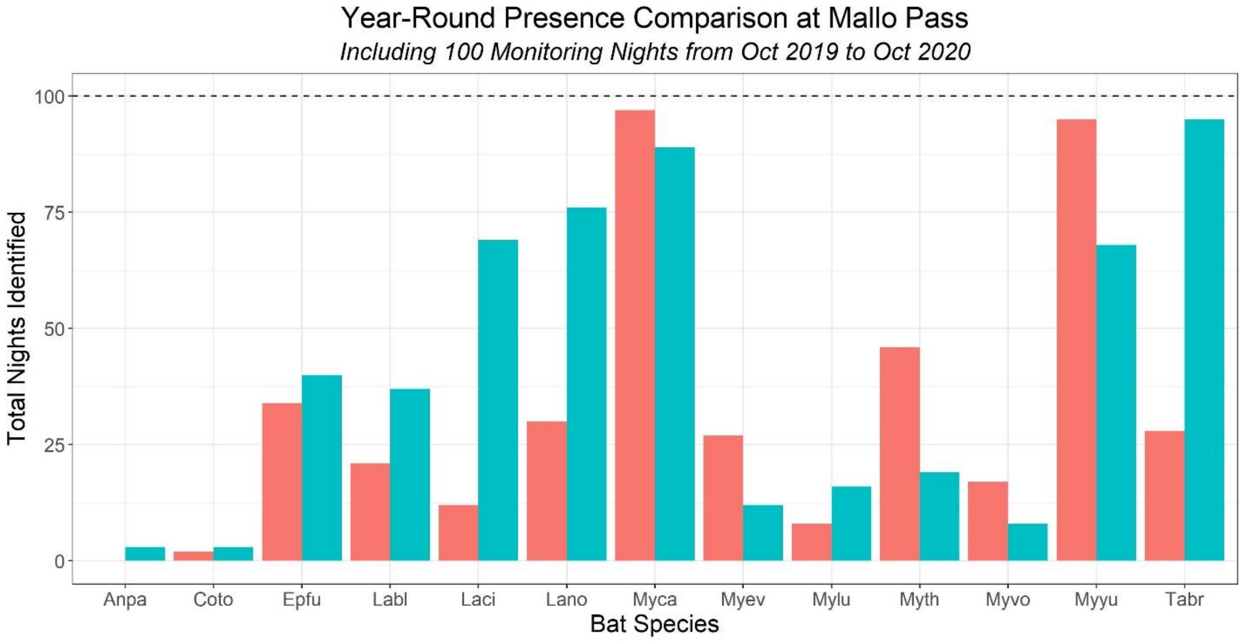


Figure 3: Paired comparison of species presence and activity results at Armstrong, with red bars = ‘Ground’ detections and blue bars = ‘Treetop’ detections. *Myotis* species are detected more frequently at ‘Ground’ and migratory tree bats (western red, ‘Labl’; hoary, ‘Laci’; silver-haired, ‘Lano’; Mexican free-tailed, ‘Tabr’) are detected more frequently at ‘Treetop.’



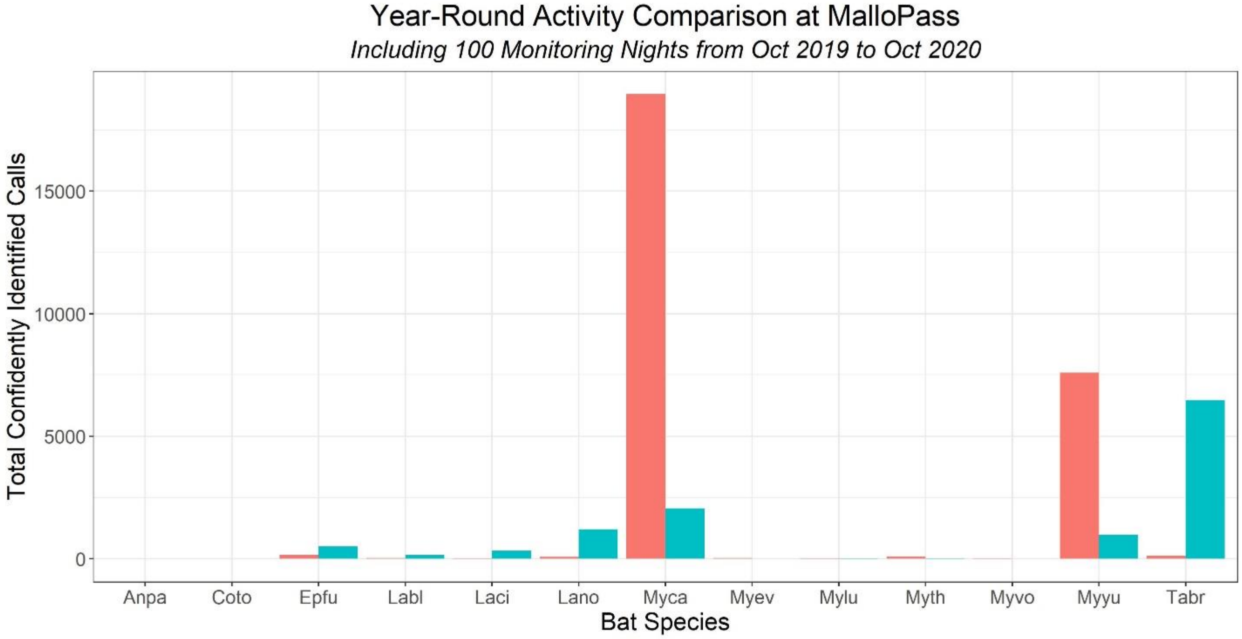


Figure 4: Paired comparison of species presence and activity results at Mallo Pass, with red bars = ‘Ground’ detections and blue bars = ‘Treetop’ detections. The same pattern observed at Armstrong also holds at this much shorter forest: *Myotis* species are detected more frequently at ‘Ground’ and migratory tree bats (western red, ‘Labl’; hoary, ‘Laci’; silver-haired, ‘Lano’; Mexican free-tailed, ‘Tabr’) are detected more frequently at ‘Treetop.’

Table 2: Proportion of each species' calls relative to all calls identified at detector location, with results omitted for rarely detected species (Townsend’s big-eared bat, pallid bat, and long-legged myotis).

Species	**Angelo**		**Armstrong**		**Caspar**		**Lyme**		**Mallo Pass**	
	G	**T**	**G**	**T**	**G**	**T**	**G**	**T**	**G**	**T**
Big brown bat	3.0%	0.2%	8.5%	1.4%	0.8%	3.4%	1.8%	5.1%	0.6%	4.3%
Western red bat	3.5%	2.5%	0.3%	0.3%	0.1%	0.0%	0.1%	1.0%	0.2%	1.4%
Hoary bat	1.4%	10.8%	0.5%	7.1%	0.4%	7.7%	0.1%	4.7%	0.1%	2.8%
Silver-haired bat	6.7%	30.1%	1.9%	11.5%	0.9%	48.0%	3.1%	22.1%	0.3%	10.2%
California myotis	9.2%	3.3%	27.5%	3.1%	77.9%	20.5%	82.1%	31.3%	69.8%	17.4%
Long-eared myotis	2.1%	0.4%	1.5%	0%	0%	0.1%	5.2%	2.1%	0.1%	0.1%
Little brown bat	35.4%	2.4%	0.3%	0.2%	0.1%	0.3%	0.1%	1.0%	0.1%	0.2%
Fringed myotis	1.0%	0.6%	39.3%	0.5%	0.1%	0.1%	3.0%	2.8%	0.3%	0.2%
Yuma myotis	25.0%	0.6%	14.0%	0.7%	19.5%	1.6%	2.2%	3.5%	28.0%	8.3%
Mexican free-tailed bat	11.7%	48.9%	2.0%	74.9%	0.1%	18.3%	0.9%	26.2%	0.4%	55.0%

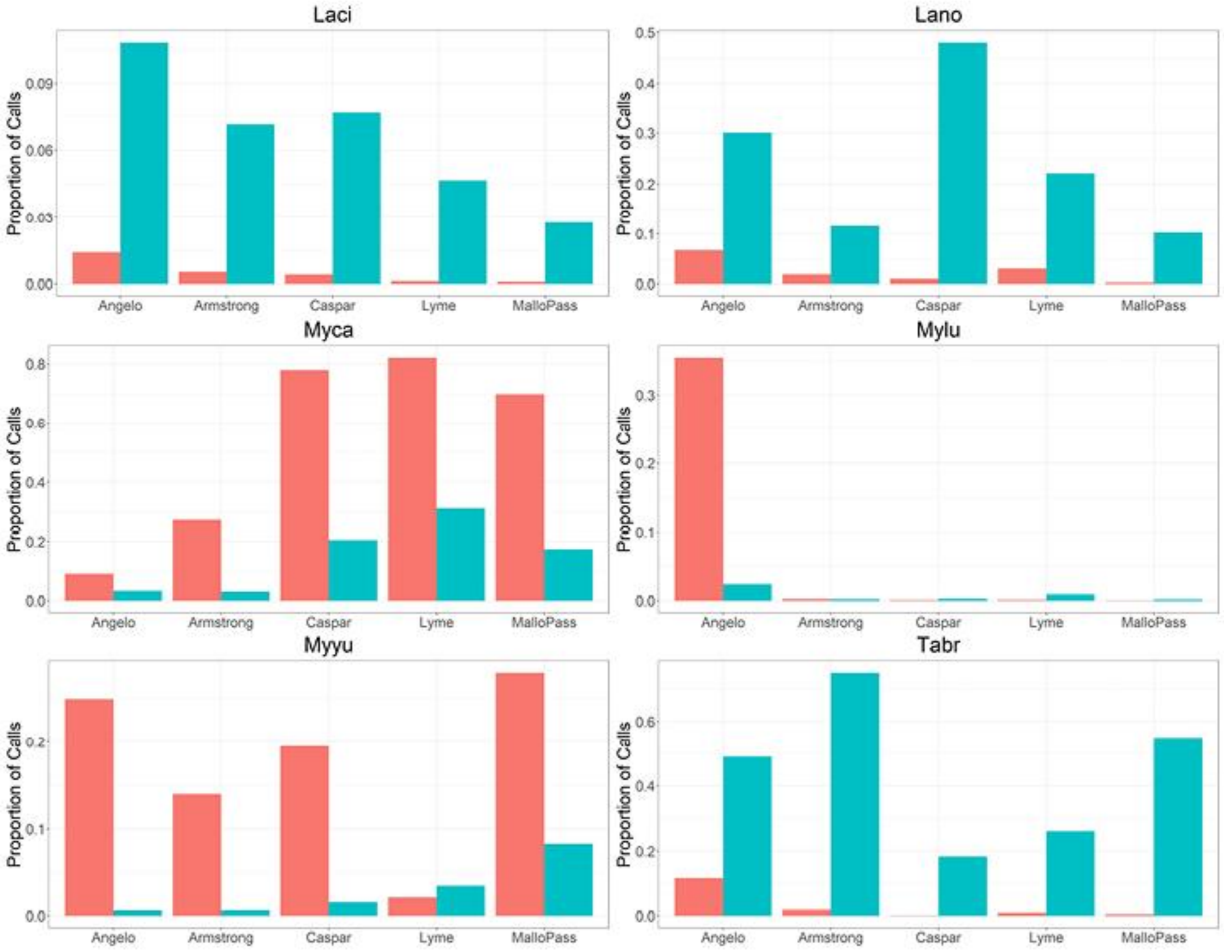


Figure 5: Species calls calculated as proportion of total calls at each of the ten detector sites, with results presented for hoary bat (Laci), silver-haired bat (Lano), California myotis (Myca), little brown bat (Mylu), Yuma myotis (Myyu), and Mexican free-tailed bat (Tabr).

3.3 Species activity model results

The ANOVA results from this multi-site, year-round canopy study revealed significant differences in bat activity between ground-level and treetop (Table 3). The activity of 6 species: hoary bats, silver-haired bats, California myotis, fringed myotis, Yuma myotis, and Mexican free-tailed bats, varied significantly (p-value < 0.05) between study sites (5-level factor), detector location (‘Ground’ or ‘Treetop’), and site:location interaction (10-level factor). However, as is clearly demonstrated by the plots of model predictions (Fig. 6-8), the direction of the location effect on species activity varied depending on the species.

Table 3: ANOVA was applied to fitted species activity models to test whether group means were different for model terms. P-values < 0.05 are reported below and non-significant p-values are indicated as 'n.s.'

Species	Site	Location	Site:Location
Big brown bat	7.11E-09	n.s.	6.15E-11
Western red bat	< 2e-16	n.s.	0.00138
Hoary bat	< 2e-16	< 2e-16	< 2e-16
Silver-haired bat	< 2e-16	< 2e-16	3.96E-15
California myotis	< 2e-16	< 2e-16	8.90E-06
Long-eared myotis	0.0013	n.s.	n.s
Little brown bat	0.00178	n.s.	n.s
Fringed myotis	1.94E-11	4.01E-11	1.75E-11
Yuma myotis	< 2e-16	< 2e-16	1.97E-06
Mexican free-tailed bat	< 2e-16	< 2e-16	< 2e-16

Hoary bats (Fig. 6), silver-haired bats (Fig. 7), and Mexican free-tailed bats (Supporting Info) were detected more frequently at treetop relative to ground-level at all study sites, including old-growth stands and working forests. This pattern generally held throughout the year as illustrated by the former spline above the latter (Figs. 6 and 7). The primary exception was a brief period in late spring when Mexican free-tailed bats detections were higher at ground-level than treetop at Angelo (Supporting Info). Hoary bats and silver-haired bats generally showed significant peaks in activity in the spring and fall, though this varied slightly by site. Some sites only showed a peak during one season and there was no clear evidence of a peak in activity for hoary bats or silver-haired bats at Armstrong. Mexican free-tailed bat activity varied significantly by site, with activity at some sites peaking in known migration seasons, fall and spring, while other sites peaked during summer and winter (Supporting Info). Although activity levels varied across seasons, these three species were all detected throughout the year, including in the winter, as indicated by both the predicted splines and the plotted activity data points.

In contrast, California myotis, fringed myotis, and Yuma myotis were detected more frequently at ground-level than treetop throughout the year (Fig. 8). These three species and other *Myotis* species showed strong summer peaks in activity, and most activity occurred between March – November, as indicated by both the predicted splines and the plotted activity data points. However, most species were also detected during the winter (December – February) on at least one monitoring night, and this winter activity appeared to be more frequent at Armstrong than other sites.

The activity of two species: big brown bat and western red bat, varied significantly (p-value < 0.05) between study sites and site:location interaction. This significant interaction effect can be visualized from model prediction plots (Supporting Info). The treetop and ground-level splines for big brown bats and western red bats were not consistently shifted in either direction; at some sites there was higher species activity at treetop and at others there was higher activity at ground-level. Similar to hoary bats and silver-haired bats, western red bats generally showed significant peaks in activity in the spring and fall, though this varied slightly by site. During the winter, western red bats were still detected on multiple monitoring nights at Angelo, Lyme, and Mallo Pass. Big brown bat activity generally occurred between spring-fall and peaked during the summer, similar to *Myotis* species. However, limited winter activity was detected at ground-level at Angelo, Armstrong, Mallo Pass, and at treetop at Caspar.

For the final two species activity models, long-eared myotis and little brown bat, the only significant model term was Site. Average activity did not vary significantly between canopy and ground level. Similar to other *Myotis* species, activity generally peaked during the summer and winter activity was extremely limited, though the long-eared myotis was also detected on multiple nights in February at Armstrong. Data points reveal that little brown bats were detected in exceptionally high numbers during the summer at Angelo, though this trend is not fully reflected in the Angelo ground detector spline.

For each of these ten species activity model, full ANOVA results, model summary, and gam.check( ) results with residual diagnostics plots can be found in Supporting Information.

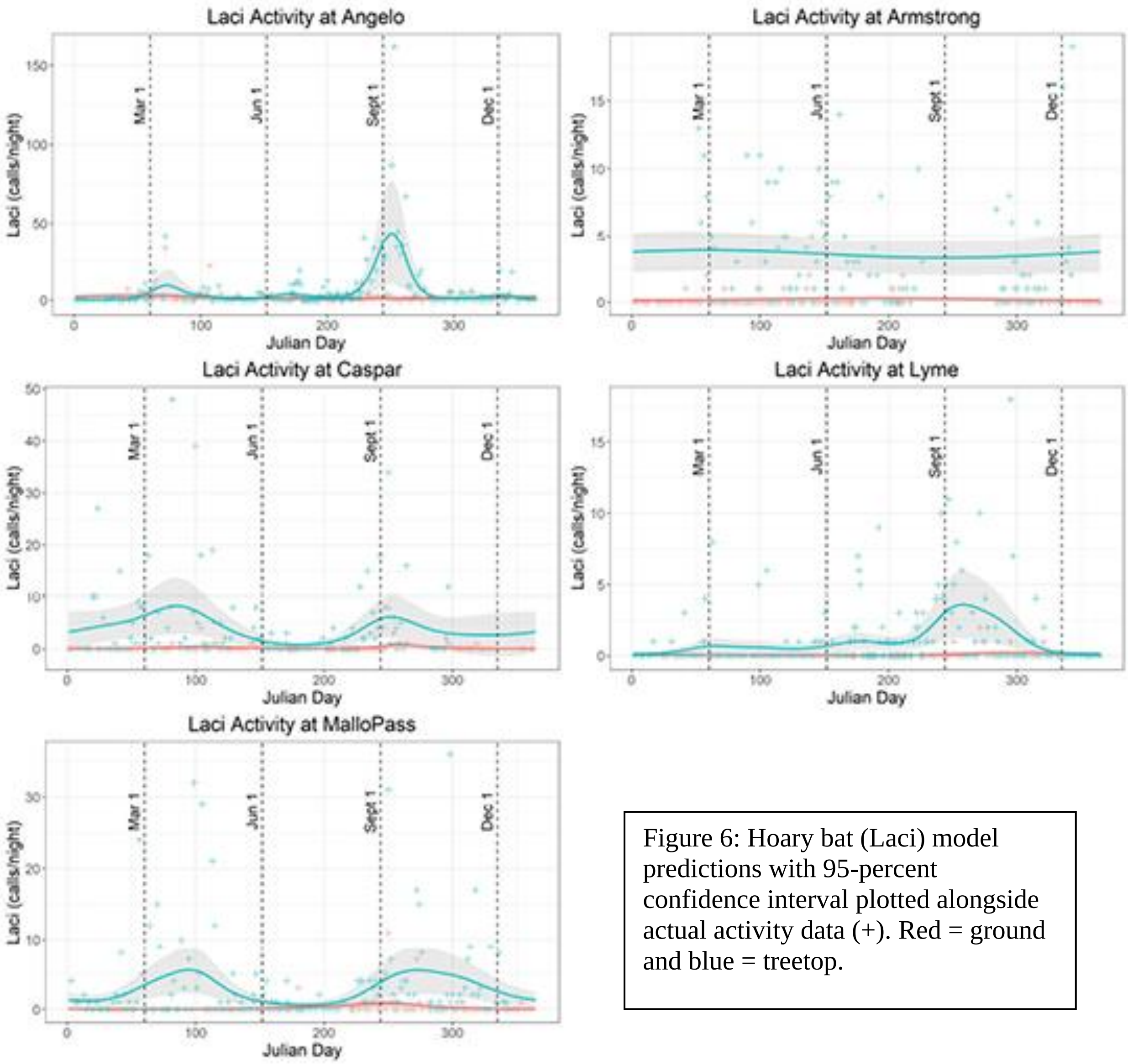


Figure 6: Hoary bat (Laci) model predictions with 95-percent confidence interval plotted alongside actual activity data (+). Red = ground and blue = treetop.

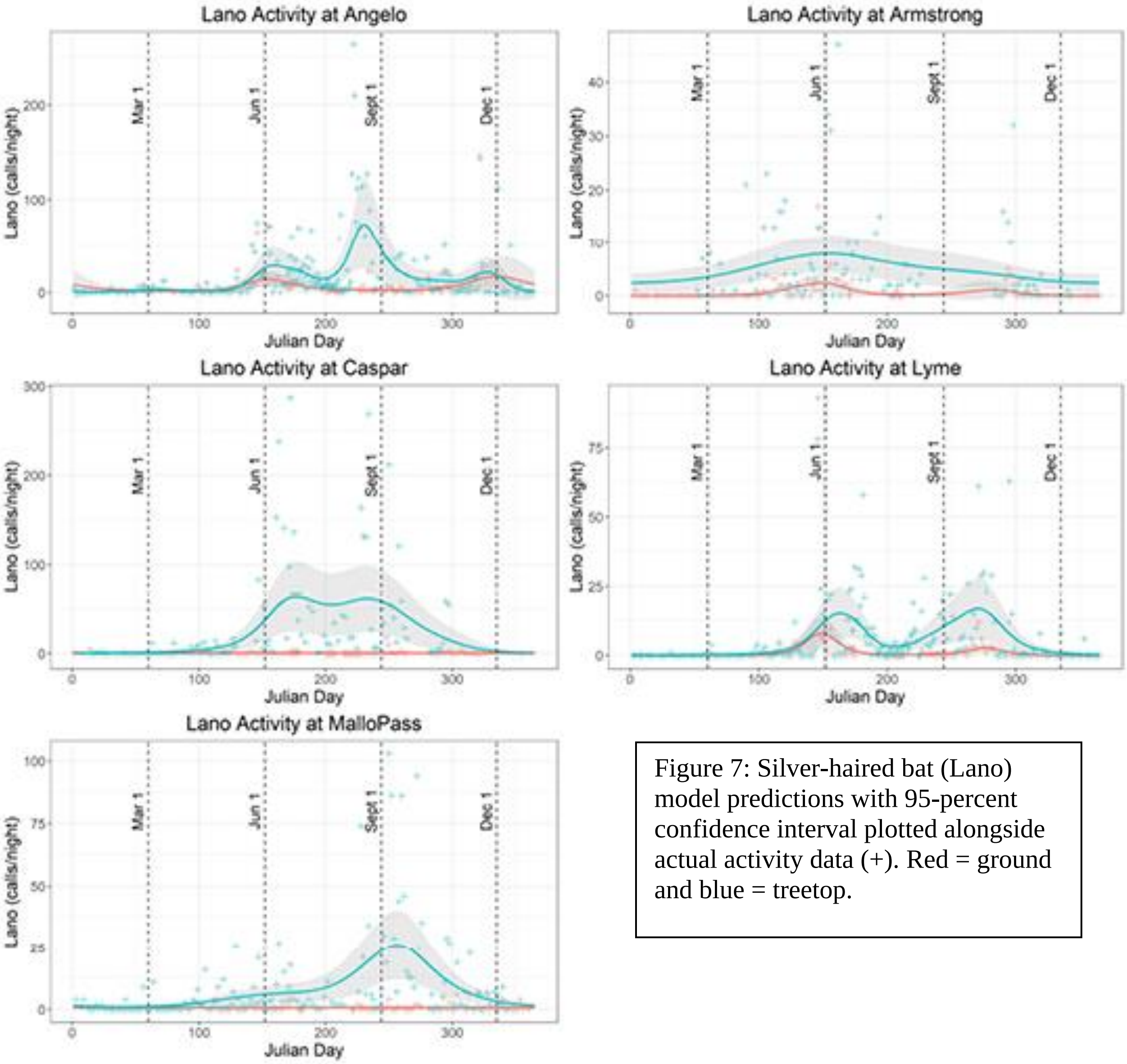


Figure 7: Silver-haired bat (Lano) model predictions with 95-percent confidence interval plotted alongside actual activity data (+). Red = ground and blue = treetop.

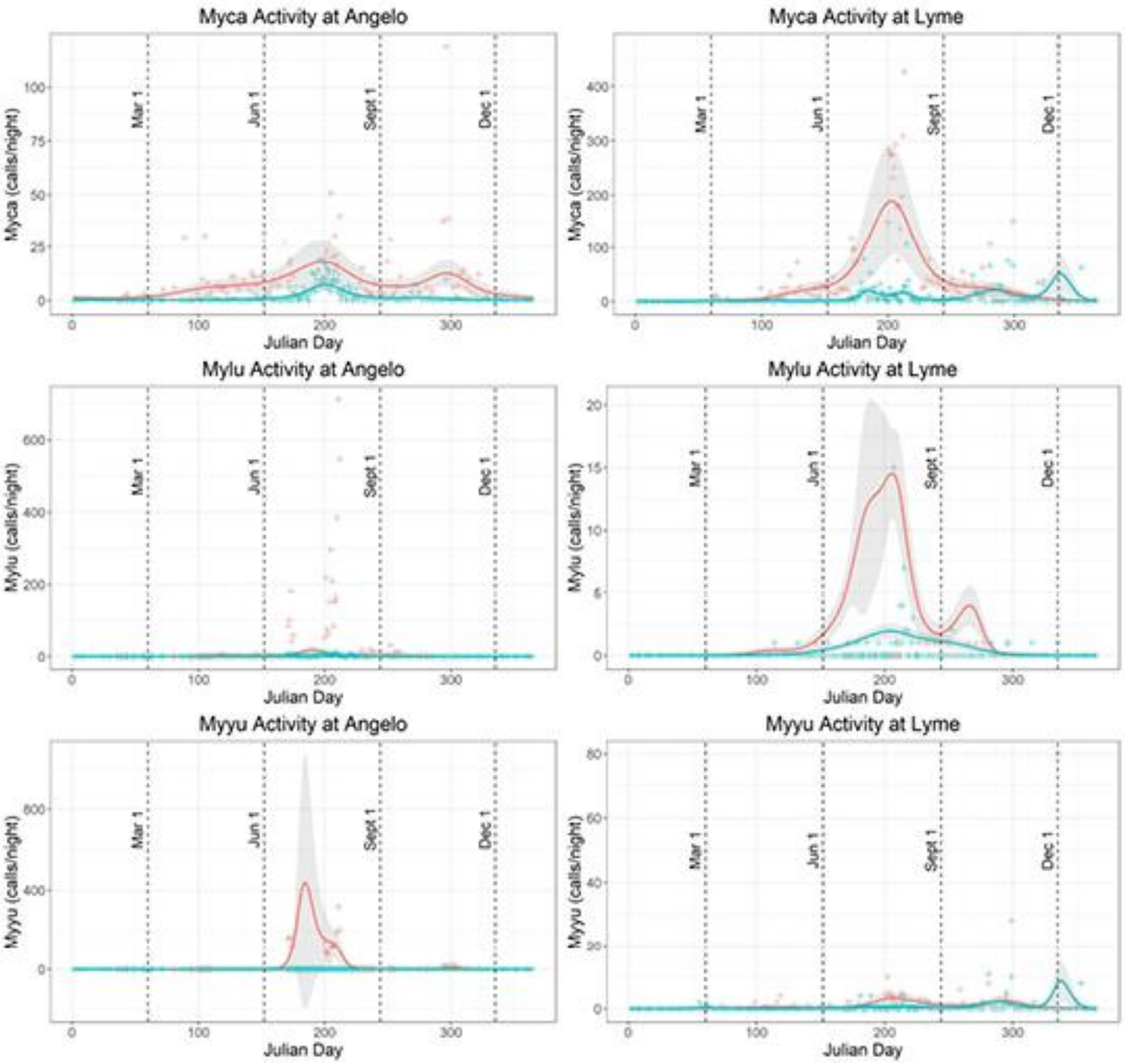


Figure 8: California myotis (Myca), little brown bat (Mylu), and Yuma myotis (Myyu) model predictions with 95-percent confidence interval plotted alongside actual activity data (+) for neighboring sites Angelo and Lyme. Red = ground and blue = treetop.

4. Discussion

Niche partitioning and forest management implications

Results from this multi-site, year-round canopy study show that vertical niche partitioning occurred across working forests as well as old-growth sites. Consistent with the earlier study of bat activity across the vertical gradient of a redwood forest, *Myotis* species comprised the majority of calls at ground-level while non-*Myotis* comprised the majority of calls higher in the forest canopy (Kennedy et al., 2014). Similar results have been found using canopy studies in other forest habitat; open-space and edge-space adapted species are detected significantly more frequently higher in the forest canopy, while clutter-adapted species are detected more frequently closer to the ground (Kalcounis et al., 1999; Menzel et al., 2005).

There were a lot of nights when hoary bats, silver-haired bats, and Mexican free-tailed bats were detected at treetop that the species was not detected at ground-level. As a result, conventional monitoring methods may underrepresent the value of redwood habitat for these species. This is an important reminder for bat conservation that non-detection does not mean absence. Given that standard survey methods in tall habitat are limited by acoustic detection range being less than the height of the habitat, especially for bats which emit quieter calls, forest managers should be mindful that high-flying, elusive species may be present even if they are undetected and manage for biodiversity accordingly.

Interestingly, this clear vertical niche partitioning did not hold across all sites for western red bats and big brown bats. This finding was initially surprising because the previous redwood canopy survey of bat activity detected western red bats, an edge-space adapted species, only at treetop, so I expected to similarly detect more calls for this species at treetop than ground-level (Kennedy et al., 2014). Likewise, studies in other forest habitat have found that big brown bats, an open-space adapted species, are also more active above the tree canopy (Menzel et al., 2005). Closer inspection revealed that big brown bats were detected more frequently at ground-level at the old-growth sites Angelo and Armstrong, and at other sites this species was detected more frequently at treetop. Western red bats were detected slightly more frequently at ground-level at Angelo, and relatively equally at ground-level and treetop at Armstrong.

The habitat structure of old-growth forests is significantly less dense and cluttered than working forests. Additionally, Angelo has a significantly wider and more open riparian corridor than the other sites. These site-level differences suggest that western red bats and big brown bats may be able to exploit lower forest habitat better at old-growth sites and in large riparian areas, whereas they may avoid cluttered habitat in younger forests by flying closer to treetop. This explanation for site-level differences is supported by other studies that have found that species adapted to edge-space and open-space foraging are less active in cluttered forest (Loeb, 2020). Species niche partitioning in redwood forests may thus vary significantly depending on forest management's influence on habitat structure, and this is the first study in redwood forests to incorporate vertical habitat gradient when studying this management influence on bats.

Not only were *Myotis* species more prevalent at ground-level, but the vast majority of calls at ground-level at three of the sites pertained to one species, California myotis. At old-growth sites, Angelo and Armstrong, calls detected at ground-level were still predominantly *Myotis* species, but no single species accounted for the majority of the calls. Given that conventional monitoring approaches survey at ground-level, understanding of bat activity in redwood forests is highly biased to these frequently detected species that are often only classified to the genus level. (Walters et al., 2012). By distinguishing the species, it is clear that California myotis, a generalist and clutter-adapted species, were far more common than all other species in working forest sites and the other *Myotis* species accounted for a greater proportion of calls at old-growth sites.

Seasonal activity patterns at regional and site-level

These results also support other study findings that many species of bats are active to some degree in redwood forest habitat year-round (Weller and Stricker, 2012; Zielinski and Gellman, 1999). However, whereas other studies attained this finding from capture methods (Weller and Stricker, 2012) and guano sampling of roosts (Gellman and Zielinski, 1996), my results demonstrate that acoustic surveys can be an effective non-invasive tool for studying seasonal activity patterns. Additionally, whereas mist net surveys in redwood forests had previously highlighted that silver-haired bats are more active than other species during the winter (Weller and Stricker, 2012), my study revealed that other migratory species, including hoary bats and Mexican free-tailed bats, are significantly active throughout the winter as well. But this activity may be overlooked because it largely occurs above the range of conventional survey methods. Consequently, this may lead natural resource managers and others concerned with bat conservation to underestimate the value of redwood forests as winter habitat for sensitive bat species.

Applying generalized additive models to multi-site monitoring studies can also inform understanding of site-level differences in species ecology across a larger landscape. Hoary bats, silver-haired bats, western red bats, and Mexican free-tailed bats are all migratory species and generally assumed to pass through the redwood ecosystem in the fall and spring. Although my results did suggest strong peaks in activity corresponding to migration events at most sites, hoary bat activity at my most southern site, Armstrong, appeared surprisingly consistent over the entire study. Our understanding of winter activity at Armstrong at treetop is unfortunately limited because that microphone was broken at this site from December 11, 2019 until February 19, 2020. However, species detections in early December and late February suggest hoary bats may be present in this habitat year-round.

Other species, including big brown bats and several *Myotis* species also showed signs of winter activity, especially at Armstrong. Evidence of winter activity has important implications because bats that are normally active and foraging during the winter might be more resilient to WNS than hibernating populations (Grider et al., 2016). More research should be done to understand winter activity patterns, including to what extent species are successfully foraging opposed to only becoming active to drink water or switch roosts.

Conclusions and future research directions

My study results demonstrate that incorporating innovative methods such as multi-site, year-round canopy studies and generalized additive model statistical approaches can provide important insights into enhancing understanding of forest bat ecology. These approaches can be effectively applied to biodiversity monitoring for other taxa as well to better under species ecology across sites and seasons and to inform conservation planning.

There is still much to be learned about species distribution patterns on both a regional and finer scale. For example, long-eared myotis and little brown bat activity varied significantly across sites but not between canopy and ground level. The significance of this effect for little brown bats appeared to be driven primarily by high detections at the old growth site in Angelo Coast Range Reserve and relatively low numbers of detections at the other sites. As detailed in my description of study sites, Angelo was the property with by far the most heterogeneous habitat. It is possible that little brown bat activity is influenced by habitat effects that are not present at the more homogeneous redwood habitat sites. Long-eared myotis were detected relatively infrequently at all sites, though detections were slightly higher at neighboring sites Angelo and Lyme than the other three study sites. Given that little brown bat populations have been especially devastated by WNS, and long-eared myotis and four other species found in redwood habitat are also susceptible to the disease, additional surveys should be done to understand patterns driving species distribution across this region and understand baseline populations before they are affected (Cheng et al., 2021; “White-Nose Syndrome,” 2021).

Some observed peaks in species activity did not coincide with migration behavior, including a peak in summer activity for many *Myotis* species. Other studies have also detected species-specific changes in activity patterns during the summer (Loeb et al., 2019). Further work on food availability and maternity season behavior may help explain changes in peak activity.

Also, this study largely focused on monitoring near riparian corridors because that is the habitat where bats are most active in this ecosystem. Expanding the number of detectors to allow for sampling in the uplands away from riparian habitat could reveal important differences in species assemblage between riparian and upland areas. For example, the sites which had a high number of Yuma myotis calls all had large, perennial stream corridors. This was expected because this species is known to be associated with open water and to forage extensively in stream areas (Braun et al., 2015). It would be interesting to examine how other species presence and activity patterns are influenced by proximity to streams and whether this also influences species comparisons between treetop and ground detectors. This expansion would further extend our understanding of bat activity across the entire redwood forest landscape but would require long-term monitoring at a fine spatial scale to accommodate low detection rates away from freshwater sources. Future research should also consider how acoustic presence and activity data can be used to derive estimates of abundance to better understand how species’ populations change seasonally in the ecosystem and across field sites.

References

Adams, A.M., Jantzen, M.K., Hamilton, R.M., Fenton, M.B., 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods Ecol Evol 3, 992–998. https://doi.org/10.1111/j.2041-210X.2012.00244.x

Armstrong, A., 2021. Use of redwood basal hollows by bats: a focus on the Townsend's big-eared bat on the North Coast of California. HSU theses and projects.

Bender, M.J., Castleberry, S.B., Miller, D.A., Bently Wigley, T., 2015. Site occupancy of foraging bats on landscapes of managed pine forest. Forest Ecology and Management 336, 1–10. https://doi.org/10.1016/j.foreco.2014.10.004

Bogan, M.A., Cryan, P.M., Valdez, E.W., Ellison, L.E., O'Shea, T.J., 2003. Western crevice and cavity-roosting bats (Federal Government Series), Western crevice and cavity-roosting bats. U.S. Geological Survey, Reston, VA.

Bombaci, S.P., Russell, R.E., St. Germain, M.J., Dobony, C.A., Ford, W.M., Loeb, S.C., Jachowski, D.S., 2021. Context dependency of disease-mediated competitive release in bat assemblages following white-nose syndrome. Ecosphere 12, e03825. https://doi.org/10.1002/ecs2.3825

Braun, J.K., Yang, B., González-Pérez, S.B., Mares, M.A., 2015. Myotis yumanensis (Chiroptera: Vespertilionidae). Mammalian Species 47, 1–14. https://doi.org/10.1093/mspecies/sev001

Britzke, E.R., Gillam, E.H., Murray, K.L., 2013. Current state of understanding of ultrasonic detectors for the study of bat ecology. Acta Theriol 58, 109–117. https://doi.org/10.1007/s13364-013-0131-3

Burns, E.E., Campbell, R., Cowan, P.D., 2018. State of Redwoods Conservation Report. Save the Redwoods League.

Carter, T.C., Menzel, M.A., Saugey, D.A., 2003. Population trends of solitary foliage-roosting bats In: O'Shea TJ and Bogan MA, Editors. Monitoring trends in bat populations of the United States and territories: problems and prospects. US Geological Survey Biological Resources Discipline, Information and Technology Report, USGS/BRD/ITR–2003–0003 1–274.

California Department of Forestry and Fire Protection, 2016. Jackson Demonstration State Forest Management Plan.

CDFW, 2019. Deadly Bat Fungus Detected in California. CDFW News. URL https://cdfgnews.wordpress.com/2019/07/05/deadly-bat-fungus-detected-in-california/ (accessed 1.13.22).

Cheng, T.L., Reichard, J.D., Coleman, J.T.H., Weller, T.J., Thogmartin, W.E., Reichert, B.E., Bennett, A.B., Broders, H.G., Campbell, J., Etchison, K., Feller, D.J., Geboy, R., Hemberger, T., Herzog, C., Hicks, A.C., Houghton, S., Humber, J., Kath, J.A., King, R.A., Loeb, S.C., Massé, A., Morris, K.M., Niederriter, H., Nordquist, G., Perry, R.W., Reynolds, R.J., Sasse, D.B., Scafini, M.R., Stark, R.C., Stihler, C.W., Thomas, S.C., Turner, G.G., Webb, S., Westrich, B.J., Frick, W.F., 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35, 1586–1597. https://doi.org/10.1111/cobi.13739

Coretta, S., 2022. tidymv: Tidy Model Visualisation for Generalised Additive Models.

Cowan, P., Burns, E.E., Campbell, R., 2017. A GIS approach to identifying the distribution and structure of coast redwood across its range.

Cryan, P.M., 2003. Seasonal Distribution of Migratory Tree Bats (Lasiurus and Lasionycteris) in North America. Journal of Mammalogy 84, 579–593. https://doi.org/10.1644/1545-1542(2003)084<0579:SDOMTB>2.0.CO;2

Cryan, P.M., Stricker, C.A., Wunder, M.B., 2014. Continental-scale, seasonal movements of a heterothermic migratory tree bat. Ecological Applications 24, 602–616. https://doi.org/10.1890/13-0752.1

Deeley, S.M., Kalen, N.J., Freeze, S.R., Barr, E.L., Ford, W.M., 2021. Post-white-nose syndrome passive acoustic sampling effort for determining bat species occupancy within the mid-Atlantic region. Ecological Indicators 125, 107489. https://doi.org/10.1016/j.ecolind.2021.107489

Denzinger, A., Schnitzler, H.-U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in Physiology 4, 164. https://doi.org/10.3389/fphys.2013.00164

Duff, A.A., Morrell, T.E., 2007. Predictive Occurrence Models for Bat Species in California. Journal of Wildlife Management 71, 693–700. https://doi.org/10.2193/2005-692

Fellers, G.M., Pierson, E.D., 2002. Habitat Use and Foraging Behavior of Townsend’s Big-Eared Bat (Corynorhinus Townsendii) in Coastal California. Journal of Mammalogy 83, 167–177. https://doi.org/10.1644/1545-1542(2002)083<0167:HUAFBO>2.0.CO;2

Fenton, M.B., 1990. The foraging behaviour and ecology of animal-eating bats. Can. J. Zool. 68, 411–422. https://doi.org/10.1139/z90-061

Flory, A.R., Kumar, S., Stohlgren, T.J., Cryan, P.M., 2012. Environmental conditions associated with bat white-nose syndrome mortality in the north-eastern United States. Journal of Applied Ecology 49, 680–689.

Foley, J., Clifford, D., Castle, K., Cryan, P., Ostfeld, R.S., 2011. Investigating and Managing the Rapid Emergence of White-Nose Syndrome, a Novel, Fatal, Infectious Disease of Hibernating Bats. Conservation Biology 25, 223–231. https://doi.org/10.1111/j.1523-1739.2010.01638.x

Fox, John, Weisberg, Sanford, Price, Brad, 2021. Companion to Applied Regression.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. Journal of Applied Ecology 50, 252–261. https://doi.org/10.1111/1365-2664.12034

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M., Kunz, T.H., 2010. An Emerging Disease Causes Regional Population Collapse of a Common North American Bat Species. Science 329, 679–682.

Frick, W.F., Puechmaille, S.J., Hoyt, J.R., Nickel, B.A., Langwig, K.E., Foster, J.T., Barlow, K.E., Bartonička, T., Feller, D., Haarsma, A.-J., Herzog, C., Horáček, I., van der Kooij, J., Mulkens, B., Petrov, B., Reynolds, R., Rodrigues, L., Stihler, C.W., Turner, G.G., Kilpatrick, A.M., 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24, 741–749. https://doi.org/10.1111/geb.12290

Froidevaux, J.S., Fialas, P.C., Jones, G., 2018. Catching insects while recording bats: impacts of light trapping on acoustic sampling. Remote Sensing in Ecology and Conservation 4, 240–247.

gam.check function - RDocumentation [WWW Document], n.d. URL https://www.rdocumentation.org/packages/mgcv/versions/1.8-38/topics/gam.check (accessed 1.9.22).

Global Biodiversity Information Facility (GBIF) [WWW Document], n.d. URL https://www.gbif.org/ (accessed 1.12.22).

Gellman, S.T., Zielinski, W.J., 1996. Use by Bats of Old-Growth Redwood Hollows on the North Coast of California. Journal of Mammalogy 77, 255–265. https://doi.org/10.2307/1382726

Grider, J.F., Larsen, A.L., Homyack, J.A., Kalcounis-Rueppell, M.C., 2016. Winter Activity of Coastal Plain Populations of Bat Species Affected by White-Nose Syndrome and Wind Energy Facilities. PLOS ONE 11, e0166512. https://doi.org/10.1371/journal.pone.0166512

Hastie, T.J., 1992. Generalized Additive Models, in: Statistical Models in S. Routledge.

Hulme, P.E., 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42, 784–794. https://doi.org/10.1111/j.1365-2664.2005.01082.x

Jetz, W., McGeoch, M.A., Guralnick, R., Ferrier, S., Beck, J., Costello, M.J., Fernandez, M., Geller, G.N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F.E., Pereira, H.M., Regan, E.C., Schmeller, D.S., Turak, E., 2019. Essential biodiversity variables for mapping and monitoring species populations. Nat Ecol Evol 3, 539–551. https://doi.org/10.1038/s41559-019-0826-1

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. PNAS 107, 4533–4538. https://doi.org/10.1073/pnas.0915062107

Jones, G., Vaughan, N., Parsons, S., 2000. Acoustic identification of bats from directly sampled and time-expanded recordings of vocalizations. Acta Chiropterologica 2, 155–170.

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., Kalko, E.K.V., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. Journal of Applied Ecology 49, 523–531. https://doi.org/10.1111/j.1365-2664.2012.02116.x

Kalcounis, M.C., Hobson, K.A., Brigham, R.M., Hecker, K.R., 1999. Bat Activity in the Boreal Forest: Importance of Stand Type and Vertical Strata. Journal of Mammalogy 80, 673–682. https://doi.org/10.2307/1383311

Kennedy, J.-P., Sillett, S.C., Szewczak, J.M., 2014. Bat Activity Across the Vertical Gradient of an Old-Growth Sequoia sempervirens Forest. Acta Chiropterologica 16, 53–63. https://doi.org/10.3161/150811014X683264

Klingbeil, B.T., Willig, M.R., 2009. Guild-Specific Responses of Bats to Landscape Composition and Configuration in Fragmented Amazonian Rainforest. Journal of Applied Ecology 46, 203–213.

Kühnert, E., Schönbächler, C., Arlettaz, R., Christe, P., 2016. Roost selection and switching in two forest-dwelling bats: implications for forest management. Eur J Wildl Res 62, 497–500. https://doi.org/10.1007/s10344-016-1021-1

Kunz, T.H., Arnett, E.B., Erickson, W.P., Hoar, A.R., Johnson, G.D., Larkin, R.P., Strickland, M.D., Thresher, R.W., Tuttle, M.D., 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Frontiers in Ecology and the Environment 5, 315–324. https://doi.org/10.1890/1540-9295(2007)5[315:EIOWED]2.0.CO;2

Kunz, T.H., Fenton, M.B., 2005. Bat Ecology. University of Chicago Press.

Lacki, M.J., Hayes, J.P., Kurta, A., 2007. Bats in Forests: Conservation and Management. JHU Press.

Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H., Marm Kilpatrick, A., 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecology Letters 15, 1050–1057. https://doi.org/10.1111/j.1461-0248.2012.01829.x

Loeb, S.C., 2020. Qualitative synthesis of temperate bat responses to silvicultural treatments—where do we go from here? Journal of Mammalogy 101, 1513–1525. https://doi.org/10.1093/jmammal/gyaa089

Loeb, S.C., Hines, B.A., Armstrong, M.P., Zarnoch, S.J., 2019. Effects of Omnidirectional Microphone Placement and Survey Period on Bat Echolocation Call Quality and Detection Probabilities. acta 21, 453–464. https://doi.org/10.3161/15081109ACC2019.21.2.019

Loeb, S.C., Rodhouse, T.J., Ellison, L.E., Lausen, C.L., Reichard, J.D., Irvine, K.M., Ingersoll, T.E., Coleman, J.T.H., Thogmartin, W.E., Sauer, J.R., Francis, C.M., Bayless, M.L., Stanley, T.R., Johnson, D.H., 2015. A plan for the North American Bat Monitoring Program (NABat). Gen. Tech. Rep. SRS-208. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 208, 1–100. https://doi.org/10.2737/SRS-GTR-208

Mazurek, M.J., Zielinski, W.J., 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecology and Management 193, 321–334. https://doi.org/10.1016/j.foreco.2004.01.013

Menzel, J.M., Menzel, M.A., Kilgo, J.C., Ford, W.M., Edwards, J.W., McCRACKEN, G.F., 2005. Effect of Habitat and Foraging Height on Bat Activity in the Coastal Plain of South Carolina. The Journal of Wildlife Management 69, 235–245. https://doi.org/10.2193/0022-541X(2005)069<0235:EOHAFH>2.0.CO;2

Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson, J.-F., Villegas, S.E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R., Jenkins, R.K.B., Jung, K.G., Kingston, T., Kunz, T.H., Cristina MacSwiney Gonzalez, M., Moya, I., Patterson, B.D., Pons, J.-M., Racey, P.A., Rex, K., Sampaio, E.M., Solari, S., Stoner, K.E., Voigt, C.C., von Staden, D., Weise, C.D., Kalko, E.K.V., 2011. Accounting for detectability improves estimates of species richness in tropical bat surveys. Journal of Applied Ecology 48, 777–787. https://doi.org/10.1111/j.1365-2664.2011.01976.x

Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Veith, M., Fenton, B., 2013. From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height. Forest Ecology and Management 306, 179–184. https://doi.org/10.1016/j.foreco.2013.06.043

Neuweiler, G., 1983. Echolocation and Adaptivity to Ecological Constraints, in: Huber, F., Markl, H. (Eds.), Neuroethology and Behavioral Physiology. Springer, Berlin, Heidelberg, pp. 280–302. https://doi.org/10.1007/978-3-642-69271-0_21

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W., Purvis, A., 2018. Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. PLOS Biology 16, e2006841. https://doi.org/10.1371/journal.pbio.2006841

O'Shea, T.J., Bogan, M.A., 2003. Monitoring trends in bat populations of the United States and territories: problems and prospects. Publications of the US Geological Survey 16.

Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by Bats in Cleared, Thinned and Unharvested Boreal Forest. Journal of Applied Ecology 40, 646–657.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science. https://doi.org/10.1126/science.1246752

Plank, M., Fiedler, K., Reiter, G., 2012. Use of forest strata by bats in temperate forests. Journal of Zoology 286, 154–162. https://doi.org/10.1111/j.1469-7998.2011.00859.x

Polis, G.A., Power, M.E., Huxel, G.R., Huxel, G.R., 2004. Food Webs at the Landscape Level. University of Chicago Press.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Russo, D., Cistrone, L., Jones, G., 2005. Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats Barbastella barbastellus. Ecography 28, 769–776. https://doi.org/10.1111/j.2005.0906-7590.04343.x

Sauer, J.R., Link, W.A., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J., Jr., 2013. The North American Breeding Bird Survey 1966–2011: Summary Analysis and Species Accounts. North American Fauna 1–32. https://doi.org/10.3996/nafa.79.0001

Saunders, M.B., Barclay, R.M.R., 1992. Ecomorphology of Insectivorous Bats: A Test of Predictions Using Two Morphologically Similar Species. Ecology 73, 1335–1345. https://doi.org/10.2307/1940680

Save-the-Redwoods League, Noss, R.F., 2013. The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Chicago, United States.

Sillett, S.C., Van Pelt, R., Carroll, A.L., Kramer, R.D., Ambrose, A.R., Trask, D., 2015. How do tree structure and old age affect growth potential of California redwoods? Ecological Monographs 85, 181–212. https://doi.org/10.1890/14-1016.1

Szewczak, J.M., Parsons, S., Morrison, M.L., 2011. Automated Acoustic Identification of Bats. Humboldt State Univ Arcata, CA.

Torregrosa, A., Combs, C., Peters, J., 2016. GOES-derived fog and low cloud indices for coastal north and central California ecological analyses. Earth and Space Science 3, 2015EA000119. https://doi.org/10.1002/2015EA000119

Walters, C.L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M.K., Puechmaille, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. Journal of Applied Ecology 49, 1064–1074. https://doi.org/10.1111/j.1365-2664.2012.02182.x

Weller, T.J., Castle, K.T., Liechti, F., Hein, C.D., Schirmacher, M.R., Cryan, P.M., 2016. First Direct Evidence of Long-distance Seasonal Movements and Hibernation in a Migratory Bat. Sci Rep 6, 34585. https://doi.org/10.1038/srep34585

Weller, T.J., Stricker, C.A., 2012a. Northern California redwood forests provide important seasonal habitat for migrant bats. In: Standiford, Richard B.; Weller, Theodore J.; Piirto, Douglas D.; Stuart, John D., tech. coords. Proceedings of coast redwood forests in a changing California: A symposium for scientists and managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 447-457 238, 447–457.

Weller, T.J., Stricker, C.A., 2012b. Northern California redwood forests provide important seasonal habitat for migrant bats. pp. 447–457.

White-Nose Syndrome [WWW Document], n.d. URL https://www.whitenosesyndrome.org/static-page/bats-affected-by-wns (accessed 12.29.21).

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., RStudio, 2021. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics.

Wood, S., 2021. mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation.

Zielinski, W.J., Gellman, S.T., 1999. Bat Use of Remnant Old-Growth Redwood Stands. Conservation Biology 13, 160–167. https://doi.org/10.1046/j.1523-1739.1999.97424.x

Chapter 3:

Microclimatic drivers of winter bat activity in coastal forests

Abstract

Bats represent one of the most diverse mammal assemblages on earth, but due to their cryptic nature little is known about many species even in well-studied areas such as North America. Bats face myriad long-term threats including habitat loss, wind energy development, and climate change, but the most immediate threat for North American bats is the fungal disease white-nose syndrome (WNS), which has led to die offs throughout the northeast and is spreading west. Bat ecology, especially winter activity and roosting behavior, influences species susceptibility to WNS. If bats are normally active during the winter, then these populations may be more resilient to mortality from WNS than hibernating populations. Therefore, to predict and mitigate future WNS disease impacts we need to determine how overwintering behavior for both migratory and resident species varies in relation to environmental conditions. This study investigated the environmental conditions under which winter bat activity was detected in a coast redwood forest ecosystem with mild winter temperatures. Generalized linear mixed models were used to relate acoustic detection probability for eight species found in coast redwood forests of California to daytime and nighttime temperature and relative humidity. Because different species are active at different levels of tall forest habitat (Chapter 2), I also examined the effect of acoustic detector placement (treetop or ground-level). The results indicate that daytime maximum temperature was the microclimate variable that best explained variation in nightly probability of bat acoustic presence. The species detected most frequently during the winter included California myotis, which was detected on 43% of ground-detector nights, and Mexican free-tailed bat, which was detected on 49% of treetop-detector nights. Nine other species were also detected as active between December through February, suggesting that coastal California may provide important winter habitat and possibly a WNS disease refugia for both migratory and resident species.

Introduction

Globally, 80% of the 1236 known bat species reviewed by the International Union for the Conservation of Nature (IUCN) require conservation or research attention, including 18% listed as threatened, 15% listed as data-deficient and over 50% of species classified as having unknown or decreasing population trends (Frick et al., 2020). This dearth of knowledge is especially troubling given the severe disease-induced population declines of several North American bat species, especially the little brown bat (*Myotis lucifugus*) which was once ubiquitous and is now considered endangered (Frick et al., 2010; "The IUCN Red List of Threatened Species," 2022).

White-nose syndrome (WNS), a wildlife disease caused by the fungal pathogen *Pseudogymnoascus destructans*, affects North American hibernating bat populations by altering their physiology so that they awake more frequently from winter torpor (Reeder et al., 2012). Although bats normally arouse periodically during the winter, this increased arousal in cold climates causes bats to expend additional energy, and mortality occurs when bats deplete their fat reserves to the point of starvation (Verant et al., 2014). Even if bats survive the winter, the stress of the disease may impact their reproductivity and indirectly result in population declines (Maslo et al., 2015). Although the devastation of WNS was initially limited to the northeastern United States where it was first detected in 2006, it has spread west, and models predict that it will ultimately affect 80% of counties of the contiguous U.S. (O'Regan et al., 2015). The detection of the pathogen on the west coast of the U.S. in 2016 has accelerated the urgency to understand how the disease will impact western North American bat populations (Lorch et al., 2016).

In order to predict and mitigate future disease impacts, we need to better understand the winter ecology of western bats. Little is known about western bat overwintering locations or their winter activity patterns because they do not form large hibernacula colonies like their eastern counterparts but rather roost individually or in small groups (Weller et al., 2018). An extensive review of winter bat survey records from 11 western states found that 95% of aggregations of *Myotis* species were composed of ≤ 10 individuals (Weller et al., 2018). It is possible that this dispersion will confer resilience to western bat populations because the pathogen will not spread as easily as it does between bats that are socially gregarious or hibernate in large groups (Langwig et al., 2012). However, this also complicates both local and continental efforts to monitor the impacts of disease on populations (Cheng et al., 2021). Forest bats are especially hard to survey because they generally roost inconspicuously in trees instead of caves or human structures, and they frequently switch roosts (Fellers and Pierson, 2002; Kunz and Fenton, 2005; Zielinski and Gellman, 1999). This means that forest bat population trends cannot be monitored using standard roost survey methods, and they may be vulnerable to habitat loss and disturbance associated with timber harvests or forest conversion.

Coastal habitat with mild climates may be an important refuge for North American bat populations because there is evidence that healthy bats in these areas are more active during the winter than inland populations of the same species (Falxa, 2007; Grider et al., 2016; Parker et al., 2020). Bats in climatically mild and relatively stable areas may survive the winter through a combination of remaining active to opportunistically forage and using torpor to conserve resources when foraging is not feasible or energetically cost-effective (Turbill and Geiser, 2008). Some migratory species, such as hoary bats (*Lasiurus cinereus*), 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 (Marín et al., 2021; Weller et al., 2016). Because the fungal pathogen *P. destructans* grows at higher rates under relatively warm and humid winter conditions (Verant et al., 2012), this could conversely result in disease impacts being more severe for hibernating bats in mild winter areas (Langwig et al., 2012). Determining how overwintering behavior for both migratory and resident species varies in relation to environmental conditions is thus critical for assessing population susceptibility to WNS.

The primary objective of this study was to evaluate the environmental conditions that are conducive to detecting winter bat activity in order to inform efforts to monitor cryptic bat populations. More specifically, I investigated the relationship between microclimate and insectivorous bat activity in coast redwood forests of California during December through February. Generalized linear mixed models are used to explore how temperature and humidity variables influenced nightly probability of detection, and how detection probability was additionally influenced by locating detectors at treetop versus ground-level. I hypothesized that nightly detection probability would be positively associated with temperature variables and negatively associated with relative humidity because bats would be more active under warmer and drier conditions when flight is less energetically costly and prey more likely to be available than when the weather is cold and wet. Based on previous comparisons of treetop versus ground-level detector placement (Chapter 2), I conducted analysis for both survey locations across five study sites. California coast redwood forests experience mild winter temperatures, and while six susceptible species and three additional species that carry the fungal pathogen are known to occur in these forests, there is no evidence of infection to date (“White-Nose Syndrome,” 2022). Understanding the normal winter activity patterns of bat populations before the arrival of a novel disease can be applied to help scientists and natural resource managers to anticipate the relative susceptibility of diverse species and to proactively identify habitat important for species conservation.

2 Materials and Methods

2.1 Study sites

I studied winter bat activity at five coast redwood forest sites in Mendocino and Sonoma Counties of Northern California (Figure 1). The study area is characterized by mild but wet winters, with 55% of annual precipitation (43.16 in annually) normally occurring between December through February (National Centers for Environmental Information, U.S. Climate Normals). December is normally the coldest month of the year, with a mean minimum temperature of 4.3 ^{o}C and a mean maximum temperature of 10.8 ^{o}C (National Centers for Environmental Information, U.S. Climate Normals). Study sites were selected to be representative of the mosaic of diverse forest management types of the redwood ecosystem, including two commercial timber properties (“Lyme” and “Mallo Pass”), Jackson Demonstration State Forest (“Caspar”), one 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. 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 forest bat activity is generally found to be highest along large stream corridors (Seidman and Zabel, 2001).

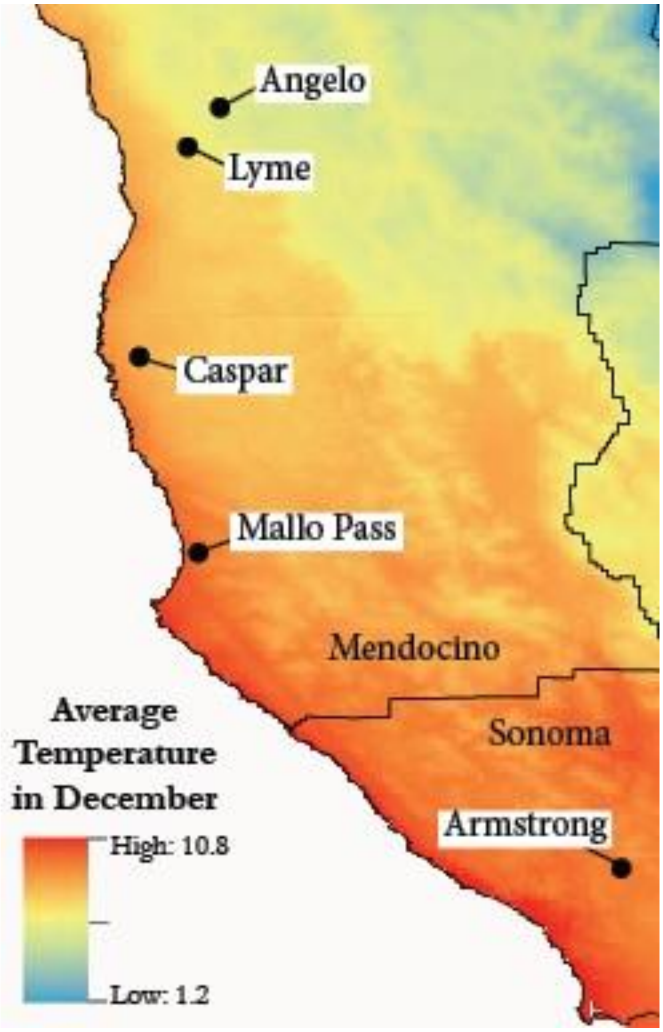


Figure 1: Five redwood forest study sites located between 2 to 15 km of the coast were selected to represent diverse management types of the Northern California coast redwood ecosystem. Map shows historical average temperature (in ⁰C) for the month of December based on the WorldClim version 2.1 climate data for 1970-2000 at 30 second (~1 km^2) spatial resolution (Fick and Hijmans, 2017).

2.2 Field data collection

I monitored winter bat activity at fixed locations from December 1, 2019 to February 29, 2020 using Wildlife Acoustics Song Meter SM2BAT 384 kHz (SM2) and SM4BAT (SM4) full-spectrum bat detectors with omnidirectional microphones (Wildlife Acoustics Inc., Maynard, MA). Coast redwood forests are the tallest forests in the world, with mature trees regularly exceeding heights of 90 m (Sillett et al., 2015). Consequently, canopy-level bat activity in this habitat is regularly beyond the range of ground-based ultrasonic detectors (Agranat, 2014; Kennedy et al., 2014). Therefore, at each site, one detector was placed at ground-level at the edge of the riparian corridor and another detector was placed at the top of the highest nearby tree. The same model of detector (SM2 or SM4) was used at paired ground and treetop locations at each site. The microphones of ground-level detectors were sited at least 2 m from vegetation and elevated 3-4 m above the ground on telescopic poles. The microphones of treetop detectors were attached to telescopic poles and extended horizontally from the tree 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 as follows: Armstrong, 78 m; Angelo, 60.5 m; Caspar, 49.5 m; Lyme, 38 m; and Mallo Pass, 33 m.

Each model of detector was deployed using the recommended settings for that model in California forest habitat. For SM2 detectors: gain = 10 dB, trigger window = 2 s, maximum trigger length = 5 s, trigger level = 12 SNR, division ratio = 8. For SM4 detectors: gain = 12 dB, minimum duration = 1.5 ms, minimum trigger frequency = 16 kHz, trigger window = 3 s, maximum trigger length = 15 s., trigger level = 12 SNR, division ratio = 8. SM2 detectors were powered by three 6 V 12 Ah lead-acid batteries set in parallel, and the newer model SM4 detectors were powered by two 6 V 12 Ah lead-acid batteries set in parallel. These setups were sufficient for the detectors to record from sunset to sunrise every other night before the batteries needed to be recharged during monthly site visits. During each site visit, I also collected the 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. I counted each full night that a detector was functional as a “detector night.”

To relate bat activity to weather and microclimate, I monitored ambient temperature and relative humidity at each study site using iButton Hygrochron DS1923 sensors (Maxim Integrated Products Inc, San Jose, CA). A sensor was hung from vegetation near each ground-based detector and shielded from precipitation and sunlight by a plastic hood. The sensors sample temperature and humidity every 30 minutes.

2.3 Species presence identification

To determine bat species presence for each detector night, I used SonoBat bat call analysis software (Arcata, CA) to identify recorded bat passes to species. I first filtered out non-bat and poor-quality call files using the SonoBat Batch Attributer 6.5. I then auto-classified calls to species using SonoBat with the Northwest California regional classifier. I manually vetted the data by visually reviewing auto-classified call files for each detector night and confirming that there was at least one confidently identified call for each species that SonoBat had identified. If at least one call was confidently identified, then I counted the species as “present” on that monitoring night at that detector location. I 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, I calculated the proportion of nights that each species was present at each of the ten detector locations, as well as across all ground-detector nights and across all treetop-detector nights. I plotted both 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 location.

2.4 Weather and climate data analysis

I analyzed iButton data recorded in the field to characterize the daily and nightly temperature and relative humidity for each study site. Because iButtons needed to be briefly handled during each monthly field visit to collect data and this may affect the first temperature reading, I omitted the first data point for each monitoring round. I used R statistical analysis software (R Core Team, 2021) with package ‘suncalc’ to calculate sunset and sunrise times for each detector night based on the latitudinal and longitudinal coordinates of the field site. I filtered data to begin at sunrise of the first monitoring night date (12/1/2019) and end at sunrise following the last monitoring night (2/29/2020). If iButton data was logged at or after sunrise and before sunset, then it was considered ‘daytime.’ If it was logged at or after sunset and before sunrise then it was considered ‘nighttime.’ I then calculated the following statistics for both temperature and relative humidity at each study site for each monitoring night date: minimum, maximum, and mean values for both ‘daytime’ and ‘nighttime.’ Even though the iButton sensors were shielded beneath a plastic hood, some logged relative humidity values were above 100%, erroneous values that result from the sensor being exposed to a wet environment. To correct this error, I adjusted these relative humidity values to be 100.

After calculating the ‘daytime’ and ‘nighttime’ temperature and relative humidity statistics for each detector night, I combined this data with the bat species detection data. Because microclimate was only logged at ground-level at each field site, the same microclimate data was paired with both the ground and treetop bat detection data. I also plotted the daytime maximum temperature, nighttime maximum temperature, and nighttime minimum relative humidity by Julian date to observe temporal trends in microclimate conditions and how this varied across the study sites. Daily maximum temperature values from the GridMET dataset (Abatzoglou, 2013) were retrieved to provide historical meteorological data. Specifically, I used the period from January 1, 2010 until December 31, 2020 for each of the five study site coordinates and filtered the data to only include winter months (January, February, and December).

2.5 Species presence models

I developed species-specific generalized linear mixed models (GLMMs) for eight species to relate microclimate explanatory variables to nightly detection of bat species presence. I omitted species models for the three most rarely detected species: little brown bat (present on 4 detector nights), pallid bat (4 detector nights), and long-eared bat (7 detector nights) because there were too few detections for the models to converge. I used binomial distribution models with a logit-link function because this is appropriate for a binary outcome of nightly presence or non-detection. All statistical and model analyses were conducted using R version 4.1.2 (R Core Team, 2021).

To test my hypothesis that bats were more likely to be active on nights when relative humidity was lower, indicating drier weather, I included the explanatory variable nighttime minimum relative humidity (‘Night.Min.Humid’) as the relative humidity variable of interest. To test my hypotheses that bats were more likely to be active on warmer nights and on nights following warmer daytime conditions, I tested both nighttime maximum temperature (‘Night.Max.Temp’) and daytime maximum temperature (‘Day.Max.Temp’). However, before running statistical models, I used ‘cor( )’ function in R to check the Spearman correlation coefficients of potential explanatory variables and found that daytime and nighttime temperature statistics were highly correlated with a correlation coefficient of .84 (see Supporting Information for correlation table). I therefore included these variables in separate models. I included detector location (‘Location’, factor with 2 levels: ‘ground’ and ‘treetop’) as a fixed effect and study site (‘Site’, factor with 5 levels) as a random effect in all models. I examined the following candidate models for each species:

Null: Presence ~ (1|Site)

Location: Presence ~ Location + (1|Site)

RH: Presence ~ Night.Min.Humid + Location + (1|Site)

Day: Presence ~ Day.Max.Temp + Location + (1|Site)

Night: Presence ~ Night.Max.Temp + Location + (1|Site)

Day + RH: Presence ~ Night.Min.Humid + Day.Max.Temp + Location + (1|Site)

Night + RH: Presence ~ Night.Min.Humid + Night.Max.Temp + Location + (1|Site)

Day x RH: Presence ~ Night.Min.Humid + Day.Max.Temp +
    Night.Min.Humid x Day.Max.Temp + Location + (1|Site)

Night x RH: Presence ~ Night.Min.Humid + Night.Max.Temp +
    Night.Min.Humid x Night.Max.Temp + Location + (1|Site)

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, I first ran the full models that included the interaction of the humidity variable with the daytime or nighttime temperature variable. If there were any convergence warnings when I used glmer( ) to run the initial models, then I used function lme4::allFit( ) with additional packages dfoptim (Varadhan et al., 2020) and optimx (Nash et al., 2021) to fit the models with alternative optimizers. Seven species models were fit without convergence issues using the default glmer( ) settings. The model for western red bat initially had model convergence issues, but this was resolved by setting the optimizer to “bobyqa.” I tested fitted models for dispersion and residual diagnostics by using the DHARMa package (Hartig and Lohse, 2021) (see Supporting Information for residual diagnostics plots).

After confirming that there were no convergence issues with the full fitted models, I used function ‘model.sel’ from package MuMIN to perform model selection. I 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 ΔAICc ≤ 2 as top models (Burnham and Anderson, 2002). I reported maximized log-likelihood, number of estimable parameters, and Akaike weights of top models, as well as model estimates of variables that had a significant effect for the best model for each species.

To predict when these species are most likely to be active during the winter, I used the ‘predict.merMod’ function to examine the effect of daytime maximum temperature (strongest explanatory variable from the GLMM analysis) on probability of species detection for both ground and treetop detector locations. To generate new data values, I used the range of daytime maximum temperatures observed: 4.1ºC to 21.8ºC and also included the mean observed daytime maximum temperature (10.2ºC). For the fitted model object, I used the model Presence ~ Day.Max.Temp + Location + (1|Site). Because the predict function is unable to return the standard error for the predicted values of models including random effects, I used function 'bootMER' to apply a bootstrapping approach and derive a 95% confidence interval from simulated predictions. I plotted the predicted probability of species presence in relation to daytime maximum temperature to visually examine how probabilities varied by species and detector location. As an additional method to compare winter detections across species, I plotted species-specific probability of detection under mean observed daytime maximum temperature.

Finally, I identified the range of daytime maximum temperatures at which species were predicted to have at least a 50% probability of detection at either ground-level or treetop and examined how often these temperatures normally occur across the study area based on the historical meteorological data. This data was filtered and combined for all five sites (4,965 total winter days) to calculate how often maximum temperature was greater than or equal to temperature values from 11 ºC to 22 ºC. I plotted the result as the average number of days per winter at which the maximum temperature occurs at or above each threshold value.

3 Results

3.1 Species presence results

This field study resulted in a total of 315 detector nights at ten locations and the total functional detector nights at each of the other detector locations ranged from 26 to 45 nights (Table 1), with the exception of Armstrong at treetop (nights = 10) and Angelo at ground-level (nights = 13) which experienced significant equipment failures. 4,762 bat calls were classified to the following 11 species: pallid bat (*Antrozous pallidus*), big brown bat (*Eptesicus fuscus*), western red bat (*Lasiurus blossevillii*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), California myotis (*Myotis californicus*), long-eared myotis (*Myotis evotis*), little brown bat (*Myotis lucifugus*), fringed myotis (*Myotis thysanodes*), Yuma myotis (*Myotis yumanensis*), and Mexican free-tailed bat (*Tadarida brasiliensis*). The only species known to occur in this study area during other seasons that were not detected during this winter study were Townsend's big-eared bat (*Corynorhinus townsendii*) and long-legged myotis (*Myotis volans*).

Table 1: Summary of detector nights and total confidently identified calls identified to species by study site and detector location.

Site	Treetop Mic Hgt (m)	Detector Location	Detector Nights	Confident ID Calls	Mean Calls/Night
Angelo	60.5	Ground	13	69	5.3
		Treetop	43	491	11.4
Armstrong	78	Ground	45	296	6.6
		Treetop	10	1,174	117.4
Caspar	49.5	Ground	38	52	1.4
		Treetop	26	206	7.9
Lyme	38	Ground	31	11	0.4
		Treetop	45	724	16.1
MalloPass	33	Ground	28	438	15.6
		Treetop	36	1,301	36.1

As shown in figure 2, the proportion of nights for which bat activity was detected varied by species, study site and detector location. For example, the species detected most frequently by ground-level detectors was California myotis. It was detected on 43% of total ground-detector nights across the entire study, and on 31% of total treetop-detector nights. However, the proportion of ground-detector nights that the species was identified ranged from 16% to 64% across the five study sites, and the proportion of treetop-detector nights ranged from 5% to 64%. The species detected most frequently at treetop was the Mexican free-tailed bat. It was detected on 49% of treetop-detector nights across the entire study (detection at individual sites ranging from 33% to 90% of treetop-detector nights). However, it was only detected on 17% of ground-detector nights (range of 3 – 46%). Similarly, the hoary bat was detected on 46% of treetop-detector nights (range of 11 – 90%) but only 12% of ground-detector nights (range of 3 – 46%); and the silver-haired bat was detected on 24% of treetop-detector nights (range of 2 – 40%) but only 8% of ground-detector nights (range of 0 – 100%). Another species which was detected more frequently at treetop than ground-level was the western red bat; it was detected on 9% of treetop-detector night and 4% of ground-detector nights.

Five species were detected more frequently at treetop, and six species were detected more frequently at ground-level. The most rarely detected species included pallid bat, long-eared myotis, and little brown bat. The little brown bat was detected as present on a single night at treetop at four of the five study sites, and it was not detected at all at ground-level. Conversely, the long-eared myotis and pallid bat were detected only at ground-level.

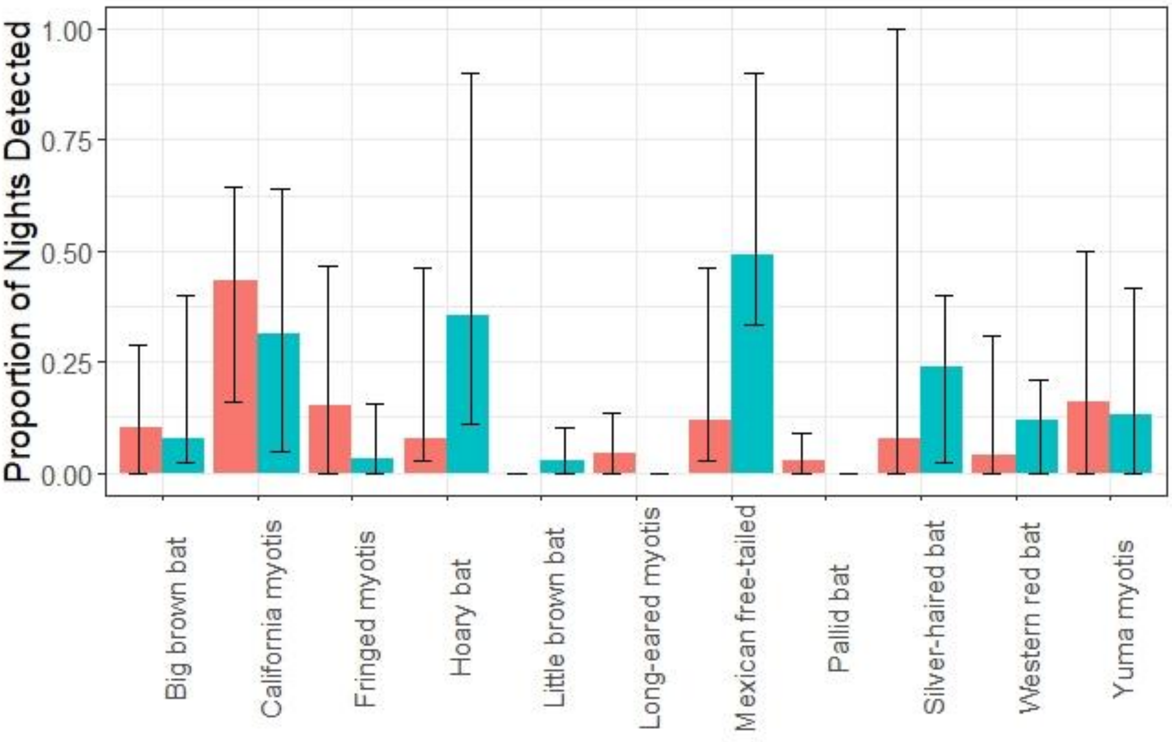


Figure 2: Red bars show the proportion of nights the species was detected across all ground-detector nights and blue bars show the proportion of nights detected across all treetop-detector nights. Error bars show the range in proportion of nights detected across the five study sites.

3.2. Microclimate data results

Maximum daytime temperature ranged from 2.6ºC to 21.8ºC, with a mean of 10.2ºC across the five study sites. Maximum nighttime temperature ranged from 2.6ºC to 14.1ºC, with a mean of 8.6ºC. 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 humidity at 100% on all nights across the five study sites (Figure 3). As demonstrated by figure 3, similar temporal trends in microclimate were observed across the five study sites, though greater variation between sites in relative humidity and maximum daytime temperature statistics was observed in February. It is evident from the February data the most inland site, Angelo, experienced a higher maximum daytime temperature and lower minimum nighttime relative humidity than the other sites. The most coastal study site, Mallo Pass, continued to have a minimum nighttime relative humidity of 100% on most nights during February.

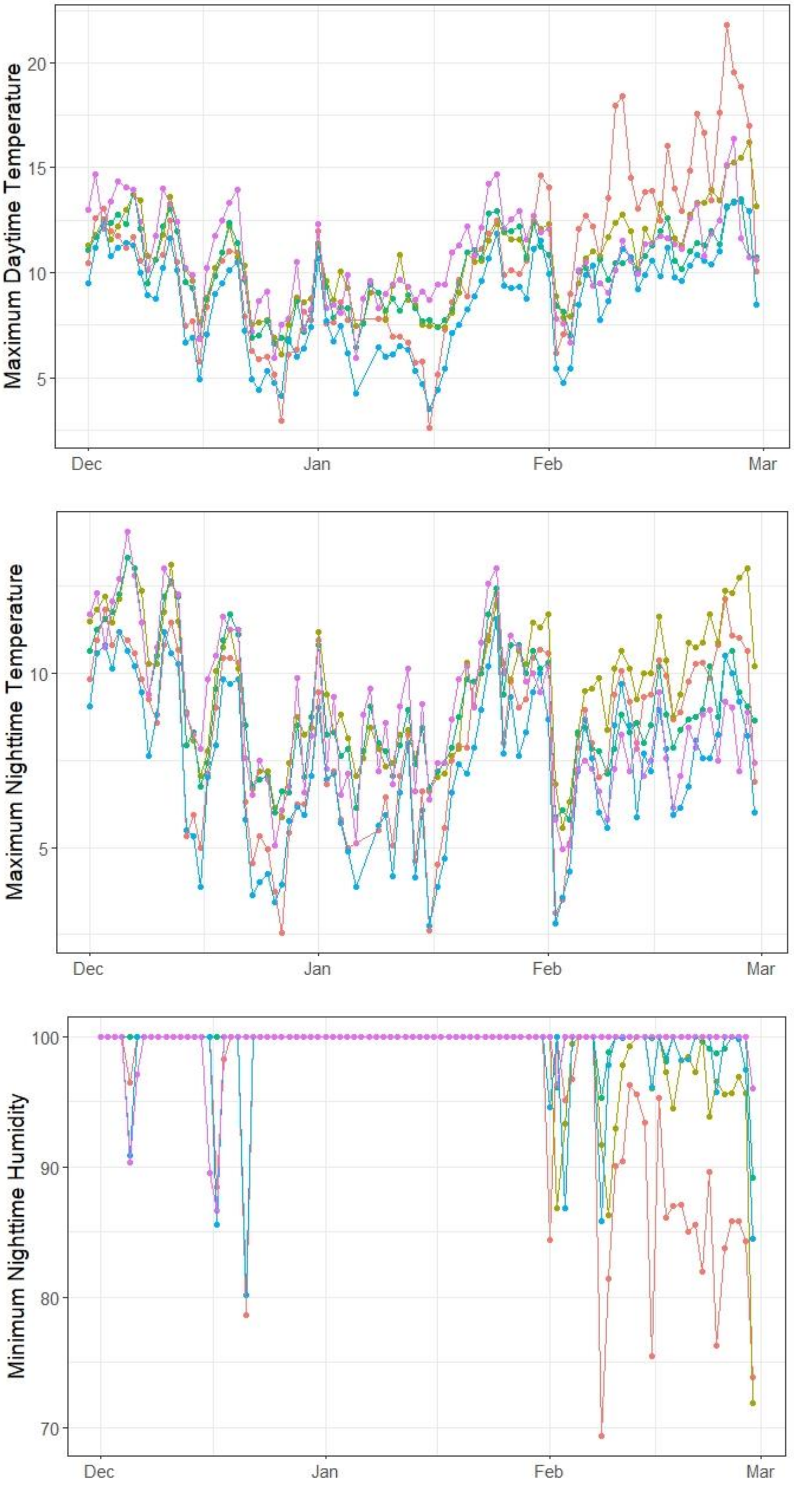


Figure 3: Plots show daily temperature and relative humidity statistics calculated from iButton data logged from December 2019 to February 2020 at the five study sites: Angelo (red), Armstrong (yellow), Caspar (green), Lyme (blue) and Mallo Pass (purple). 100% RH was observed across all sites in January.

3.4. 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 2). The top model for six of the eight species included daytime maximum temperature as the only microclimate explanatory variable. The top model for big brown bat included both daytime maximum temperature and relative humidity. The top model for Yuma myotis included the interaction of daytime maximum temperature and relative humidity.

Table 2: Top generalized linear mixed models ranked by AICc for each species nightly probability of presence. Explanatory variables included: daytime maximum temperature (Day), nighttime maximum temperature (Night), nighttime minimum relative humidity (RH), and the interaction between temperature variable and relative humidity. All models also included detector location (ground or treetop) as a fixed effect and study site as a random effect.

Species	Model	K	logLik	AICc	delta	weight
Big brown bat	Day + RH	5	-78.83	167.85	0	0.446
	Day + RH + Day x RH	6	-78.73	169.73	1.88	0.174
	Night	4	-80.81	169.75	1.902	0.172
Western red bat	Day	4	-74.43	156.99	0	0.399
	Day + RH + Day x RH	6	-72.43	157.13	0.139	0.372
	Day + RH	5	-74.39	158.97	1.976	0.149
Hoary bat	Day	4	-117.8	243.73	0	0.5
	Day + RH	5	-117.21	244.61	0.883	0.321
Silver-haired bat	Day	4	-109.82	227.77	0	0.638
	Day + RH	5	-109.77	229.73	1.958	0.24
California myotis	Day	4	-182.99	374.11	0	0.577
	Day + RH	5	-182.91	376.02	1.916	0.221
Fringed myotis	Day	4	-70.06	148.25	0	0.45
	Day + RH	5	-70	150.19	1.939	0.171
Yuma myotis	Day + RH + Day x RH	6	-102.27	216.81	0	0.759
Mexican free-tailed bat	Day	4	-134.44	277.02	0	0.623

Daytime maximum temperature had a positive significant effect (Pr(>|z|) < 0.05) on probability of presence for all eight species (Table 3; Figure 4). Probability of presence of big brown bat was positively associated with relative humidity. Probability of presence of Yuma myotis was positively associated with the interaction of daytime maximum temperature and relative humidity. Location also had a significant effect on the probability of nightly detection for four species. Hoary bat, silver-haired bat, and Mexican free-tailed bat were detected significantly more frequently at treetop, whereas fringed myotis were detected significantly more frequently at ground-level (Figure 5).

Table 3: GLMM model results from each species' best model for nightly presence as shown in Table 2 and only including estimates and standard error for fixed effects which had a significant effect (Pr(>|z|) < 0.05) on species presence. Explanatory variables that had a significant effect included: maximum daytime temperature (Day), relative humidity (RH), the interaction Day x RH, and detector location (Location).

Species	Variable	Coefficient	SE	z value	Pr(>|z|)
Big brown bat	Day	1.27	0.35	3.67	< .001
	RH	1.03	0.51	2.00	0.045
Western red bat	Day	0.58	0.21	2.80	0.005
Hoary bat	Day	1.26	0.21	5.98	< .001
	Location	-1.24	0.21	-5.91	< .001
Silver-haired bat	Day	1.08	0.20	5.49	< .001
	Location	-0.80	0.20	-4.10	< .001
California myotis	Day	0.69	0.16	4.39	< .001
Fringed myotis	Day	0.79	0.32	2.50	0.01
	Location	0.60	0.29	2.05	0.04
Yuma myotis	Day	0.63	0.27	2.32	0.02
	Day x RH	0.96	0.41	2.35	0.02
Mexican free-tailed bat	Day	1.29	0.20	6.43	< .001
	Location	-1.28	0.18	-6.99	< .001

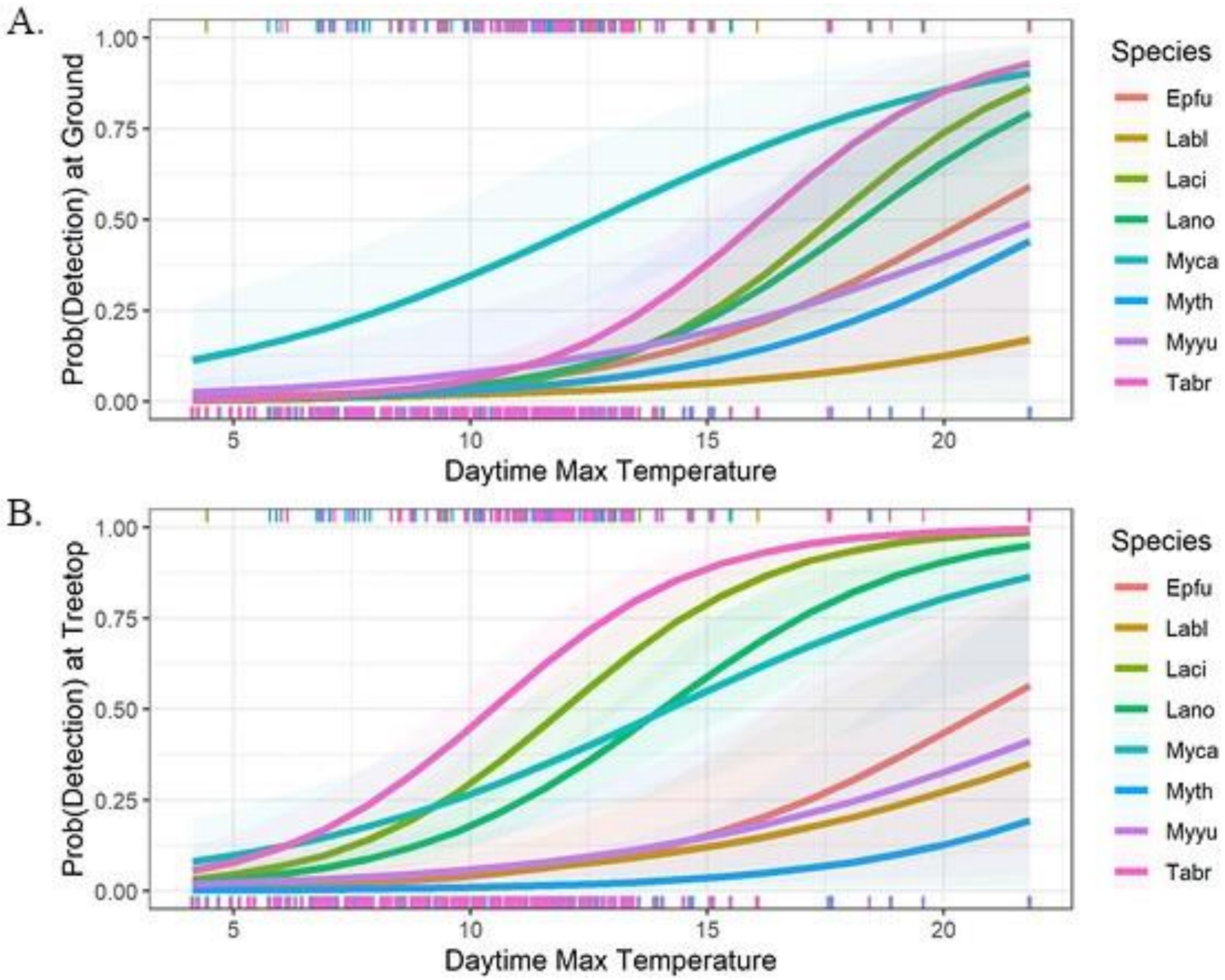


Figure 4: Plots showing how predicted probability of species detection is positively associated with daytime maximum temperature for all species when detector is (A) at ground-level and (B) when detector is at treetop with 95% confidence intervals.

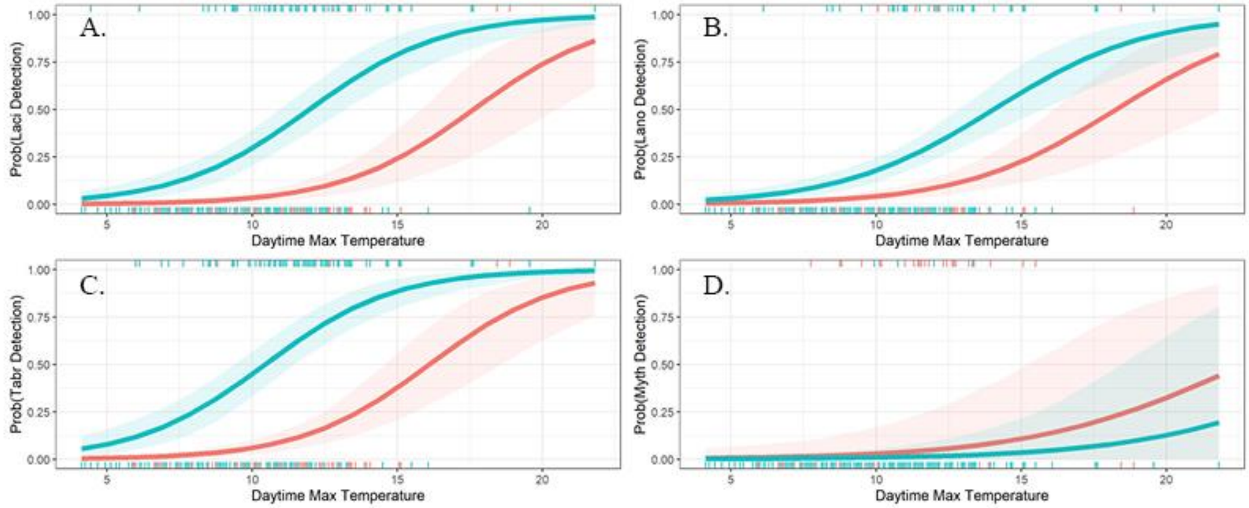


Figure 5: Plots comparing how predicted probability of presence varies for ground detectors (blue line) and treetop detectors (red line) for the four species for which detector location had a significant effect: A) hoary bat (Laci), B) silver-haired bat (Lano), C) Mexican free-tailed bat (Tabr), and D) fringed myotis (Myth).

Probability of detecting a species at 10.2ºC, the mean winter daytime maximum temperature observed across the study sites, varied by species and detector location (Figure 6). California myotis was predicted to have a probability of presence of .36 (95% CI = .19-.57) at ground-level and .28 (95% CI = .13-.48) at treetop. Mexican free-tailed bat was predicted to have a probability of presence of .06 (95% CI = .03-.11) at ground-level and .47 (95% CI = .34-.58) at treetop. Hoary bat was predicted to have a probability of .04 (95% CI = .01-.07) at ground-level, compared to .31 (95% CI = .22-.41) at treetop; and silver-haired bat was predicted to have a probability of .04 (95% CI = .02-.08) at ground-level, compared to .19 (95% CI = .12-.26) at treetop. Big brown bat, western red bat, fringed myotis and Yuma myotis were all predicted to have a ≤ .08 probability of presence at either location at mean winter temperature.

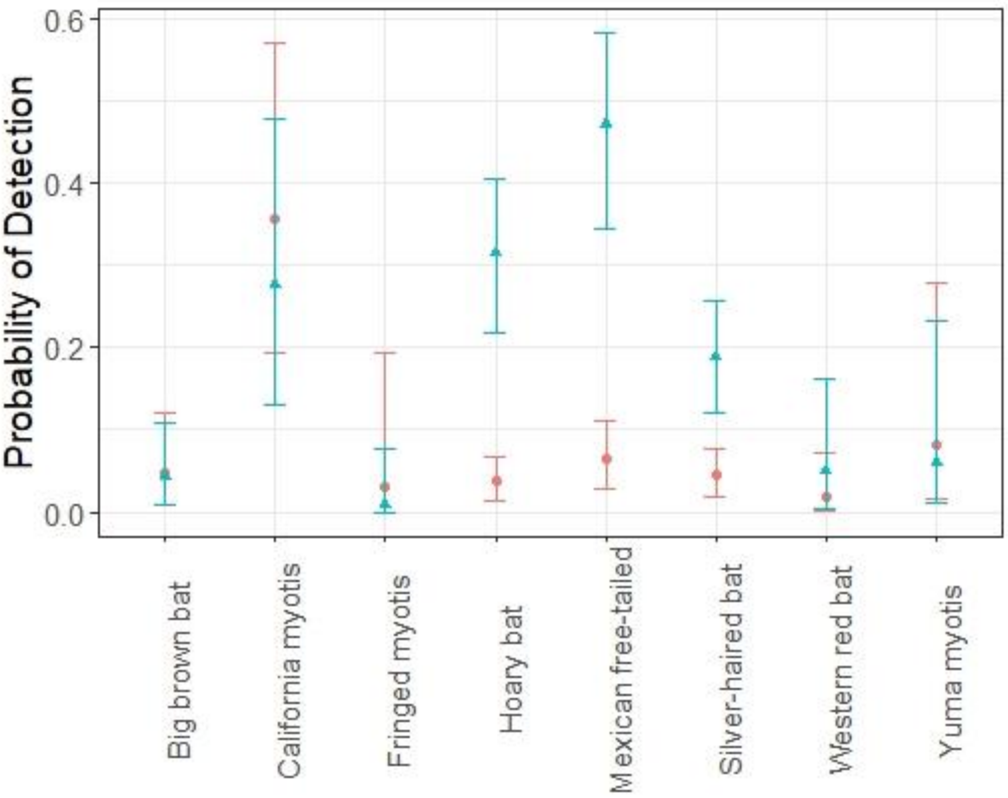


Figure 6: Plot of predicted probability of detection with 95% confidence interval for each species under mean observed winter daytime maximum temperature.

The maximum daytime temperature at which species were predicted to have a 50% probability of detection ranged from approximately 11 ºC (Mexican free-tailed bat at treetop) to approximately 22 ºC (Yuma myotis at ground-level), with most species not detected at ground-level unless the temperature was at least 16 ºC (Figure 4). Based on the historical meteorological data (2010-2020), maximum daytime temperature has exceeded 16 ºC on an average of 24 days per winter, and maximum daytime temperature has exceeded 22 ºC on an average of 2 days per winter (Figure 7). The western red bat was predicted to have significantly less than 50% probability of being detected even at the highest observed daytime maximum temperature.

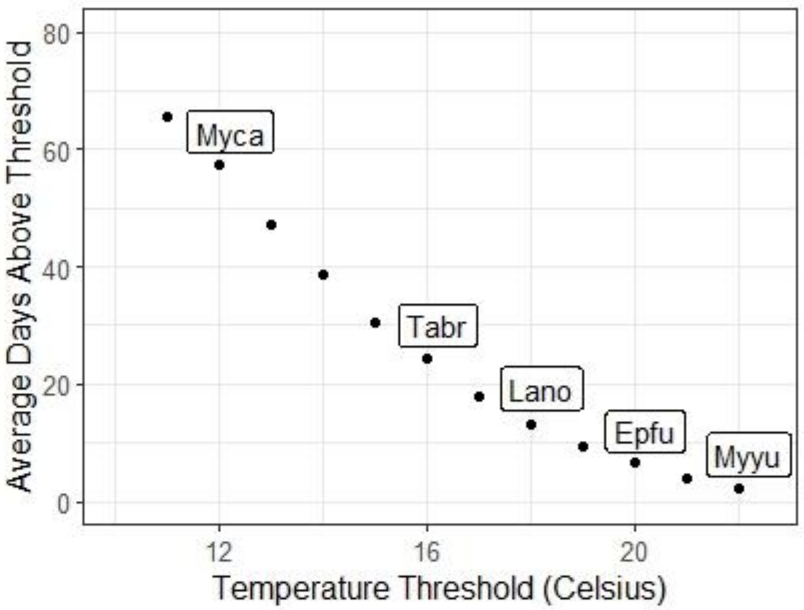


Figure 7: Plot of average number of days per winter at which maximum temperature historically exceeded temperature threshold values across the five study site locations from 2010-2020. Labels indicate the approximate temperature thresholds at which a 50% probability of detection at ground-level is predicted for the following species: California myotis (Myca), Mexican free-tailed bat (Tabr), silver-haired bat (Lano), big brown bat (Epfu), and Yuma myotis (Myyu).

Discussion

Acoustic monitoring confirmed that at least 11 of the 13 species known to occur in the coast redwood ecosystem are present during the winter season. This included five species known to be elsewhere affected by WNS: big brown bat, fringed myotis, little brown bat, long-eared bat, and Yuma myotis, as well as two additional species known to carry the fungal pathogen: Mexican free-tailed bat and silver-haired bat ("White-Nose Syndrome," 2022). By monitoring bat activity from December-February, I was able to show that these species are active along the northern California coast during months that they are generally not detected at inland habitat (Johnson et al., 2017; Schwab, 2014). This extends other research findings that coastal populations are able to take advantage of milder environmental conditions to sustain higher activity during the winter than inland populations of the same species (Falxa, 2007; Grider et al., 2016).

All species had a significantly greater probability of detection at higher temperatures. This agrees with other studies that have found ambient temperature to be positively associated with winter bat activity (Klüg-Baerwald et al., 2016; Parker et al., 2020). Other researchers have found that even in colder areas where insect prey is not available during the winter, bat arousal is triggered by warmer temperatures when it is less energetically costly to be active, and the threshold for this activity varies by species (Klüg-Baerwald et al., 2016). Interestingly, maximum daytime temperature was a better predictor of winter bat activity than maximum nighttime temperature. This may suggest that the mechanism driving bat arousal and subsequent flight activity is daytime environmental conditions more so than the conditions that bats experience when flying after sunset. However, these two variables were highly correlated, and more research is needed to investigate the precise environmental and physiological conditions underlying bat arousal from winter torpor.

Regardless of the precise mechanism triggering bat activity, my findings suggest that scientists and natural resource managers can optimize winter bat surveys to detect species presence by strategizing acoustic monitoring to be on nights following warmer daytime temperatures. However, most species are not predicted to be detected by conventional ground-level monitoring until maximum daytime temperature is at least 17 ºC (Figure 4). This temperature threshold is typically reached or exceeded on only 18 days per winter in this study area (Figure 7). Several species are not likely to be detected at ground-level until maximum daytime temperature is at least 20 ºC, which has historically occurred on fewer than 10 days per winter. This means that even though many of these species were also detected at lower temperatures over the course of the field study, they have a low probability of being detected on an individual night during the winter unless acoustic monitoring is conducted following these relatively rare warm days.

Model results revealed that relative humidity had a significant effect on big brown bat, and the interaction of relative humidity and maximum daytime temperature had a significant effect on Yuma myotis. However, the direction of this effect was contrary to my hypothesis that bats would be less active and less likely to be detected under wetter conditions. Instead, these species were positively associated with relative humidity. One explanation for this is that these species are selecting to hibernate in habitat with higher relative humidity to reduce water loss during torpor. An alternative explanation for this positive association is that relative humidity is higher closer to the coast where the influence of marine fog is more intense than inland sites even within the coast redwood ecosystem (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 generally milder and more stable environment, and big brown bats and Yuma myotis may be more active in this milder coastal habitat. Future research to explore this association with relative humidity should include more study sites to mitigate the possibility that there are confounding site-level effects driving the presence of these species. Also, future research should untangle the influence of relative humidity from precipitation because it is possible that more species have a positive association with humidity, but that this relationship is obscured by rain events. Rain may suppress bat activity due to either the increased thermoregulatory costs of being wet or because rain drops interfere with bat perception of echolocation calls (Geipel et al., 2019; Voigt et al., 2011)

Detector placement had a significant effect in four of the eight species models, with three species having a higher probability of detection at treetop and one species having a higher probability of detection at ground-level. Notably, the three species that models revealed to be more frequently detected at treetop were migratory species: hoary bat, Mexican free-tailed bat, and silver-haired bat. These species are known to have significant migration events through the study area during the spring and fall migration seasons (see Chapter 2). At some study sites, these species were detected on ≥ 90% of winter monitoring nights (Figure 1). This high frequency of detection suggests that at least some individuals of these migratory populations may overwinter in the study area and remain active. However, their winter presence in this ecosystem may be underestimated because previous winter monitoring has primarily been conducted using standard ground-level acoustic surveys, guano sampling of tree cavities, or mist netting from the forest floor (Gellman and Zielinski, 1996; Weller and Stricker, 2012; but see Kennedy et al., 2014;). Also, the little brown bat was exclusively detected at treetop, though it was too rarely detected to be modeled. Although the logistics of monitoring at treetop may not be feasible for conventional surveying, my finding of higher detections at treetop for these species is a pertinent reminder that standard ground-based monitoring may not capture all species that are active in a forest habitat on a survey night. Additional survey nights may be necessary to detect high-flying and other elusive species.

Another key finding of my study was that the most frequently detected species was California myotis. Although this species is ubiquitous in the ecosystem, it is notable how much more frequently this species was detected as present compared to Yuma myotis, a similarly sized myotis species that is commonly detected at these study sites during other seasons. During my summer study in the coast redwood ecosystem, 42% of total identified calls were classified as California myotis and 41% of calls were classified as Yuma myotis (see Chapter 1). However, California myotis was detected on 43% of total ground-detector nights during the winter, whereas Yuma myotis was only detected on 16% of ground-detector nights. Modeling probability of detection suggests that this difference is even more pronounced at colder temperatures (Figure 4). At mean observed daytime maximum temperature, California myotis is predicted to have a 36% probability of detected presence, whereas Yuma myotis is predicted to have an 8% probability (Figure 6).

Because California myotis and Yuma myotis emit similar high frequency echolocation calls, these two species are often combined into one species group in acoustic studies that rely on autoclassification software to reduce the probability of misidentification (Johnson et al., 2017; Schwab, 2014). My results suggest that this grouping obscures critical differences in species ecology. California myotis continues to be frequently detected in the coast redwood ecosystem during the winter, suggesting that this may be a species which uses shallow torpor in order to take advantage of warmer temperatures to rewarm passively and possibly forage (Turbill and Geiser, 2008). In contrast, Yuma myotis is rarely detected indicating that this species is also overwintering in the ecosystem but spends long periods in torpor. This has important conservation implications because Yuma myotis is a species which has been documented elsewhere in North America with symptoms of white-nose syndrome. Big brown bat, fringed myotis, and little brown bat are other WNS-susceptible species which I detected as present in the redwood ecosystem during the winter but rarely active.

The propensity of California myotis to be active during the winter, even at relatively low temperatures, may confer greater resilience to white-nose syndrome than these other species. Studies in areas where little brown bat populations have been severely impacted by white-nose syndrome have found that the decline of this formerly abundant species led to other species shifting their spatial and temporal niche partitioning (Jachowski et al., 2014) or broadening their diet (Morningstar et al., 2019). However, it is unknown whether this competitive release will lead to population growth of other species, especially since bat populations also are vulnerable to climate change and anthropogenic disturbance (Jachowski et al., 2014). Further research should be done to understand the baseline foraging ecology of all of these species in order to detect whether this changes in the future, as this may be a helpful way to monitor future impacts of disease on cryptic bat communities. Importantly, future monitoring of bat overwintering habitat should also sample insect abundance because the availability of prey will likely be a key factor in the resilience of affected bat populations to mortality from WNS, especially for species which are not normally active during the winter. Protecting coastal forest habitat where bats are active and able to forage during the winter may be an effective conservation strategy to not only support local bat populations but have wider implications for the conservation of species that are severely declining across North America.

References

Abatzoglou, J.T., 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33, 121–131. https://doi.org/10.1002/joc.3413

Agranat, I., 2014. Detecting Bats with Ultrasonic Microphone. Wildlife Acoustics, Inc.

Bates, D., Maechler, M., Bolker [aut, B., cre, Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., simulate.formula), P.N.K. (shared copyright on, 2021. lme4: Linear Mixed-Effects Models using "Eigen" and S4.

Burnham, K.P., Anderson, D.R. (Eds.), 2002. Information and Likelihood Theory: A Basis for Model Selection and Inference, in: Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY. https://doi.org/10.1007/978-0-387-22456-5_2

Cheng, T.L., Reichard, J.D., Coleman, J.T.H., Weller, T.J., Thogmartin, W.E., Reichert, B.E., Bennett, A.B., Broders, H.G., Campbell, J., Etchison, K., Feller, D.J., Geboy, R., Hemberger, T., Herzog, C., Hicks, A.C., Houghton, S., Humber, J., Kath, J.A., King, R.A., Loeb, S.C., Massé, A., Morris, K.M., Niederriter, H., Nordquist, G., Perry, R.W., Reynolds, R.J., Sasse, D.B., Scafini, M.R., Stark, R.C., Stihler, C.W., Thomas, S.C., Turner, G.G., Webb, S., Westrich, B.J., Frick, W.F., 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35, 1586–1597. https://doi.org/10.1111/cobi.13739

Cryan, P.M., Stricker, C.A., Wunder, M.B., 2014. Continental-scale, seasonal movements of a heterothermic migratory tree bat. Ecological Applications 24, 602–616. https://doi.org/10.1890/13-0752.1

Falxa, G., 2007. WINTER FORAGING OF SILVER-HAIRED AND CALIFORNIA MYOTIS BATS IN WESTERN WASHINGTON. nwnt 88, 98–100. https://doi.org/10.1898/1051-1733(2007)88[98:WFOSAC]2.0.CO;2

Fellers, G.M., Pierson, E.D., 2002. Habitat Use and Foraging Behavior of Townsend's Big-Eared Bat (Corynorhinus Townsendii) in Coastal California. Journal of Mammalogy 83, 167–177. https://doi.org/10.1644/1545-1542(2002)083<0167:HUAFBO>2.0.CO;2

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol 37, 4302–4315. https://doi.org/10.1002/joc.5086

Frick, W.F., Kingston, T., Flanders, J., 2020. A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences 1469, 5–25. https://doi.org/10.1111/nyas.14045

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M., Kunz, T.H., 2010. An Emerging Disease Causes Regional Population Collapse of a Common North American Bat Species. Science 329, 679–682.

Geipel, I., Smeekes, M.J., Halfwerk, W., Page, R.A., 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. Journal of Experimental Biology 222, jeb192005. https://doi.org/10.1242/jeb.192005

Gellman, S.T., Zielinski, W.J., 1996. Use by Bats of Old-Growth Redwood Hollows on the North Coast of California. Journal of Mammalogy 77, 255–265. https://doi.org/10.2307/1382726

Grider, J.F., Larsen, A.L., Homyack, J.A., Kalcounis-Rueppell, M.C., 2016. Winter Activity of Coastal Plain Populations of Bat Species Affected by White-Nose Syndrome and Wind Energy Facilities. PLOS ONE 11, e0166512. https://doi.org/10.1371/journal.pone.0166512

Hartig, F., Lohse, L., 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Jachowski, D.S., Dobony, C.A., Coleman, L.S., Ford, W.M., Britzke, E.R., Rodrigue, J.L., Leung, B., 2014. Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. Diversity & Distributions 20, 1002–1015. https://doi.org/10.1111/ddi.12192

Johnson, J.S., Treanor, J.J., Lacki, M.J., Baker, M.D., Falxa, G.A., Dodd, L.E., Waag, A.G., Lee, E.H., 2017. Migratory and winter activity of bats in Yellowstone National Park. Journal of Mammalogy 98, 211–221. https://doi.org/10.1093/jmammal/gyw175

Kennedy, J.-P., Sillett, S.C., Szewczak, J.M., 2014. Bat Activity Across the Vertical Gradient of an Old-Growth Sequoia sempervirens Forest. Acta Chiropterologica 16, 53–63. https://doi.org/10.3161/150811014X683264

Klüg-Baerwald, B.J., Gower, L.E., Lausen, C.L., Brigham, R.M., 2016. Environmental correlates and energetics of winter flight by bats in southern Alberta, Canada. Can. J. Zool. 94, 829–836. https://doi.org/10.1139/cjz-2016-0055

Kunz, T.H., Fenton, M.B., 2005. Bat Ecology. University of Chicago Press.

Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H., Marm Kilpatrick, A., 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecology Letters 15, 1050–1057. https://doi.org/10.1111/j.1461-0248.2012.01829.x

Lorch, J.M., Palmer, J.M., Lindner, D.L., Ballmann, A.E., George, K.G., Griffin, K., Knowles, S., Huckabee, J.R., Haman, K.H., Anderson, C.D., Becker, P.A., Buchanan, J.B., Foster, J.T., Blehert, D.S., 2016. First Detection of Bat White-Nose Syndrome in Western North America. mSphere 1, e00148-16. https://doi.org/10.1128/mSphere.00148-16

Marín, G., Ramos-H, D., Cafaggi, D., Sierra-Durán, C., Gallegos, A., Romero-Ruiz, A., Medellín, R.A., 2021. Challenging hibernation limits of hoary bats: the southernmost record of Lasiurus cinereus hibernating in North America. Mamm Biol 101, 287–291. https://doi.org/10.1007/s42991-020-00080-4

Maslo, B., Valent, M., Gumbs, J.F., Frick, W.F., 2015. Conservation implications of ameliorating survival of little brown bats with white-nose syndrome. Ecological Applications 25, 1832–1840. https://doi.org/10.1890/14-2472.1

Morningstar, D.E., Robinson, C.V., Shokralla, S., Hajibabaei, M., 2019. Interspecific competition in bats and diet shifts in response to white-nose syndrome. Ecosphere 10, e02916. https://doi.org/10.1002/ecs2.2916

Nash, J.C., Varadhan, R., Grothendieck, G., 2021. optimx: Expanded Replacement and Extension of the “optim” Function.

O’Regan, S.M., Magori, K., Pulliam, J.T., Zokan, M.A., Kaul, R.B., Barton, H.D., Drake, J.M., 2015. Multi-scale model of epidemic fade-out: Will local extirpation events inhibit the spread of white-nose syndrome? Ecological Applications 25, 621–633. https://doi.org/10.1890/14-0417.1

Parker, K.A., Jr., Li, H., Kalcounis-Rueppell, M.C., 2020. Species-specific environmental conditions for winter bat acoustic activity in North Carolina, United States. Journal of Mammalogy 101, 1502–1512. https://doi.org/10.1093/jmammal/gyaa133

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reeder, D.M., Frank, C.L., Turner, G.G., Meteyer, C.U., Kurta, A., Britzke, E.R., Vodzak, M.E., Darling, S.R., Stihler, C.W., Hicks, A.C., Jacob, R., Grieneisen, L.E., Brownlee, S.A., Muller, L.K., Blehert, D.S., 2012. Frequent Arousal from Hibernation Linked to Severity of Infection and Mortality in Bats with White-Nose Syndrome. PLOS ONE 7, e38920. https://doi.org/10.1371/journal.pone.0038920

Schwab, N.A., 2014. Winter Acoustic Activity of Bats in Montana. nwnt 95, 13–27. https://doi.org/10.1898/NWN13-03.1

Seidman, V.M., Zabel, C.J., 2001. Bat activity along intermittent streams in northwestern california. Journal of Mammalogy 82, 738–747. https://doi.org/10.1644/1545-1542(2001)082<0738:BAAISI>2.0.CO;2

Sillett, S.C., Van Pelt, R., Carroll, A.L., Kramer, R.D., Ambrose, A.R., Trask, D., 2015. How do tree structure and old age affect growth potential of California redwoods? Ecological Monographs 85, 181–212. https://doi.org/10.1890/14-1016.1

The IUCN Red List of Threatened Species [WWW Document], 2022. IUCN Red List of Threatened Species. URL https://www.iucnredlist.org/en (accessed 3.5.22).

Torregrosa, A., Combs, C., Peters, J., 2016. GOES-derived fog and low cloud indices for coastal north and central California ecological analyses. Earth and Space Science 3, 2015EA000119. https://doi.org/10.1002/2015EA000119

Turbill, C., Geiser, F., 2008. Hibernation by tree-roosting bats. J Comp Physiol B 178, 597. https://doi.org/10.1007/s00360-007-0249-1

Varadhan, R., University, J.H., Borchers, H.W., Research, A.C., Bechard, and V., University), H.M. (Montreal, 2020. dfoptim: Derivative-Free Optimization.

Verant, M.L., Boyles, J.G., Waldrep, W., Wibbelt, G., Blehert, D.S., 2012. Temperature-Dependent Growth of Geomyces destructans, the Fungus That Causes Bat White-Nose Syndrome. PLoS One 7, e46280. https://doi.org/10.1371/journal.pone.0046280

Verant, M.L., Meteyer, C.U., Speakman, J.R., Cryan, P.M., Lorch, J.M., Blehert, D.S., 2014. White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. BMC Physiology 14, 10. https://doi.org/10.1186/s12899-014-0010-4

Voigt, C.C., Schneeberger, K., Voigt-Heucke, S.L., Lewanzik, D., 2011. Rain increases the energy cost of bat flight. Biology Letters 7, 793–795. https://doi.org/10.1098/rsbl.2011.0313

Weller, T.J., Castle, K.T., Liechti, F., Hein, C.D., Schirmacher, M.R., Cryan, P.M., 2016. First Direct Evidence of Long-distance Seasonal Movements and Hibernation in a Migratory Bat. Sci Rep 6. https://doi.org/10.1038/srep34585

Weller, T.J., Rodhouse, T.J., Neubaum, D.J., Ormsbee, P.C., Dixon, R.D., Popp, D.L., Williams, J.A., Osborn, S.D., Rogers, B.W., Beard, L.O., McIntire, A.M., Hersey, K.A., Tobin, A., Bjornlie, N.L., Foote, J., Bachen, D.A., Maxell, B.A., Morrison, M.L., Thomas, S.C., Oliver, G.V., Navo, K.W., 2018. A review of bat hibernacula across the western United States: Implications for white-nose syndrome surveillance and management. PLOS ONE 13, e0205647. https://doi.org/10.1371/journal.pone.0205647

Weller, T.J., Stricker, C.A., 2012. Northern California redwood forests provide important seasonal habitat for migrant bats. pp. 447–457.

White-Nose Syndrome [WWW Document], n.d. URL https://www.whitenosesyndrome.org/static-page/bats-affected-by-wns (accessed 12.29.21).

Zielinski, W.J., Gellman, S.T., 1999. Bat Use of Remnant Old-Growth Redwood Stands. Conservation Biology 13, 160–167. https://doi.org/10.1046/j.1523-1739.1999.97424.x

Chapter 4:

Managing working forests for wildlife conservation: Policy insights from bats in California redwood forests

Many of the world's species need large landscape conservation. Achieving this goal is increasingly difficult as people transform earth's surface by converting habitat into agricultural and other types of development.[1] With 83% of the earth surface influenced by human use[2] and the climate changing at an unprecedented rate it is not surprising we are in the midst of the 6th mass global extinction event.[3] To protect migratory and wide-ranging species individual protected areas are often not big enough to prevent extirpation or to withstand extreme weather events. Creating new, large reserves is no longer feasible in most countries because small habitat fragments are all that remain. Conservation planners have shifted the focus to ecological networks comprised of protected areas connected by corridors.[4] Large scale land conservation initiatives at the US state and federal level call for protecting 30% of the land, freshwater, and ocean environments by 2030 (referred to as '30x30'), with the focus on ecological networks to protect biodiversity and build resilience as well as provide increased access to open space for those that need it. While these plans acknowledge the importance of working lands to meet these goals there is little emphasis on what is required for working lands for conservation and the importance of investing in land stewardship.

While ecological networks remain vital for species conservation, protected areas will not serve their intended purpose if they are surrounded by inhospitable land uses that have spillover effects into protected habitats. Rapid climate change is also forcing many species to shift their distributions out of existing parks in pursuit of suitable climate types. Working lands provide important open space and can work for conservation while sustainably providing human resources. Working lands for conservation can contribute to large landscape conservation by providing habitats and resources for some species and by facilitating dispersal and climate change adaptation for others. At the same time, maintaining diversified working lands can aid in sustainable production of food, fiber, fuel, and timber and increase landscape-scale resilience to extreme events, including pest and disease outbreaks that are on the rise with climate change.

Approximately one quarter of the world's forests (1.2 billion hectares out of 4.06 billion hectares) are listed globally for the production of wood and non-wood forest products.[5]

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[1] Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. and Woolmer, G., 2002. The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience, 52*(10), pp.891-904.

[2] *Id.*

[3] Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*.

[4] Hilty, J., Worboys, G.L., Keeley, A., Woodley, S., Lausche, B., Locke, H., Carr, M., Pulsford, I., Pittock, J., White, J.W. and Theobald, D.M., 2020. Guidelines for conserving connectivity through ecological networks and corridors. *Best practice protected area guidelines series*, (30).

[5] FAO. 2020. *Global Forest Resources Assessment 2020: Main report.* Rome.

However, only 1.11 billion hectares are estimated to be primary forest,[6] revealing that the world's forests are regenerating from a history of human disturbance. In the California coast redwood ecosystem, one of the most iconic forests of the world, 93% of currently existing redwood forest has been logged at least once, and 35% continues to be managed by industrial timber companies.[7,8] Hence, the way working forests are managed will determine the long-term persistence of forest-dwelling species.

Here I provide insights from forest-dwelling bats in California's coast redwood forests as a case study for where gaps exist in legal protections for wide-ranging wildlife reliant on working forests. There is an urgent need to understand how law and policy serves, or fails to serve, as an effective tool for supporting wildlife conservation across working forest lands in order to meet the goals of 30x30 and other large landscape conservation initiatives designed to stave off extinction and protect ecosystems from climate impacts. Identifying existing oversights and conflicts between forestry and animal conservation is a crucial first step to improving legal protections and strategizing management to better support biodiversity conservation. While some endangered species such as the spotted owl[9] have influenced timber harvest planning most forest species are not accounted for in even sustainable timber harvest efforts. Bats, for example, range across vast areas of forests; many are migratory, and population decline is concerning especially with the immediate spread of a fatal disease, white-nose syndrome, and increasing drought conditions associated with climate change. Exploring what is known about bat conservation reveals where forest and wildlife regulations could be improved to make working forests work for conservation – a necessary step for large landscape conservation to be successful.

Taking a case study approach allows me to apply my understanding of forest bat ecology to assess the implications of different forest management regulations and thus identify what opportunities may exist to increase protections for sensitive species in the face of rising threats. Here I explore these questions by reviewing the laws and policies that either directly or indirectly protect wildlife on public and privately owned timberland in the coast redwood ecosystem. This includes protections that are afforded all wildlife under principles of public trust, as well as extra protections that are reserved for those species which state or federal laws have declared special. I take a closer look at two examples of how bats have been previously considered in relation to forest management protection. Finally, I recommend changes that could be made to make working forests work more effectively for bat conservation.

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[6] *Id.*

[7] Burns, E.E., Campbell, R., Cowan, P.D., 2018. State of Redwoods Conservation Report. Save the Redwoods League.

[8] Cowan, P., Burns, E.E., Campbell, R., 2017. A GIS approach to identifying the distribution and structure of coast redwood across its range.

[9] Marcot, B.G., 1997. *Of Spotted Owls, Old Growth, and New Policies: A History Since the Interagency Scientific Committee Report*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Background: bats and redwood forests

At least thirteen species of bats inhabit coast redwood forests, and recent concerns about the vulnerability of California bat populations are bringing these cryptic creatures into the limelight. California bat populations are increasingly at risk from white-nose syndrome (WNS), a wildlife disease that has decimated North American bat populations and pushed several vulnerable species toward the brink of regional extinctions.[10,11,12] Since its initial detection in New York in 2006, WNS has been spreading west, and in 2018, the fungal pathogen was detected for the first time in California. This has raised alarm about what the future holds for California bats. Six of the species found in coast redwood forests have elsewhere been identified with WNS symptoms, including the little brown bat (*Myotis lucifugus*), a once ubiquitous species which is now being reviewed by the U.S. Fish and Wildlife Service for listing under the Endangered Species Act.[13] Three additional species have been found to carry the causative fungal pathogen,[14] and even if they are not susceptible, may contribute to the spread of the pathogen in the ecosystem.

Bats are also threatened by climate change. Bats have high rates of evaporative water loss,[15] and their reproductive success can decline dramatically when local water sources drop below a critical threshold.[16] Consequently, the higher temperatures and longer dry periods that are forecasted for California may lead to significant population declines.[17,18] Historically, the coast redwoods have been buffered from the temperature extremes that other parts of the state experience. Coastal effects create a highly stable environment year-round[19] and fog rolling in

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[10] Lorch, J. M. et al. First Detection of Bat White-Nose Syndrome in Western North America. mSphere 1, e00148-16 (2016).

[11] White-Nose Syndrome. Available at: https://www.whitenosesyndrome.org/static-page/bats-affected-by-wns.

[12] Hoyt, J.R., Kilpatrick, A.M. & Langwig, K.E. Ecology and impacts of white-nose syndrome on bats. *Nat Rev Microbiol* **19,** 196–210 (2021). https://doi.org/10.1038/s41579-020-00493-5

[13] https://www.batcon.org/article/protecting-endangered-species/

[14] White-Nose Syndrome. Available at: https://www.whitenosesyndrome.org/static-page/bats-affected-by-wns.

[15] Adams, R.A. Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91: 2437–2445 (2010).

[16] Adams, R.A., Hayes, M.A. Water Availability and Successful Lactation by Bats as Related to Climate Change in Arid Regions of Western North America. Journal of Animal Ecology 77 (6): 1115–21 (2008).

[17] Williams, A. P. et al. Contribution of anthropogenic warming to California drought during 2012-2014: GLOBAL WARMING AND CALIFORNIA DROUGHT. Geophysical Research Letters 42, 6819–6828 (2015).

[18] Amorim, F., et al. Effects of a drought episode on the reproductive success of European free-tailed bats (Tadarida teniotis). Mammalian Biology 80: 228–236 (2015).

[19] Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J. and P.P. Pasteris, 2008. Physiographically sensitive mapping of climatological temperature and Precipitation across the conterminous United States. Int. J. Climatol. 28: 2031–2064.

from the ocean provides a valuable freshwater resource to the ecosystem.[20,21,22,23] Therefore, coast redwoods might serve as a critical climate refugia. It is thus especially critical that we understand the habitat value of the redwood ecosystem for California bat populations as a whole.

Conserving bats is especially challenging because, as the only volant mammals, bats regularly cross property boundaries. Furthermore, bats are far ranging in both their nightly foraging, and for some species, their seasonal migrations. Even individuals of the same species may have different roosting requirements depending on their sex and the stage of their life cycle.[24,25,26] As a result, bats rely on extensive habitat, and their varying seasonal ecology needs generally cannot be met on one property.

The coast redwood ecosystem has experienced a long history of intensive logging, and only 110,000 acres of old-growth forest remains.[27] The other 95% of the habitat has been logged at least once, and while the heydays of the California timber industry may have passed, 77% of redwood forest is still privately owned and not protected.[28] This has resulted in a fragmented ecosystem under a mosaic of different ownerships. Each of these ownerships is guided by different principles and subject to different regulations depending on the management type. These differences affect the habitat value of redwood forest and can have significant ramifications for the conservation of wildlife in the ecosystem.

Wildlife as a public resource

In the United States, both federal and state courts have long held that wildlife resources are held in trust by government for the benefit of present and future citizens.[29] U.S. wildlife policies date back to colonial America, when diminishing wildlife populations created a need for

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[20] Hiatt, C., D. Fernandez, and C. Potter. 2012. Measurements of Fog Water Deposition on the California Central Coast. Atmospheric and Climate Sciences 2 (4): 525–31.

[21] Fischer, D.T., C.J. Still, C.M. Ebert, S.A. Baguskas, and A.P. Williams. 2016. Fog Drip Maintains Dry Season Ecological Function in a California Coastal Pine Forest. Ecosphere 7 (6).

[22] Sawaske, S.R., and D.L. Freyberg. 2015. Fog, Fog Drip, and Streamflow in the Santa Cruz Mountain of the California Coast Range. Ecohydrology 8 (4): 695–713.

[23] Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476–485.

[24] Weller, T. J. and C.A. Stricker. Northern California redwood forests provide important seasonal habitat for migrant bats. 2012. In: Standiford, Richard B.; Weller, Theodore J.; Piirto, Douglas D.; Stuart, John D., tech. coords. Proceedings of coast redwood forests in a Changing California: A symposium for scientists and managers. Gen. Tech. Rep. PSW GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 447-457 238, 447–457.

[25] Gellman, S., and W. Zielinski. 1996. Use by bats of oldgrowth redwood hollows on the north coast of California. Journal of Mammalogy, 77: 255–265.

[26] Adams, R.A., and M.A. Hayes. 2008. Water Availability and Successful Lactation by Bats as Related to Climate Change in Arid Regions of Western North America. Journal of Animal Ecology 77 (6): 1115–21.

[27] "https://www.savetheredwoods.org/redwoods/coast-redwoods/"

[28] *Id.*

[29] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (770); *Ex Parte Maier* (1894) 103 Cal. 476, 483

regulations limiting methods of harvest and how many animals could be taken.[30] The first federal U.S. court case to establish that wildlife were public resources, held by the state in trust for the people, was *Martin v. Waddell (1842)*.[31] The U.S. Supreme Court drew upon British law, in which the king held game animals in trust for the people, to conclude that the plaintiff did not have the right to exclude other people from taking oysters from a riparian area.[32]

Subsequent court cases eventually applied the same principles to nonaquatic wildlife species. For example, in the landmark case *State v. Rodman* (1894), the Minnesota Supreme Court ruled that a person does not have a right to take or kill deer or other wild game except as authorized by state laws.[33] In this case, the Court stated that "the ownership of wild animals, so far as they are capable of ownership, is in the state, not as proprietor, but in its sovereign capacity, as the representative, and for the benefit, of all its people in common."[34] A key justification for this police power of that state was the principle that "the preservation of such animals as are adapted to consumption as food, or to any other useful purpose, is a matter of public interest"[35] and thus the state was entrusted to “enact such laws as will best preserve such game, and secure its beneficial use in the future to the citizens."[36] It is evident from this language that the focus of wildlife regulation in this case continued to be on consumable or otherwise “useful” animals.

For much of the next century, the focus of wildlife regulation continued to be on fish and game species or other economically valuable animals. However, these same principles were ultimately extended to all wildlife species. In *Betchart v. Department of Fish and Game* (1984), the court stated in the first sentence of its ruling that “the state has a duty to protect and preserve wildlife.”[37] The court referenced Fish and Game Code section 1801 and declared that it was “state's policy to conserve and maintain wildlife for citizens' use and enjoyment, for their intrinsic and ecological values, and for aesthetic, educational and nonappropriative uses.”[38] The court’s reference of the non-appropriative public value of wildlife signifies how by this time both legislation and case law had evolved to encompass non-game species within state protections. While Fish and Game Code section 1801 defined the policies and objectives of the state

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[30] North American Wildlife Policy and Law (2018); edited by Bruce D. Leopold, Winifred B. Kessler, James L. Cummins. Page 27

[31] *Id.*

[32] Martin v. Waddell, 41 U.S. 367 (1842)

[33] State v. Rodman, 58 Minn. 393 (1894)

[34] *Id.*

[35] *Id.*

[36] *Id.*

[37] *Betchart v. Department of Fish Game*, 158 Cal.App.3d 1104, 1106 (Cal. Ct. App. 1984)

[38] *Betchart v. Department of Fish Game*, 158 Cal.App.3d 1104, 1106 (Cal. Ct. App. 1984); Fish and Game Code Section 1801, subds. (a), (b), (c), (d)

regarding protection of wildlife, it is section 1802 that defined the jurisdiction of the California Department of Fish and Game (DFG)[39] as "trustee for fish and wildlife resources."[40]

Although DFG was responsible for maintaining and conserving all wildlife, bat conservation remained largely out of the agency's radar until 1986, when zoology professor Dan Williams reviewed the status of all mammals in California.[41] Williams designated 36 species as "Mammals of Special Concern," including seven California bat species. DFG responded by calling a meeting with Williams and several California bat researchers, and this led to the first state-funded research project for bats.[42] Subsequent efforts were made to monitor for bats on public land, including at federal and state parks, and to include information on bats in public education.[43]

However, despite over thirty years of efforts to raise attention to the vulnerability of California bat populations, including surveys indicating serious species declines,[44] California bat species still elude standardized public regulations. For example, California Department of Fish and Wildlife (CDFW) provides public information on survey protocols for monitoring for many sensitive species, [45] but CDFW does not have standardized protocols for surveying bats. One reason for this is that it is inherently difficult to standardize best practices for surveying this diverse taxon. California has 25 native species, and these species have different behaviors and habitats, so survey protocols need to vary by species and project.[46] This lack of state agency guidance on surveying protocols suggests one of the challenges that CDFW is having in fulfilling its duties as a trustee agency when it comes to advising on how human actions might impact bats.

CDFW's public recommendations regarding bats have instead focused on what to do if someone encounters a bat in their home and how to report a sick or dead bat.[47] This reflects an additional challenge to the protection of bats in the form of negative stigmas as pests roosting in buildings and carriers of rabies. These perceptions of bats as nuisances and threats lower the estimation of their public value. Recently, public efforts to counter these stereotypes have gained traction and CDFW is part of this effort by recognizing bats as "vital to maintaining a healthy ecosystem" on the agency website.[48] However, the value of bats has largely been based on the argument that bats provide important ecosystem services, such as insect control.[49] Recent scientific studies have sought to quantify the ecosystem service value that bats provide by

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[39] DFG's name changed to California Department of Fish and Wildlife (CDFW) effective January 1, 2013 to reflect the department's responsibilities to all wildlife species, not just its traditional responsibilities to game species. https://cdfgnews.wordpress.com/2012/12/31/department-name-change-effective-tomorrow/

[40] Fish and Game Code Section 1802

[41] (https://www.batcon.org/article/vbat-conservation-in-california/)

[42] (https://www.batcon.org/article/vbat-conservation-in-california/)

[43] *Id.*

[44] *Id.*

[45] https://wildlife.ca.gov/Conservation/Survey-Protocols#377281285-mammals

[46] Personal communication with CDFW personnel. May 7, 2020.

[47] *Id.*

[48] https://wildlife.ca.gov/Conservation/Mammals/Bats/Report-Colony

[49] *Id.*

suppressing insect pests which would otherwise damage agricultural crops.[50] However, this ecosystem service justification for protecting bats carries less weight in the context of the redwood forest ecosystem because redwood trees already are naturally resistant to insect pests because of their thick bark that contains tannins, chemical substances which are toxic to most insects.[51]

Given these challenges, what has determining that all wildlife species are protected in the public trust translated to in practice for California forest bats? It really depends on the management regime. Public trust considerations are built into the Forest Practice Act, the Forest Practice Rules, the California Environmental Quality Act, as well as other state and federal statutes protecting wildlife.[52] In management types, such as California state parks, where the public mandate to protect natural resources takes precedence, these considerations hold more weight. In other management types, such as commercial timber properties, where conservation of wildlife must be weighed more critically against economic development and feasibility standards, bat conservation might be relegated to a back seat. In the context of working forests, where do laws protecting bats and other wildlife have teeth, and where are they only bluffing?

The Forest Practice Act and Forest Practice Rules

For much of the history of the United States, the California timber industry faced few environmental regulations. The forest resources of the country seemed inexhaustible, and there was little understanding of how far the impacts of logging operations reached. A Board of Forestry was first established in California in 1885 and a state forester was appointed in 1905, but the original focus of these entities was fire protection.[53] In 1945, the first California Forest Practices Act was enacted, and this resulted in the creation of four Forest District Boards which were each given the authority to establish forestry regulations for their district.[54] However, these boards were primarily composed of timber industry representatives, and thus were effectively self-regulating.[55]

This system began to change after a series of studies were conducted by California Senate committees between 1957-1967 that identified timber harvesting and related activities as a major threat to state watershed resources, and it was concluded that a "relatively simple elevation in the

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[50] https://www.sciencedirect.com/science/article/abs/pii/S0167880920302486; https://pubmed.ncbi.nlm.nih.gov/21449963/ Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. Ecosystem services provided by bats. Ann N Y Acad Sci. 2011 Mar;1223:1-38. doi: 10.1111/j.1749-6632.2011.06004.x. PMID: 21449963.

[51] https://www.nps.gov/parkhistory/online_books/shirley/sec6.htm

[52] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005. (774)

[53] Valachovic, Y., L. Quinn-Davidson and R. Standiford. 2015. Can the California Forest Practice Rules adapt to address conifer encroachment? In Standiford, Richard B.; Purcell, Kathryn L., tech. cords. 2015. Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world. Gen. Tech. Rep. PSW-GTR-251. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 579 p.

[54] *Id.*

[55] *Id.*

overall standards of forest practices would go far toward minimizing these long-term consequences."[56] These studies were closely followed by a court case that was instrumental in pushing the State Board of Forestry to reform. In *Bayside Timber v. Board of Supervisors* (1971), the Court held that the existing Forest Practice Act was unconstitutional because it delegated legislative power to individuals who had a financial interest in the industry that they were regulating.[57] It was additionally declared in this court case that "few, if any, industries adversely affect the rights of others, and the public generally, as do timber and logging operations."[58] The California timber industry would no longer be permitted to proceed without significantly more safeguards to protect the state's environment and other public resources.

The Z'berg-Nejedly Forest Practice Act of 1973 (FPA) which emerged from this litigation radically changed how private forests were managed in California. The new FPA overhauled the existing Board and created a new structure with nine members appointed by the California Governor, of which five seats were held by members of the public with no direct financial interest in the timber industry.[59] The FPA has two purposes: to manage forest resources for "maximum sustained production of high-quality timber products," and to protect natural resources and related values for the public.[60]

The Forest Practice Act and Forest Practice Rules together now serve as the certified regulatory program under the California Environmental Quality Act (CEQA) and therefore all timber harvest plans are reviewed under the FPA to meet CEQA compliance. In *Natural Resources Defense Council, Inc v. Arcata National Corp.* (1976), the court ruled that the California Department of Forestry's (CDF) approval of a THP amounted to a project under CEQA and was therefore subject to the requirements of CEQA as well as the FPRs.[61] The court determined that THPs were the "functional equivalent" of the Environmental Impact Report (EIR) process under CEQA, and were thus eligible to file the THP as effectively an abbreviated EIR for timber operations instead of a "full scale EIR."[62] The implications of this were realized in a couple of later court cases.

To accomplish these new goals, a new regulatory framework was also enacted. The Board of Forestry was made responsible for defining and implementing the goals of the FPA by establishing regulations known as the Forest Practice Rules (FPRs).[63] The FPRs established standards by which to evaluate whether site-specific forest practices are meeting the goals of the

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[56] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (2).; Assembly Subcommittee on Forest Practices and Watershed Management, *Man's Effect Upon the California Watershed*, 1965-1967

[57] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (2).; *Bayside Timber v. Board of Supervisors* (1971) 20 Cal. App. 3d 1.

[58] *Bayside Timber v. Board of Supervisors* (1971) 20 Cal. App. 3d 1.

[59] CA Pub. Res. Code § 731

[60] CA Pub Res Code § 4513

[61] *Natural Resources Defense Council, Inc. v. Arcata National Corporation* (1976) 59 Cal. App. 3d 959

[62] *Natural Resources Defense Council, Inc. v. Arcata National Corporation* (1976) 59 Cal. App. 3d 959; CA PRC § 21080.5

[63] CA Pub Res Code §§ 4551-4555

FPA.[64] Central to this regulation is the submission of Timber Harvesting Plans (THPs). Before a private landowner can legally harvest timber on their property, they must submit a detailed THP prepared by a Registered Professional Forester (RPF).[65] The California Department of Forestry and Fire Protection (CAL FIRE), which works under the direction of the Board of Forestry, reviews these THPs for compliance with the FPA and the FPRs and decides whether to approve the proposed logging plan or to require modifications. There are specific standards in Article 9 of the FPRs that pertain to wildlife protection. For example, because dead trees are known to serve as valuable wildlife habitat, the FPRs generally require that all snags are retained within the plan area, though exceptions are made for hazard reduction purposes or insect and disease control.[66] If CAL FIRE finds that a THP fails to meet all wildlife protection measures stipulated in the FPRs, then it is obligated to disapprove a plan.[67]

Although timber regulation is primarily overseen by CAL FIRE, other state agencies also advise in the review process.[68] For example, the California Department of Fish and Wildlife (CDFW), formerly known as the Department of Fish and Game, is a key player in this process. CDFW serves as a designated trustee agency for the protection of the state's wildlife resources. Under the FPRs, forest management is required to maintain functional wildlife habitat in sufficient condition for the existing wildlife community and to provide for habitat connectivity.[69] Additional restrictions exist for specific species.[70] CDFW can provide its expertise to assist CAL FIRE in evaluating whether the proposed timber operations are complying with these requirements.[71]

However, there is a critical distinction between CAL FIRE's role as the lead agency and the other agencies as advisors. Other agencies, such as CDFW, may make recommendations on THPs, but only the Director of CAL FIRE can deny a THP approval if the RPF refuses to incorporate these recommendations.[72] Members of the review team do have the option to "non-concur" in the approval recommendation, which does not overturn the decision but does require the CAL FIRE chairperson to defend the challenged recommendation in writing.[73] The ability of CAL FIRE to override decisions about fisheries, wildlife, and water quality that are entrusted to other more qualified agencies significantly limits the power of other agencies to advise on forest management and is a major criticism of the FPRs.[74]

Furthermore, other agencies are not required, nor do they have the organizational capacity, to participate in the review of every THP. CAL FIRE reviews between 500 to 1,400

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[64] CA Pub Res Code § 4552

[65] CA Pub Res Code § 4581

[66] 14 CCR § 939.1

[67] 14 CCR §§ 897(c), 898.1

[68] 14 CCR § 1037.5

[69] 14 CCR § 897(1)(B-C)

[70] 14 CCR §§ 895.1, 919.3, 939.3, 959.3

[71] 14 CCR § 1037.5(b)

[72] 14 CCR § 1037.5(f)(2)

[73] 14 CCR § 1037.5(e)

[74] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (121).

THPs every year.[75] Historically, most of these never received a pre-harvest site inspection from a representative of CDFW or another trustee agency.[76] For example, one CDFW staff person reported that the target for on-site review in the North Coast district used to be only 10% of THPs.[77] However, CDFW's capacity to review THP's has increased significantly since Assembly Bill No. 1492 was passed in 2012, and this percentage now appears to be much higher.[78] AB 1492 established the Timber Regulation and Forest Restoration Fund in the State Treasury and imposed a 1% tax on the retail sale of lumber.[79] The bill also stipulated that $1,500,000 from this new fund would be appropriated to CDFW to fund their review of THPs, instead of the funding coming out of the general fund, though it is unclear from the current statute whether that original amount is accurate.[80]

Although more THPs are receiving on-site inspection from both CAL FIRE and advising agencies, this has not resolved concerns about the agencies' capacity to conduct a review of environmental impacts because the scope of activity that needs to be reviewed is still enormous. For example, CAL FIRE may only have one day to inspect a 200-acre THP site.[81] Yet, 99 percent of submitted THPs will receive CAL FIRE approval with little challenge to their proposed plan and its evaluation of potential environmental impacts.[82] If there is a tree important for wildlife habitat on the property and leaving the tree standing is not a risk to human safety, then the THP review team can generally persuade the landowner to not log the tree.[83] However, this depends on the review team knowing that this potentially important resource was present, which might not be possible if they only have the capacity to do a cursory review.[84] Given that neither CAL FIRE nor the other trustee agencies have the capacity to review all of these THPs with a fine tooth comb, the FPA may not be meeting the expectations set forth by CEQA.

Additionally, while the THP process is not exempted from the mitigation and monitoring program requirements of CEQA, the fulfillment of these obligations receives considerable agency discretion. CAL FIRE has fulfilled these requirements though the forest practice inspection and enforcement process outlined under the FPA.[85] The FPA stipulates that forest inspections are to occur "as needed,"[86] but there are no mandatory inspections during the active period of timber operations. The FPA does mandate that CAL FIRE inspects the site within six months after the timber owner has filed a report that operations are completed,[87] but at that point,

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[75] https://www.fire.ca.gov/programs/resource-management/forest-practice/

[76] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (116).

[77] Personal communication with agency personnel. May 7, 2021.

[78] Personal communication with agency personnel. May 10, 2021.

[79] CA PRC §§ 4629.3, 4629.5

[80] CA PRC §§ 4629.6(c)

[81] Personal communication with agency personnel. May 7, 2021.

[82] https://wildcalifornia.org/how-a-timber-harvest-plan-works

[83] Personal communication with agency personnel. May 4, 2021.

[84] Personal communication with agency personnel. May 7, 2021.

[85] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (466).

[86] PRC § 4604(a)(1)-(4)

[87] PRC § 4586

any damage from the timber operations is already done and cannot be undone.[88] This is in contrast to CEQA's requirement that "the reporting or monitoring program shall be designed to ensure compliance during project implementation,"[89] which presents lingering concerns about the adequacy of FPA measures for complying with CEQA's environmental protection standards.

Cumulative impact evaluation

CEQA requires that cumulative impacts be considered in evaluating the environmental impact of a proposed project,[90] but prior to 1991, consideration of cumulative effects was not incorporated in CAL FIRE's review of THPs.[91] CAL FIRE originally contended that minimizing the effects on each individual timber harvest plan was sufficient to address cumulative effects at the level of the larger landscape.[92] However, it is now better understood that cumulative impacts are more than the sum of their parts. Environmental impacts may be synergistic, or the accumulation of effects may push the ecosystem past a critical threshold, with severe consequences for biological diversity and ecosystem integrity. In *Californians for Native Salmon and Steelhead v. Department of Forestry* (1990),[93] the court noted that "the cumulative impact of past, present, and future logging activities is 'a substantive criterion for the evaluation of the environmental impact' of a proposed timber harvest."[94] This case was resolved by the Board of Forestry adopting the CEQA definition of cumulative impacts in the FPRs, and stipulating that "Individual THPs shall be considered in the context of the larger forest and planning watershed in which they are located, so that biological diversity and watershed integrity are maintained within larger planning units and adverse cumulative impacts…are reduced."[95]

Requiring cumulative impact analysis might be especially important for assessing the adverse impacts of timber operations on forest bats. For example, the loss of roosting trees or valuable foraging habitat at the level of one THP might not account as a significant impact at the level of an individual THP. However, many of these private timber companies manage vast contiguous tracts of land or there might be other THPs in the area currently, historically, or projected in the future. The cumulative impacts of all of this activity might amount to a much greater threat to the viability of bat populations in the local area. Efforts to protect water quality and other aspects of the health of the watershed using cumulative impact analysis are also beneficial to bats because many species rely on aquatic insects as their primary prey source.

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[88] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (466-467).

[89] PRC § 21081.6(a)(1)

[90] 14 C.C.R. §§ 898, 15130, 15355

[91] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (239).

[92] *Environmental Protection Information Center (EPIC) v. Johnson* (1985) 170 Cal. App. 3d

[93] *Californians for Native Salmon and Steelhead v. Department of Forestry* (1990) 221 Cal. App. 3d 1419

[94] *Id.*

[95] 14 C.C.R. § 897(b)(2)

However, the effectiveness of impact evaluation depends on understanding the ecological relationships. For example, there is a lot of emphasis in FPRs on late seral habitat, especially remnant old growth.[96] There is much less discussion of how to review the impacts of additional disturbance on habitat that is younger but already providing important habitat value to bats and other wildlife species. For example, Chapter 1 results demonstrated that young, working forests provide habitat for at least 12 of the 13 bat species present in the coast redwood ecosystem, and seven of those species were present at every working forest site that was surveyed. It is still unknown to what extent these bats are roosting at these immature forest sites opposed to ranging into this habitat to forage. Regardless, by focusing on late seral habitat, THP review is disregarding the function of younger habitat for bat ecological needs and may therefore underestimate the impacts of new disturbance on the wildlife communities present.

This oversight is also concerning in the context of how bats have different seasonal requirements and frequently shift roosts. Bats might not be on site at the time that a survey is conducted, but they may still depend on the habitat for seasonal aspects of their ecology. For example, Chapter 2 examination of bat seasonal activity patterns revealed significant peaks in the activity of four migratory species (hoary bats, Mexican free-tailed bats, silver-haired bats and western red bats) during the fall and spring across all forest management types. However, these four species are challenging to detect in redwood forests using standard, ground-level acoustic monitoring (Chapter 2), so their presence on a landscape might be undetected or vastly underestimated even if bat surveys are conducted. In fact, Chapter 3 results suggest that at least three of these migratory species are overwintering in coast redwood forests more than previously documented, and coastal habitat may be increasingly crucial to the resilience of bat populations threatened by emerging white-nose syndrome disease. Even if bats do not overwinter or otherwise roost for extensive periods of time at the site, the habitat might be a critical stopover site during migration periods. If this habitat value is not understood, then its loss will not be accounted for in cumulative impact evaluation, and impacts will not be adequately mitigated.

Obligation to consider adverse impacts to all species

The application of CEQA to the regulation of private timber harvesting has also been instrumental in requiring that THPs consider the potential adverse impacts to all plant and animal species that may be affected by the project. Certain situations qualify as a “mandatory finding of significance.”[97] These include findings that a project may “substantially reduce the habitat of a fish or wildlife species,” “threaten to eliminate a plant or animal community,” or “substantially reduce the number or restrict the range of an ‘endangered,’ ‘rare,’ or ‘threatened’ species.”[98] Under CEQA, “endangered” species are ones whose survival are in immediate jeopardy; “rare” and “threatened” species are ones that exist in such small numbers as to be at risk of endangerment if their environment worsens or is otherwise likely to become endangered within the foreseeable future.[99] These definitions are more expansive than the qualifications for

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[96] 14 C.C.R. §§ 919.16, 939.16, 959.16

[97] CEQA § 15065

[98] CEQA § 15065(a)(1)

[99] CEQA § 15380(a), (b)(1)

‘endangered,’ ‘rare,’ and ‘threatened’ under the federal and state endangered species acts which I will discuss later. Threats to species which are not formally listed under the federal and state endangered species acts may thus also qualify as mandatory findings of significance under CEQA, provided that there is “substantial evidence” that the species is at risk.[100]

How impactful is a mandatory finding of significance for wildlife? The answer seems to be that it depends on the species in question and on the larger context. At the least, a mandatory finding of significance forces the plan submitter and CAL FIRE to identify and analyze the impacts of the proposed THP on species and habitat, and CEQA requires feasible mitigation of significant adverse impacts.[101] However, we enter a gray area when complete mitigation of the impacts is not deemed feasible. CAL FIRE may approve a THP that will have significant unmitigated impacts by adopting a “statement of overriding considerations.”[102] This means that the agency has decided that the benefits of the plan being approved outweigh the unmitigated impacts on species and habitat.[103] Notably, CAL FIRE can only decline to require full mitigation of significant impacts if the species is not listed by the federal Endangered Species Act (ESA) or the California Endangered Species Act (CESA).[104] If there will be significant impacts on a species that is listed under ESA or CESA, incidental take of these species must first be authorized by the applicable federal or state wildlife agency, not by CAL FIRE, and issuing that incidental take permit is subject to the mitigations requirements of those laws.[105]

Three bat species found in coast redwood forests are classified by CDFW as “species of special concern” and seven additional species are included on CDFW’s “special animals list.”[106] These bat species should qualify for protections under CEQA in the event of a finding of significant impact. However, CEQA is rarely triggered for forest bats because these species tend to roost solitarily or in small groups, not in the large colonies that may be found under bridges. CEQA is intended to prevent population impacts on a species, not to protect individual animals. It is therefore not sufficient for a wildlife reviewer to find that a bat roost will be impacted by timber operations for that roost to qualify for protections under CEQA.[107] The number of bats in the roost, the specific species, and most important, whether there is evidence that the roost is important for a maternity colony, would influence whether a finding of significant impact is ultimately found.[108]

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[100] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (269).

[101] CEQA § 15065

[102] CEQA §§ 15021(d), 15065(c)(4), 15093

[103] CEQA § 15251(o)

[104] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (274).

[105] CEQA § 15093

[106] California Natural Diversity Database (CNDDB). April 2021. Special Animals List. California Department of Fish and Wildlife. Sacramento, CA.

[107] Personal communication with CAL FIRE personnel. May 4, 2020. Personal communication with CDFW personnel. May 7, 2020.

[108] Personal communication with CAL FIRE personnel. May 4, 2020.

It is significant to note that even if mitigation measures are not required under CEQA, the wildlife reviewer can often still provide guidance to the landowner and persuade them to voluntarily leave the roost tree standing.[109] However, the value of leaving the tree standing might be limited if the surrounding habitat is altered or otherwise disturbed. One reason for this is that bats are extremely sensitive to the microclimate of their roosting environment and removing the surrounding trees might result in the protected tree ceasing to function as a viable roost.

Federal and State Endangered Species Acts

The federal Endangered Species Act (ESA) is widely considered to be one of the most powerful environmental laws in existence.[110] If you are looking for where the teeth are in wildlife protection, this is the body to check. The ESA was enacted because Congress was concerned that the value of endangered species was "incalculable" and therefore the protection of species from extinction should be afforded "first priority" by federal agencies over the agencies' primary missions.[111] This requirement is why CAL FIRE cannot adopt "overriding considerations" to avoid requiring full mitigation in a situation that would adversely impact an endangered species protected by the ESA.[112] If an agency action, including approval of a THP, will significantly harm or harass a species listed under the ESA, then the action cannot proceed without approval from the USFW in the form of an Incidental Take Permit (ITP). An ITP can only be issued if it will not jeopardize the continued existence of a species, and all of the impacts of an authorized take must be "minimized and fully mitigated,"[113] at least "to the maximum extent practicable."[114]

The California Endangered Species Act (CESA) is modeled after ESA, but there are a few critical distinctions to note. One way in that CESA offers stronger environmental protections than ESA is that all impacts of the authorized take must not only not jeopardize the species and be minimized, impacts must also be "fully mitigated."[115] However, it is unclear how fully mitigated is defined here because there is also a feasibility standard for what mitigation measures may be required.[116] When issuing an incidental take permit, the CDFW director must set the permit conditions based on what is "legally, technologically, economically and biologically practicable."[117]

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[109] Personal communication with CAL FIRE personnel. May 4, 2020.

[110] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (473).

[111] *Tennessee Valley Authority (TVA) v. Hill* (1973) 67; Endangered Species Act of 1973 § 7

[112] CEQA § 15065

[113] Fish and Game Code §§ 2081(b)(2), 2081(c)

[114] Clark Morrison and Scott B. Birkey, *Natural Resource Regulation in California: A Practical Guide to Agency Permitting and Procedures.* Point Arena, CA: Solano Press Books, 2019 (164).

[115] Fish and Game Code §§ 2081(b)(2), 2081(c

[116] 14 CA ADC § 783.4

[117] *Id.*

Another difference between the federal and state laws is that under the federal ESA, it is not necessary to establish that direct harm will affect individuals of a listed species in order to qualify as a "take." Harm in the form of habitat modification that would impair the species' ability to breed, shelter or otherwise fulfill its requirements for survival also qualifies.[118] CESA, on the other hand, does not explicitly apply the take prohibition to the indirect effects of habitat modification.[119] As an example of the ramifications related to this, according to the California Fish and Game Code, public agencies are recommended to not approve projects that would impair the essential habitat of a protected species.[120] However, this is framed as being "the policy of the state," rather than holding the force of law, and this recommendation is also subject to whether there are "reasonable and productive alternatives" available that are still consistent with the goals of the project being reviewed.[121] The agencies may allow projects to proceed despite unmitigated significant environmental impacts based upon "economic, social, or other" factors.[122,123]

This lack of direct protection of habitat under CESA is problematic for a species such as a bat which has highly sensitive roost requirements. Even if a bat species is listed under CESA and even if its roosting habitat is known, it might not be protected from the adverse impacts of timber projects. For example, according to a Cal Trans biologist, when there is a project by their agency that requires trees to be removed that potentially have tree roosting bats, the protocol is to remove the tree in stages.[124] First, the limbs of the tree will be removed one night. Then, the tree will be removed the next day. The theory is that the limb removal will sufficiently disturb the bats that they will roost somewhere else the next night and not be harmed when the tree is cut down.[125] A biologist for a water district described the same 2-day period protocol as being recommended when they write best management practices for tree removals.[126] They also recommend that removal trees occur outside of bat maternity roosting season and months of winter torpor.[127] However, they stipulate that if that is unavoidable then trees should just be removed when no rain is occurring or forecast and when daytime temperatures are at least 50ºF to facilitate the bats moving from the roost.[128] Such measures are presumed to protect the bats from direct harm and therefore are not subjected to additional mitigation, even though the loss of roost has made the bats vulnerable to predation and other risks of harm.

Furthermore, despite the powerful protections that both ESA and CESA provide special species, the scope of the protections for biodiversity conservation are limited by the endangered species listing processes. One point on which CESA does offer stronger environmental

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[118] Endangered Species Act of 1973 § 7

[119] Biber, Reforming CESA Draft page 8

[120] Fish and Game Code § 2053

[121] *Id.*

[122] Clark Morrison and Scott B. Birkey, *Natural Resource Regulation in California: A Practical Guide to Agency Permitting and Procedures.* Point Arena, CA: Solano Press Books, 2019 (147).; Fish and Game Code § 2054

[123] Biber, Reforming CESA Draft page 16; Public Resources Codes Section 21081

[124] Personal communication with Jennifer Greslik, Cal Trans biologist. May 4, 2021

[125] *Id.*

[126] Personal communication with Jennifer Watson, Biologist, Santa Clara Valley Water District. May 4, 2021.

[127] *Id.*

[128] *Id.*

protections than the federal ESA is the provisions that it extends to species that do not qualify for the highest level of listing. CESA candidate species which have not yet been approved for listing are subject to take provisions.[129] Under the federal ESA, species do not qualify for take provisions until they have been formally listed. This is problematic because USFWS holds a list of candidate species for which there is "sufficient information on biological vulnerability and threats to support issuance of a proposed rule to list," but ESA listing is precluded by a lack of agency resources to complete the full listing proposal.[130]

Another nuance to consider is that species listing as "endangered" or "threatened" is based on scientific and commercial data of current species population and assessment of threats to population viability. One implication of this is that in order for a species to be listed, there must be sufficient available evidence to justify a listing determination.[131] This population assessment can be a difficult standard to meet for species such as forest bats, whose nocturnal activity patterns make them especially cryptic. Many species of bats roost in large colonies in caves and buildings. That is not the case for the bat populations of the coast redwoods, which tend to roost individually or in small groups. Some species do roost in identifiable basal hollows in the trees or utilize human structures, such as bridges, on the forest property. But tree-roosting species, including hoary bat, western red bat and silver-haired bat, roost underneath sloughing bark, in crevices in the tree trunk or in the foliage itself. Their roosts are almost impossible to identify on the landscape, which makes it difficult to conduct a population assessment or to even recognize the impact that timber operations might have on unidentified bat roosts.

Wildlife monitoring for many species includes capture or camera trapping methods that can be used to estimate abundance on the landscape. Although mist netting is technically a capture method too, bats can easily elude capture by flying over or around the nets, so it is not a reliable method for assessing population or even identifying all bat species present at a site. Acoustic monitoring is much more effective at detecting species presence, and passive acoustic monitors can be left a site for multiple nights to collect much more data than most capture studies. However, acoustic data can only be used to identify species and cannot distinguish between individuals. Ten bats passing by is indistinguishable from the same bat passing by ten times. Also, some bat species emit quieter calls than others, including Townsend's big-eared bat. Acoustic monitors routinely fail to detect these species when they are present in the habitat. Bat survey protocols are thus limited in their power to assess species abundance. Even if bat monitoring provides evidence that populations are declining on the landscape, it might be difficult to substantiate this against the strong opposition of the timber industry and other interests that do not want to see bat species listed.

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[129] Clark Morrison and Scott B. Birkey, *Natural Resource Regulation in California: A Practical Guide to Agency Permitting and Procedures.* Point Arena, CA: Solano Press Books, 2019 (165).; Fish and Game Code § 2080.1

[130]https://www.federalregister.gov/documents/2020/11/16/2020-24198/endangered-and-threatened-wildlife-and-plants-review-of-domestic-species-that-are-candidates-for

[131] Duggan, Sharon, and Tara Mueller. *Guide to the California Forest Practice Act and Related Laws*. Point Arena, CA: Solano Press Books, 2005 (479).

Natural Community Conservation Plans

California's Natural Community Conservation Planning (NCCP) program provides an alternative route for landowners to obtain CDFW authorization for take of listed species and species which might be listed in the future by voluntarily cooperating with agencies to develop early and broad-based planning for development projects and their impacts on wildlife.[132] Developing an NCCP agreement is substantially more involved than the CESA ITP application process, but it comes with multiple advantages. At the foremost, there are regulatory assurances that if actions approved by the NCCP agreement later result in the take of a listed species, there will not be further restrictions on development. For example, if an unlisted species covered by the NCCP is later listed under CESA, planned logging operations can proceed without requiring new ITP authorizations because incidental take was already authorized at the time of plan approval.[133] Such regulatory assurances can be highly beneficial for landowners that need long-term certainty of their investments. NCCP thus serves as an important tool to reconcile biodiversity conservation with economic development.[134]

Whereas incidental take permits issued under ESA and CESA only focus on individual species, the NCCP program "promotes multispecies and multihabitat management and conservation" and "promotes the conservation of broad-based natural communities and species diversity."[135] Furthermore, while incidental take permits only apply to species listed under ESA and CESA, an NCPP agreement can cover non-listed species.[136] The effectiveness of this approach for conservation depends on how well the entities making the plan, including the landowner, the regulating agencies, and their advisors, understand the ecological relationships at the site. To facilitate this, NCCP agreements must establish a process for the inclusion of independent scientific input to assist the department and plan participants in developing the plan.[137] The plan must also include a monitoring program that integrates adaptive management strategies and that is periodically reviewed to ensure that the plan is conserving covered species and ecosystems as intended.[138] Given the scope of these requirements, these agreements are therefore more appropriate for large landowners with contiguous holdings and substantial development interests, and there are several timber companies in the coast redwood ecosystem that meet that description.

One large timber company called Mendocino Redwoods Company (MRC) enacted a NCCP agreement in 2003. In keeping with NCCP planning agreement requirements, an independent scientific advisory committee reviewed the proposed plan, and their recommendations are kept publicly available. One detail that I found striking is that the committee recognized that no mitigation measures for bats were included in the NCCP proposal nor were any plans made to monitor for bats on the property, even though several sensitive bat

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[132] Cal. Fish & Game Code §§ 2801, 2835

[133] Cal. Fish & Game Code § 2835

[134] Biber, CESA Reform draft, page 12; Cal. Fish & Game Code § 2801

[135] Cal. Fish & Game Code § 2801(d)

[136] Cal. Fish & Game Code § 2805(e)

[137] Cal. Fish & Game Code § 2810(b)(5)

[138] Cal. Fish & Game Code § 2820

species were known to occur on adjacent lands.[139] This omission was recognized but no change was recommended.

The pallid bat was later included in 2017 in Mendocino Redwood Company's Habitat Conservation Plan, which is the federal equivalent of an NCCP. It is the only bat species included in the list of "threatened, endangered, and sensitive species known to occur on MRC forestlands."[140] However, I included three of MRC's properties in my own research study, and by using acoustic monitoring methods, I routinely detected other species considered to be sensitive by CBWG's "special animals list."[141] It is possible that these species were not detected using the earlier non-acoustic survey methods. This is another example of how bats are being omitted from wildlife protections simply because the interested parties and the public cannot advocate to conserve a resource if they lack evidence that it is present, let alone endangered.

However, there is increasing recognition from private landowners and the public that bats are both a valued part of healthy ecosystems, and also a threatened public resource. The fact that the little brown bat, a formerly ubiquitous species, has been so decimated in the past decade by a wildlife disease that it is now being considered for listing under the federal ESA is a wake-up call for landowners who have never had to consider bats.[142] The impacts of white-nose syndrome appear to be inevitably spreading west, with the pathogen first detected in California in July 2019.[143] Although no bats with the symptoms have been yet reported, CDFW noted that similar surveillance results have preceded white-nose syndrome occurrence in bat populations elsewhere by one to three years.[144] If these species do ultimately become listed by ESA or CESA, this will have consequences in the form of extra costs and administrative hurdles for timber operations. This creates a timely opportunity to encourage timber owners to take advantage of the NCCP for the reasons that it was designed for: "protecting California's natural diversity while reducing conflicts between protection of the state's wildlife heritage and reasonable use of natural resources for economic development."[145]

The case of Townsend's big-eared bat

The Center of Biological Diversity had submitted a petition to the Fish and Game Commission in November 2012 to list Townsend's as threatened or endangered pursuant to CESA. CDFW reviewed the best scientific information available and ultimately decided in June 2016 that listing was not warranted. There had been some quantitative data suggesting massive declines of Townsend's at certain colonies where they had previously been found, but when CDFW reviewed the distribution across the state, it seemed from the available data, of which the

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[139] MRC Natural Community Conservation Plan, Habitat Conservation Plan, Report of Science Advisors, page 28

[140] MRC Management Plan, August 2017, Appendix B, page 1

[141] California Natural Diversity Database (CNDDB). April 2021. Special Animals List. California Department of Fish and Wildlife. Sacramento, CA.

[142] https://www.batcon.org/article/protecting-endangered-species/

[143] https://wildlife.ca.gov/Conservation/Laboratories/Wildlife-Health/Monitoring/WNS

[144] *Id.*

[145] Cal. Fish & Game Code § 2801(c)

quantitative data was mostly coming from public lands, that the species was still well-distributed across the state, so listing was not warranted at that time.[146]

Nevertheless, when Townsend's was being considered for listing, the agencies and timber industry began to get a look at what shape CESA-listing protections for bats might take. During the years in which Townsend's status was being reviewed, measures for the species were beginning to be preemptively incorporated in THPs.[147] One issue that came up in the redwood forest ecosystem is that timber owners would contend that they did not need to consider environmental impacts to Townsend's because their THP area did not constitute likely roosting habitat. They argued that "a vast majority of the reporting sighting and various roost sites [of this species] are not found within the forested landscape."[148] Of course, one reason that Townsend's presence was not being documented in forests, especially on private timber properties, is that no one was being required to survey for them. Townsend's are an especially cryptic bat because they emit quieter calls than other species. However, I know from own acoustic monitoring surveys that Townsend's are present in redwood habitat (Chapter 1) even though I have never identified a Townsend's roost.

The timber companies also noted in their THP that there were no trees with "extremely large (cavernous) basal cavities" known to occur in the THP area.[149] As a result, they argued that the proposed THPs activities would not cause CESA "take" and "since there are no known feasible ways to even determine if such an event were to occur, we have chosen not to speculate further per CEQA."[150] However, the CAL FIRE wildlife reviewer pushed back on this assessment in the review comments because "there is no published literature that provides minimum dimensions of trees that can be utilized as maternity roosts or hibernacula."[151] The timber companies were citing a 2004 study that was not intended to provide criteria for what tree size qualifies as a potential Townsend's roost.[152] In fact, the author of the study communicated to the agency wildlife reviewer that "it is grossly inappropriate to use the data from my small, anecdotal, and observational General Note to suggest any sort of minimum dbh for potential roosts for any type of Townsend's big-eared bat."[153] This highlights the challenge of protecting even listed species from adverse environmental impacts when there is a lack of data on the species' habitat and ecological needs or understanding of how timber operations and other human activities impact these. These data gaps will need to be filled before sensitive bat populations can be effectively protected even under ESA or CESA.

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[146] Personal communication with CDFW personnel. May 7, 2020.

[147] Personal communication with Cal Fire personnel. May 4, 2020. See for example: Timber Harvest Plan No. 2-15-051-BUT(l) – Preacher; Ramblin THP #2-15-025-TRI.

[148] Timber Harvest Plan No. 2-15-051-BUT(l) – Preacher. August 10, 2015

[149] Timber Harvest Plan No. 2-15-051-BUT(l) – Preacher September 2, 2015; Ramblin THP #2-15-025-TRI. June 3, 2015

[150] Timber Harvest Plan No. 2-15-051-BUT(l) – Preacher

[151] Emershy 15-025-TRI #2, July 7, 2015

[152] Emershy 15-025-TRI #2, July 7, 2015, page 2

[153] *Id.*

Once CDFW decided that Townsend's did not warrant listing, all of the provisions for assessing and mitigating impact that had begun to be developed were dissolved.[154] The THPs that had included provisions for Townsend's under the circumstance that it was listed did not need to fulfill those provisions. No further surveying for sensitive bat species has been required.

Concluding recommendations

When it comes to working forest lands in California, measures encoded in the Forest Practice Act, Forest Practice Rules, and CEQA provide some protection for wildlife, but as discussed, few direct protections exist for species such as bats. This is especially true for forest bat populations that do not roost in the large colonies found elsewhere, and thus might not qualify for protections under CEQA even if these species are being significantly impacted by the cumulative effects of many roost trees being logged without meaningful mitigation to provide for the persistence of the populations. If these species are ultimately listed under ESA or CESA, there will be new requirements to survey for bats on timber properties, but the recent history of when Townsend's big-eared bat was considered for listing suggests that this process will not be easy for public agencies or private landowners. We need to revise forest management policy so that wildlife conservation is more compatible with economic development and other public values.

Improvements are needed to the Forest Practice Act to meet the intentions of CEQA and protect species across working forests. Current policy emphasizes protections for species already listed under endangered species acts. We need to be more proactive about protecting sensitive species before they reach the brink of population collapse and are unable to recover. However, we cannot effectively advocate for and protect species if we do not even know that they are present in the habitat. A key first step for reforming the Forest Practice Act is requiring that surveys are conducted for sensitive species such as bats before timber harvesting occurs. As illustrated by my dissertation research (Chapters 1-3), acoustic monitoring offers a non-invasive sampling approach to collect enormous amounts of data on bat species presence and activity patterns. Furthermore, tremendous efforts have recently been made to standardize best practices for monitoring North American bats, providing a helpful reference guide for conducting bat surveys across large landscapes.[155] Although there are limitations to acoustic surveys, such as the inability to directly assess population abundance and the challenges of detecting quieter or higher-flying species, acoustic monitoring can nevertheless provide a beneficial understanding of species presence and population trends. Requiring this level of monitoring for non-listed species is especially justified for forest bats given both the challenges to accurately assessing the

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[154] Personal communication with Cal Fire personnel. May 4, 2020.

[155] Loeb, S.C., Rodhouse, T.J., Ellison, L.E., Lausen, C.L., Reichard, J.D., Irvine, K.M., Ingersoll, T.E., Coleman, J.T.H., Thogmartin, W.E., Sauer, J.R., Francis, C.M., Bayless, M.L., Stanley, T.R., Johnson, D.H., 2015. A plan for the North American Bat Monitoring Program (NABat). Gen. Tech. Rep. SRS-208. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 208, 1–100. https://doi.org/10.2737/SRS-GTR-208

population status of cryptic species and the known severity of threats, such as white-nose syndrome, already decimating North American bat populations.[156]

We need to not only have standardized methods for detecting species presence before timber harvesting occurs but also require standardized surveys afterwards to assess short and long-term impacts on species populations. These surveys should be reviewed by CDFW and CAL FIRE, and the records should be made publicly available. Not only would this inform future management of the surveyed property but developing this population assessment record would improve agency and general scientific understanding of how timber management affects bats on a larger scale. This could shed much needed light on the extent to which cumulative impacts of roosting or foraging habitat loss are impacting local and regional populations.

Importantly, bat surveys must be species-specific. Earlier research and monitoring studies in the redwood ecosystem often aggregated species because it was not possible to confidently identify calls to species, and this is still common practice in many places for the *Myotis* genus.[157] However, Chapter 1 findings demonstrate that species in this ecosystem vary in their sensitivity to both habitat disturbance and microclimate. For example, three species (pallid bat, long-eared myotis, and fringed myotis) were significantly positively associated with canopy height, which was used as a proxy for forest maturity. Townsend's big-eared bat was only detected at mature forests sites, indicating this species may be especially sensitive to working forest habitat conditions. Other species may be better adapted to working forests because of their morphology or foraging style. This includes the California myotis, which is the species which was by far the most ubiquitous species at working forest sites in my year-round study of bat activity (Chapter 2). If *Myotis* species and other acoustic guilds are not studied at the individual species level, then natural resource managers may fail to detect the species-specific impacts of forest management practices on local and regional bat populations.

Another reason why it is important to monitor species-specific impacts is that Chapter 3 findings of winter activity patterns suggest that species will also be differentially susceptible to emerging disease, and white-nose syndrome is projected to spread to this region in the near future.[158] For example, the California myotis was the species most frequently detected as active in this ecosystem during the winter (Chapter 3). In contrast, the Yuma myotis, a species that was detected approximately as frequently as the California myotis during the summer (Chapter 1), was rarely detected as active during the winter. This difference in winter behavior has critical implications because Yuma myotis is known to be elsewhere affected by white-nose syndrome. These two species emit similar echolocation calls and are therefore often combined into one

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[156] Lorch, J.M., Palmer, J.M., Lindner, D.L., Ballmann, A.E., George, K.G., Griffin, K., Knowles, S., Huckabee, J.R., Haman, K.H., Anderson, C.D., Becker, P.A., Buchanan, J.B., Foster, J.T., Blehert, D.S., 2016. First Detection of Bat White-Nose Syndrome in Western North America. *mSphere* 1, e00148-16.

[157] Walters, C.L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M.K., Puechmaille, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. Journal of Applied Ecology 49, 1064–1074. https://doi.org/10.1111/j.1365-2664.2012.02182.x

[158] White-Nose Syndrome [WWW Document], n.d. URL https://www.whitenosesyndrome.org/press-release/state-and-federal-partners-in-california-and-arizona-ask-public-to-help-detect-and-prevent-spread-of-fungus-deadly-to-bats (accessed 3.31.22).

species group in acoustic studies that rely on autoclassification software.[159] This may seem like a prudent approach to reduce the probability of species misidentification, but given the differences in species' susceptibility to emerging threats of climate change and disease, it is essential that scientists and natural resource managers take advantage of advancements in acoustic technology and classification software to monitor population changes at the individual species level.

Given that bats have distinct seasonal ecology requirements and occupy different landscapes at different times of the year, consideration must be given to the timing of surveys. The limited attention that has been given to protecting forest bat roosting habitat has mostly focused on summer maternity roosts. Protecting maternity roosts is absolutely essential for population persistence, but we must also identify and protect habitat that is critical for other aspects of species' ecology. For example, male and female silver-haired bats sexually segregate for most of the year, but there is evidence that female silver-haired bats migrate to redwood forests to overwinter and mate.[160] Redwood habitat is also known to provide important stopover and winter habitat for other sensitive tree bat species such as hoary bats.[161] If we only survey redwood habitat during the summer, then we would underestimate the importance of the habitat for these species and may overlook how forest management affects these populations.

This more comprehensive understanding of sensitive species and their ecological needs should also be incorporated into natural community conservation plans and habitat conservation plans. NCCPs and HCPs can be powerful tools for reconciling biodiversity conservation with economic development goals. However, their effectiveness for conservation is contingent on what species are included and how well ecological relationships are understood. In the example of previous incidences of these plans being implemented in redwood forests, the timber company did not include any bat species in its 2003 NCCP and the only species that was included in the 2017 HCP was the pallid bat. This species generally roosts in large basal hollows in the redwood forest, and it forages by gleaning prey from the ground, which is unusual for bats in this ecosystem. Bats have species-specific foraging and roosting needs, and species respond differently to silvicultural treatments.[162] Therefore, including one bat species in the plan does not sufficiently cover the habitat needs of species with different ecological niches. On the other hand, there is evidence that some forest bat species might serve as umbrella species and targeting conservation efforts around these species might also protect species with overlapping niches.[163]

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[159] Johnson, J.S., Treanor, J.J., Lacki, M.J., Baker, M.D., Falxa, G.A., Dodd, L.E., Waag, A.G., Lee, E.H., 2017. Migratory and winter activity of bats in Yellowstone National Park. Journal of Mammalogy 98, 211–221. https://doi.org/10.1093/jmammal/gyw175; Schwab, N.A., 2014. Winter Acoustic Activity of Bats in Montana. nwnt 95, 13–27. https://doi.org/10.1898/NWN13-03.1

[160] Weller, T.J., Stricker, C.A., 2012. Northern California redwood forests provide important seasonal habitat for migrant bats. In: Standiford, Richard B.; Weller, Theodore J.; Piirto, Douglas D.; Stuart, John D., tech. coords. Proceedings of coast redwood forests in a changing California: A symposium for scientists and managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 447-457 238, 447–457.

[161] Weller, T.J., Castle, K.T., Liechti, F., Hein, C.D., Schirmacher, M.R., Cryan, P.M., 2016. First Direct Evidence of Long-distance Seasonal Movements and Hibernation in a Migratory Bat. Sci Rep 6, 34585.

[162] Loeb, S.C., 2020. Qualitative synthesis of temperate bat responses to silvicultural treatments—where do we go from here? Journal of Mammalogy 101, 1513–1525. https://doi.org/10.1093/jmammal/gyaa089

[163] Drake, E.C., Gignoux-Wolfsohn, S., Maslo, B., 2020. Systematic Review of the Roost-Site Characteristics of North American Forest Bats: Implications for Conservation. Diversity 12, 76. https://doi.org/10.3390/d12020076

Incorporating monitoring for umbrella species alongside the most vulnerable species would extend the scope of NCCPs and HCPs to the larger natural community.

At the moment there is significant social and political momentum to mitigate the unprecedented impacts of climate change and other global threats to biodiversity through large-scale conservation planning. This has been exemplified by the 30x30 movements that are occurring at global, national, and state scales.[164,165] Integrating working landscapes will be key to meeting these goals. However, it is evident that for working lands to work for conservation then we need to resolve existing oversights and conflicts between land management and animal conservation. I have identified some of these gaps in protection in the context of bats in California redwood forests, and I have offered recommendations for how state and federal policy could be improved to better protect sensitive species. Such changes will require new efforts on the part of policymakers, agencies, and private landowners. However, given the enormity of the challenges that species are facing globally and in our local forests, such efforts seem a necessary price to pay to uphold the public trust and conserve biodiversity for the future.

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[164] Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., Burgess, N.D., Burkart, K., Noss, R.F., Zhang, Y.P., Baccini, A., Birch, T., Hahn, N., Joppa, L.N., Wikramanayake, E., 2019. A Global Deal For Nature: Guiding principles, milestones, and targets. Science Advances.

[165] Bill Text - AB-3030 Resource conservation: land and ocean conservation goals. [WWW Document], n.d. URL https://leginfo.legislature.ca.gov/faces/billTextClient.xhtml?bill_id=201920200AB3030 (accessed 1.19.22).

Conclusion

My dissertation findings reveal details on the habitat value of coast redwood forests for 13 bat species threatened by climate change and emerging disease. Importantly, I was able to take advantage of recent advances in ultrasonic detection equipment and call classification software to identify recorded bat calls to species. This enabled me to study species-specific responses to environmental conditions, as well as examine species seasonal ecology and bat community niche partitioning. This species-level understanding can critically inform vulnerability assessments and conservation planning for target species. Furthermore, by examining species ecology across multiple forest management types, my research addressed gaps that were left by historical research tendencies to focus on protected areas, especially old-growth groves. My results demonstrated that young, working forests also serve as critical habitat for sensitive bat populations, and managing these forests for bats may thus be as important as managing in mature, protected areas.

In Chapter 1, I used a large landscape approach to study how bat species distribution and activity patterns relate to two key environmental factors: fog-dominated climate and forest maturity. I recorded bat acoustic activity over 407 summer monitoring nights at 20 sites that were selected to represent the spectrum of forest management types and the coastal gradient of fog-influenced climate. Temperature and relative humidity were actively logged at monitoring sites, and historical climatic moisture deficit data was obtained from the software application ClimateNA (Wang et al., 2016). To characterize forest habitat, I derived mean forest canopy height and stream channel area at the monitoring sites from remotely sensed data using ArcGIS. I developed generalized linear mixed models to relate species activity to these climate and habitat variables, and my findings demonstrated that the drivers influencing bat activity across the coast redwood landscape were species-specific. In particular, several species were significantly positively associated with forest canopy height, suggesting that these species may be more reliant than others on mature habitat. However, it is important to note that I studied bat activity based on echolocation behavior, and bats may forage long distances and return elsewhere to roost. Consequently, although my study demonstrates that working lands provide important foraging habitat, other studies have found that many species roost primarily in mature habitat features, such as old-growth basal hollows, and this difference in habitat value between mature and younger forests should not be discounted (Gellman and Zielinski, 1996; Mazurek and Zielinski, 2004; Zielinski and Gellman, 1999).

Another key finding of the Chapter 1 study was that while both inland and coastal sites functioned as important bat habitat, higher bat activity in the redwood ecosystem was associated with higher temperature. This was contrary to my hypothesis that bat activity would be higher closer to the coast, where temperatures are more stable and more moisture is available. One explanation for this is that habitat suitability is driven more by selection for optimal foraging conditions (Brooks et al., 2017). Future research should sample insect abundance across the study area to investigate how the positive association between bats and temperature relates to prey availability versus thermoregulatory costs. Also, it is possible that there was not a stronger association between bats and more coastal sites because the entire study area is functioning to buffer bats from the temperature extremes and drought stress experienced inland. A future research direction would be to study the influence of climate on California bats across an even larger scale, including study sites outside of the coast redwood range. Future research should also evaluate whether these relationships hold as climate change increasingly stresses the redwood ecosystem, especially if coastal fog decreases in the future (Johnstone and Dawson, 2010).

In Chapter 2, I conducted a year-round study at five sites, including both old-growth groves and young timberland, to examine bat seasonal ecology and vertical niche partitioning. By placing acoustic monitors at both ground and treetop, I discovered that treetop deployment methods significantly increased the detection of tree-roosting and migratory species across all forest management types and all seasons. This was a surprising finding for two reasons. The first is that while a previous study had observed significant changes in community composition across the vertical gradient of old-growth groves (Kennedy et al., 2014), I had not expected this finding to extend to much shorter younger forests. Also, I had expected differences between ground and treetop detections to primarily occur during the fall and spring migration seasons, when species are believed to move rapidly through the coast redwood ecosystem (Cryan, 2003; Weller and Stricker, 2012). Indeed, applying generalized additive models did illustrate strong seasonal peaks for these species during known migration periods, but treetop deployment methods also detected unexpectedly higher levels of migratory species activity across the year. Ground-level detectors frequently failed to detect migratory species presence on nights when species calls were detected in high volume at treetop. Instead, standard acoustic survey methods primarily detected clutter-adapted *Myotis* species. This bias may limit understanding of how forest management practices differentially impact bat species and underestimate the value of coast redwood habitat for tree-roosting and migratory species.

Using generalized additive models to examine seasonal activity patterns also revealed peaks in species activity that did not coincide with migration behavior, including a peak in summer activity for many *Myotis* species. Other studies have also detected species-specific changes in activity patterns during the summer (Loeb et al., 2019), but the drivers behind these changes should be explored further. Future research could investigate how fluctuations in insect prey availability or maternity season behavior may relate to activity peaks.

The findings included in Chapter 2 point to significant winter bat activity, but this activity may have been overlooked or underestimated by previous research because many species were primarily detected at treetop. Following up on this finding, Chapter 3 provides a deeper dive into the microclimatic conditions under which bats are detected during the winter. I developed species-specific generalized linear mixed models to relate ambient temperature and humidity variables to nightly detection of bat species presence. I included the location of the detector (ground or treetop) as an additional fixed effect. The modeling results indicated that maximum daytime temperature was a better predictor of winter bat activity than maximum nighttime temperature, which may suggest that the mechanism driving bat arousal and subsequent flight activity is daytime environmental conditions more so than the conditions that bats experience when flying at night. Future research should investigate the precise environmental and physiological conditions underlying bat arousal from winter torpor. Regardless of the mechanism, my findings of the daytime temperature thresholds at which different species are predicted to be active during the winter can be applied to help optimize survey efforts to detect target species.

Perhaps most importantly, the research in Chapter 3 was able to extend findings from other ecosystems that coastal populations are able to take advantage of milder environmental conditions to sustain higher activity during the winter than inland populations of the same species (Falxa, 2007; Grider et al., 2016). This has important implications because bats that are active during the winter are more resilient to white-nose syndrome than hibernating bats. My findings showed that there were tremendous differences in the propensity of species to be detected during the winter. This stark contrast was apparent between two species which were similarly ubiquitous during summer monitoring, the California myotis and the Yuma myotis, which suggests that differences in detection probability reflect real differences in overwintering strategies. Species that are detected frequently may use shallow torpor, instead of hibernating, in order to take advantage of warmer temperatures to rewarm passively and possibly forage (Turbill and Geiser, 2008). Whether and to what extent bats in the coast redwood ecosystem are able to successfully forage during the winter remains unknown, and this is a critical direction for future research. If bats are able to successfully forage during the winter, then even populations which normally hibernate may be resilient to mortality from white-nose syndrome. If that is the case, then the coast redwood ecosystem may be a priority habitat for bat conservation.

In Chapter 4, a review of the laws and policies regulating California timberland management for wildlife is provided to assess to what extent regulations are effective in protecting sensitive bat species. I then discuss ways in which regulations could be improved to make working lands management more compatible with biodiversity conservation. Measures encoded in the Forest Practice Act, Forest Practice Rules, and California Environmental Quality Act provide some protection for wildlife, but few direct protections exist for species which are not listed under the state or federal Endangered Species Act. Furthermore, even if forest bats should qualify for additional protections, their cryptic nature makes it hard to assess species population status. We need to start by at least requiring forest managers to assess species presence on the landscape. Also, current survey and mitigation measures for bats focus on summer maternity roosts, and we need to also consider their vulnerability to forest management during other seasons. This dissertation research provides evidence that coast redwood forests are serving as critical habitat to bats throughout the year and protecting winter habitat may be especially important once white-nose syndrome reaches California bat populations. Three North American bat species are currently being reviewed for possible listing under the federal Endangered Species Act, including one species that is found in the coast redwood ecosystem. However, it would be better for both working forest management and bat conservation if we could resolve conflicts in managing for multiple public values before species reach the point of population collapse. To do so, we must continue to find new ways to integrate diverse land ownerships into future conservation planning.

References

Armstrong, A., 2021. Use of redwood basal hollows by bats: a focus on the Townsend's big-eared bat on the North Coast of California. HSU theses and projects.

Brooks, J.D., Loeb, S.C., Gerard, P.D., 2017. Effect of forest opening characteristics, prey abundance, and environmental factors on bat activity in the Southern Appalachians. Forest Ecology and Management 400, 19–27. https://doi.org/10.1016/j.foreco.2017.05.045

Cryan, P.M., 2003. Seasonal Distribution of Migratory Tree Bats (Lasiurus and Lasionycteris) in North America. Journal of Mammalogy 84, 579–593. https://doi.org/10.1644/1545-1542(2003)084<0579:SDOMTB>2.0.CO;2

Falxa, G., 2007. WINTER FORAGING OF SILVER-HAIRED AND CALIFORNIA MYOTIS BATS IN WESTERN WASHINGTON. nwnt 88, 98–100. https://doi.org/10.1898/1051-1733(2007)88[98:WFOSAC]2.0.CO;2

Gellman, S.T., Zielinski, W.J., 1996. Use by Bats of Old-Growth Redwood Hollows on the North Coast of California. Journal of Mammalogy 77, 255–265. https://doi.org/10.2307/1382726

Grider, J.F., Larsen, A.L., Homyack, J.A., Kalcounis-Rueppell, M.C., 2016. Winter Activity of Coastal Plain Populations of Bat Species Affected by White-Nose Syndrome and Wind Energy Facilities. PLOS ONE 11, e0166512. https://doi.org/10.1371/journal.pone.0166512

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. PNAS 107, 4533–4538. https://doi.org/10.1073/pnas.0915062107

Kennedy, J.-P., Sillett, S.C., Szewczak, J.M., 2014. Bat Activity Across the Vertical Gradient of an Old-Growth Sequoia sempervirens Forest. Acta Chiropterologica 16, 53–63. https://doi.org/10.3161/150811014X683264

Loeb, S.C., Hines, B.A., Armstrong, M.P., Zarnoch, S.J., 2019. Effects of Omnidirectional Microphone Placement and Survey Period on Bat Echolocation Call Quality and Detection Probabilities. acta 21, 453–464. https://doi.org/10.3161/15081109ACC2019.21.2.019

Mazurek, M.J., Zielinski, W.J., 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecology and Management 193, 321–334. https://doi.org/10.1016/j.foreco.2004.01.013

Turbill, C., Geiser, F., 2008. Hibernation by tree-roosting bats. J Comp Physiol B 178, 597. https://doi.org/10.1007/s00360-007-0249-1

Wang, T., Hamann, A., Spittlehouse, D., Carroll, C., 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. PLoS ONE 11, e0156720. https://doi.org/10.1371/journal.pone.0156720

Weller, T.J., Stricker, C.A., 2012. Northern California redwood forests provide important seasonal habitat for migrant bats. In: Standiford, Richard B.; Weller, Theodore J.; Piirto, Douglas D.; Stuart, John D., tech. coords. Proceedings of coast redwood forests in a changing California: A symposium for scientists and managers. Gen. Tech. Rep. PSW-GTR-238. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. pp. 447-457 238, 447–457.

Zielinski, W.J., Gellman, S.T., 1999. Bat Use of Remnant Old-Growth Redwood Stands. Conservation Biology 13, 160–167. https://doi.org/10.1046/j.1523-1739.1999.97424.x

Chapter 1 Supporting Information

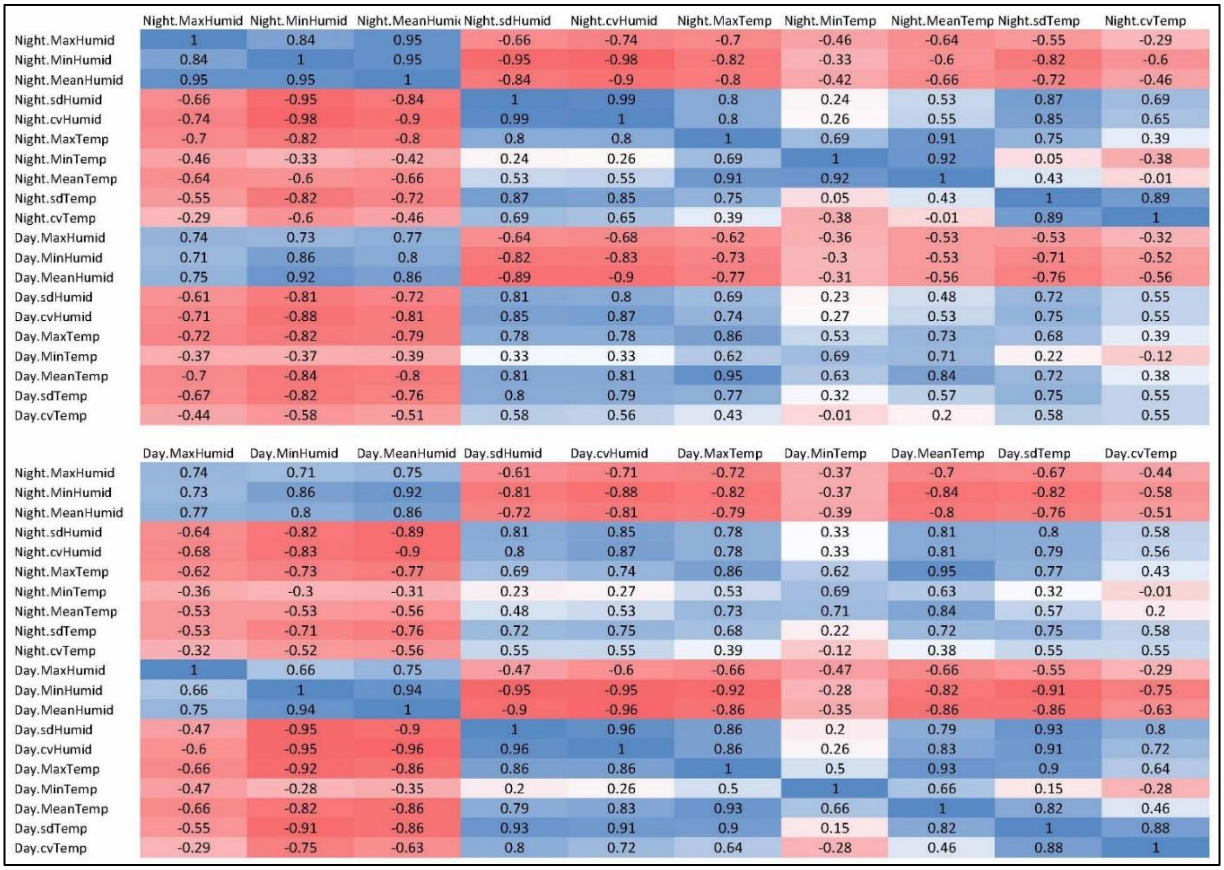
for

Influence of climate and forest management on summer bat activity in coastal forests

Contents

Appendices S1-S7

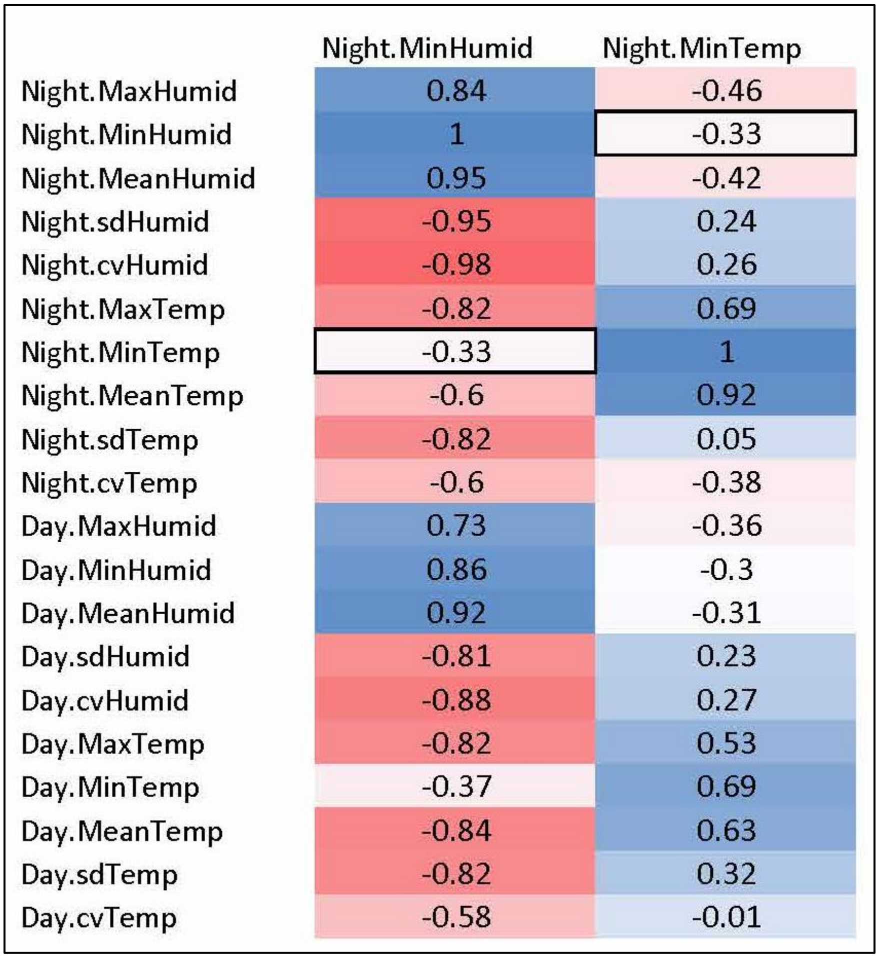
Appendix S1: Spearman’s rank correlation results between microclimate variables.



	Night.MaxHumid	Night.MinHumid	Night.MeanHumi	Night.sdHumid	Night.cvHumid	Night.MaxTemp	Night.MinTemp	Night.MeanTemp	Night.sdTemp	Night.cvTemp
Night.MaxHumid	1	0.84	0.95	-0.66	-0.74	-0.7	-0.46	-0.64	-0.55	-0.29
Night.MinHumid	0.84	1	0.95	-0.95	-0.98	-0.82	-0.33	-0.6	-0.82	-0.6
Night.MeanHumid	0.95	0.95	1	-0.84	-0.9	-0.8	-0.42	-0.66	-0.72	-0.46
Night.sdHumid	-0.66	-0.95	-0.84	1	0.99	0.8	0.24	0.53	0.87	0.69
Night.cvHumid	-0.74	-0.98	-0.9	0.99	1	0.8	0.26	0.55	0.85	0.65
Night.MaxTemp	-0.7	-0.82	-0.8	0.8	0.8	1	0.69	0.91	0.75	0.39
Night.MinTemp	-0.46	-0.33	-0.42	0.24	0.26	0.69	1	0.92	0.05	-0.38
Night.MeanTemp	-0.64	-0.6	-0.66	0.53	0.55	0.91	0.92	1	0.43	-0.01
Night.sdTemp	-0.55	-0.82	-0.72	0.87	0.85	0.75	0.05	0.43	1	0.89
Night.cvTemp	-0.29	-0.6	-0.46	0.69	0.65	0.39	-0.38	-0.01	0.89	1
Day.MaxHumid	0.74	0.73	0.77	-0.64	-0.68	-0.62	-0.36	-0.53	-0.53	-0.32
Day.MinHumid	0.71	0.86	0.8	-0.82	-0.83	-0.73	-0.3	-0.53	-0.71	-0.52
Day.MeanHumid	0.75	0.92	0.86	-0.89	-0.9	-0.77	-0.31	-0.56	-0.76	-0.56
Day.sdHumid	-0.61	-0.81	-0.72	0.81	0.8	0.69	0.23	0.48	0.72	0.55
Day.cvHumid	-0.71	-0.88	-0.81	0.85	0.87	0.74	0.27	0.53	0.75	0.55
Day.MaxTemp	-0.72	-0.82	-0.79	0.78	0.78	0.86	0.53	0.73	0.68	0.39
Day.MinTemp	-0.37	-0.37	-0.39	0.33	0.33	0.62	0.69	0.71	0.22	-0.12
Day.MeanTemp	-0.7	-0.84	-0.8	0.81	0.81	0.95	0.63	0.84	0.72	0.38
Day.sdTemp	-0.67	-0.82	-0.76	0.8	0.79	0.77	0.32	0.57	0.75	0.55
Day.cvTemp	-0.44	-0.58	-0.51	0.58	0.56	0.43	-0.01	0.2	0.58	0.55

	Day.MaxHumid	Day.MinHumid	Day.MeanHumid	Day.sdHumid	Day.cvHumid	Day.MaxTemp	Day.MinTemp	Day.MeanTemp	Day.sdTemp	Day.cvTemp
Night.MaxHumid	0.74	0.71	0.75	-0.61	-0.71	-0.72	-0.37	-0.7	-0.67	-0.44
Night.MinHumid	0.73	0.86	0.92	-0.81	-0.88	-0.82	-0.37	-0.84	-0.82	-0.58
Night.MeanHumid	0.77	0.8	0.86	-0.72	-0.81	-0.79	-0.39	-0.8	-0.76	-0.51
Night.sdHumid	-0.64	-0.82	-0.89	0.81	0.85	0.78	0.33	0.81	0.8	0.58
Night.cvHumid	-0.68	-0.83	-0.9	0.8	0.87	0.78	0.33	0.81	0.79	0.56
Night.MaxTemp	-0.62	-0.73	-0.77	0.69	0.74	0.86	0.62	0.95	0.77	0.43
Night.MinTemp	-0.36	-0.3	-0.31	0.23	0.27	0.53	0.69	0.63	0.32	-0.01
Night.MeanTemp	-0.53	-0.53	-0.56	0.48	0.53	0.73	0.71	0.84	0.57	0.2
Night.sdTemp	-0.53	-0.71	-0.76	0.72	0.75	0.68	0.22	0.72	0.75	0.58
Night.cvTemp	-0.32	-0.52	-0.56	0.55	0.55	0.39	-0.12	0.38	0.55	0.55
Day.MaxHumid	1	0.66	0.75	-0.47	-0.6	-0.66	-0.47	-0.66	-0.55	-0.29
Day.MinHumid	0.66	1	0.94	-0.95	-0.95	-0.92	-0.28	-0.82	-0.91	-0.75
Day.MeanHumid	0.75	0.94	1	-0.9	-0.96	-0.86	-0.35	-0.86	-0.86	-0.63
Day.sdHumid	-0.47	-0.95	-0.9	1	0.96	0.86	0.2	0.79	0.93	0.8
Day.cvHumid	-0.6	-0.95	-0.96	0.96	1	0.86	0.26	0.83	0.91	0.72
Day.MaxTemp	-0.66	-0.92	-0.86	0.86	0.86	1	0.5	0.93	0.9	0.64
Day.MinTemp	-0.47	-0.28	-0.35	0.2	0.26	0.5	1	0.66	0.15	-0.28
Day.MeanTemp	-0.66	-0.82	-0.86	0.79	0.83	0.93	0.66	1	0.82	0.46
Day.sdTemp	-0.55	-0.91	-0.86	0.93	0.91	0.9	0.15	0.82	1	0.88
Day.cvTemp	-0.29	-0.75	-0.63	0.8	0.72	0.64	-0.28	0.46	0.88	1

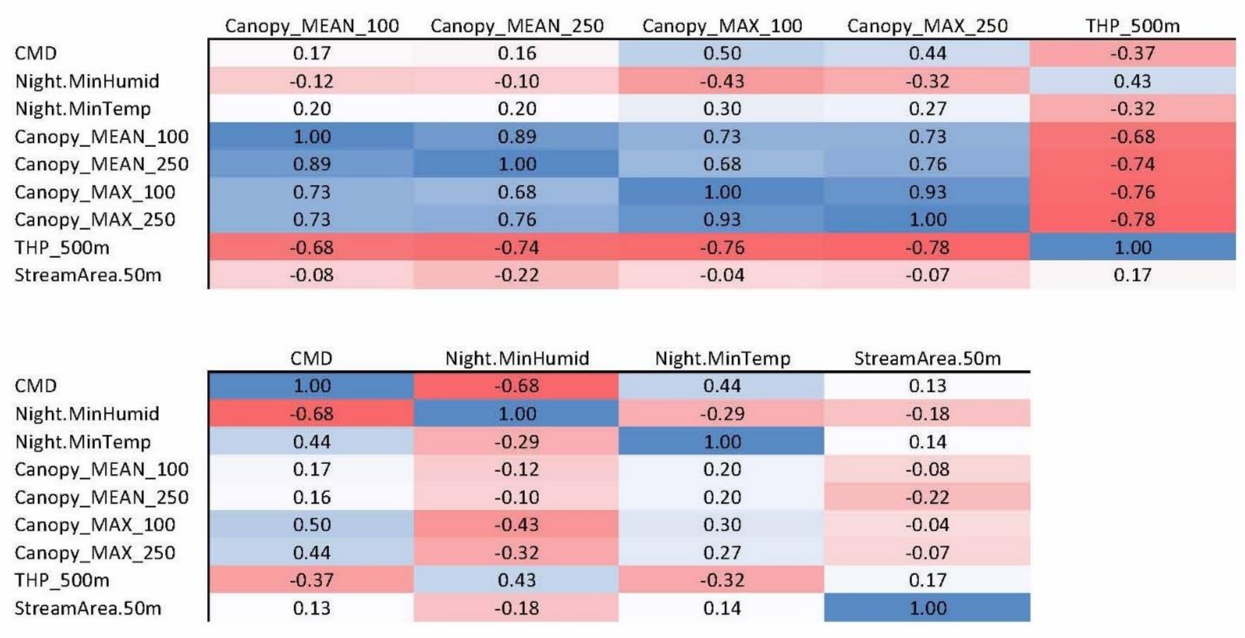
Spearman's rank correlation (rho) correlation results between all examined microclimate variables, including daytime and nighttime statistics for humidity and temperature. Microclimate variables were significantly correlated so we selected only two variables, minimum nighttime humidity and minimum nighttime temperature, which minimized correlation to an acceptable level (-0.33) while representing the microclimate variables of interest.



	Night.MinHumid	Night.MinTemp
Night.MaxHumid	0.84	-0.46
Night.MinHumid	1	-0.33
Night.MeanHumid	0.95	-0.42
Night.sdHumid	-0.95	0.24
Night.cvHumid	-0.98	0.26
Night.MaxTemp	-0.82	0.69
Night.MinTemp	-0.33	1
Night.MeanTemp	-0.6	0.92
Night.sdTemp	-0.82	0.05
Night.cvTemp	-0.6	-0.38
Day.MaxHumid	0.73	-0.36
Day.MinHumid	0.86	-0.3
Day.MeanHumid	0.92	-0.31
Day.sdHumid	-0.81	0.23
Day.cvHumid	-0.88	0.27
Day.MaxTemp	-0.82	0.53
Day.MinTemp	-0.37	0.69
Day.MeanTemp	-0.84	0.63
Day.sdTemp	-0.82	0.32
Day.cvTemp	-0.58	-0.01

Spearman's rank correlation (rho) correlation results for selected variables minimum nighttime humidity and minimum nighttime temperature.

Appendix S2: Spearman's rank correlation results between all model variables.



	Canopy_MEAN_100	Canopy_MEAN_250	Canopy_MAX_100	Canopy_MAX_250	THP_500m
CMD	0.17	0.16	0.50	0.44	-0.37
Night.MinHumid	-0.12	-0.10	-0.43	-0.32	0.43
Night.MinTemp	0.20	0.20	0.30	0.27	-0.32
Canopy_MEAN_100	1.00	0.89	0.73	0.73	-0.68
Canopy_MEAN_250	0.89	1.00	0.68	0.76	-0.74
Canopy_MAX_100	0.73	0.68	1.00	0.93	-0.76
Canopy_MAX_250	0.73	0.76	0.93	1.00	-0.78
THP_500m	-0.68	-0.74	-0.76	-0.78	1.00
StreamArea.50m	-0.08	-0.22	-0.04	-0.07	0.17

	CMD	Night.MinHumid	Night.MinTemp	StreamArea.50m
CMD	1.00	-0.68	0.44	0.13
Night.MinHumid	-0.68	1.00	-0.29	-0.18
Night.MinTemp	0.44	-0.29	1.00	0.14
Canopy_MEAN_100	0.17	-0.12	0.20	-0.08
Canopy_MEAN_250	0.16	-0.10	0.20	-0.22
Canopy_MAX_100	0.50	-0.43	0.30	-0.04
Canopy_MAX_250	0.44	-0.32	0.27	-0.07
THP_500m	-0.37	0.43	-0.32	0.17
StreamArea.50m	0.13	-0.18	0.14	1.00

Spearman's rank correlation (rho) correlation results between all examined habitat variables.

All metrics of canopy height (mean and maximum canopy height, within 100m and 250m radius of monitoring location) were significantly correlated with Timber Harvesting Plan record (proportion of area within 500m radius of monitoring location covered by any THP recorded since 1997). We selected Canopy_Mean_100 as the variable which minimized this correlation. However, we found that the correlation between this and the THP variable still caused model convergence issues. We therefore decided to omit the THP variable and only include mean canopy height within a 100 m radius of the monitoring location in our model because this variable best represented the differences in forest maturity and management history across all sites.

Although Climatic Moisture Deficit (CMD) had a similar level of correlation with minimum nighttime humidity (-0.67), this did not cause convergence issues, so we retained both variables in the model.

Appendix S3: Results of canopy height analysis with example rasters.

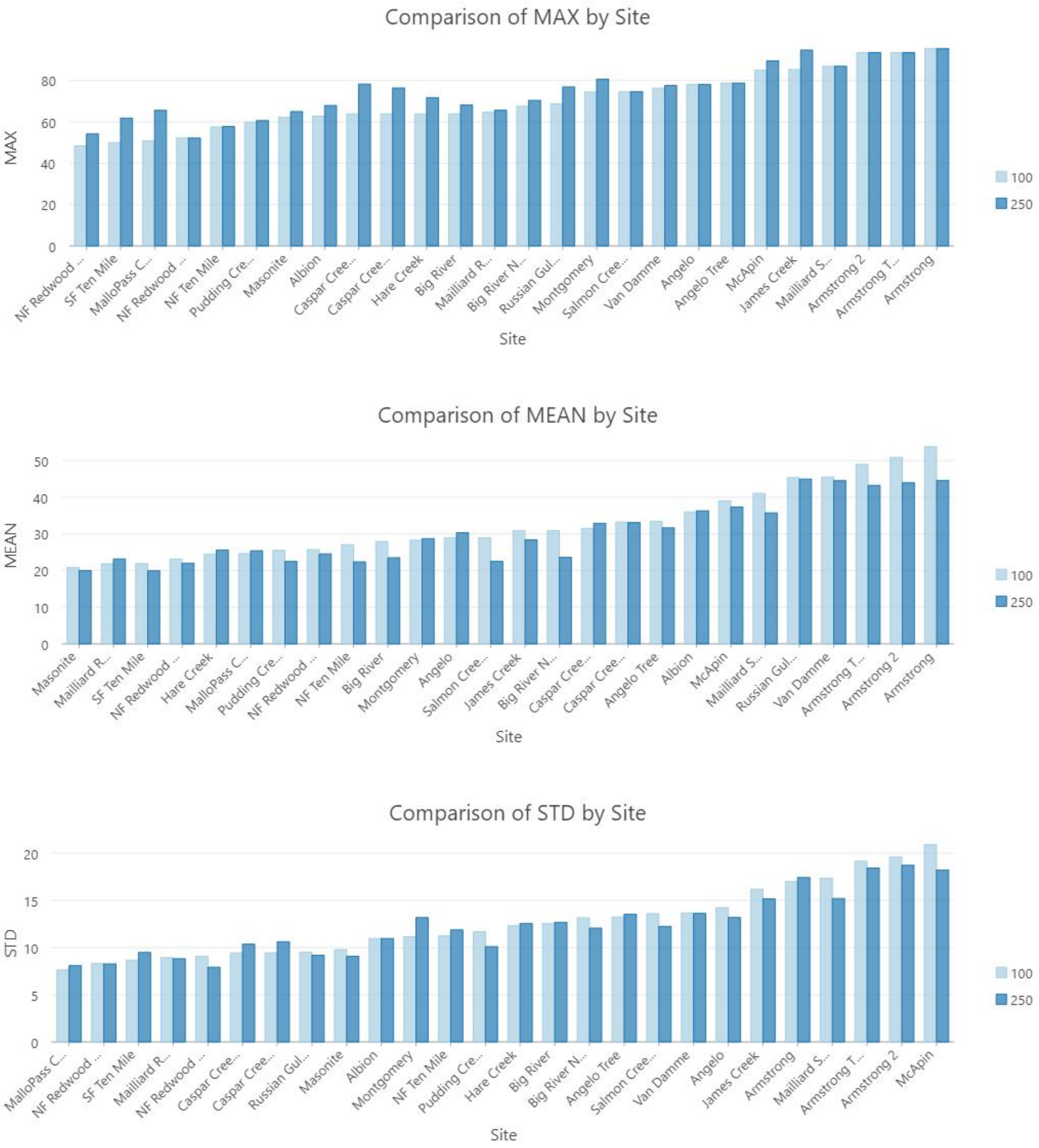
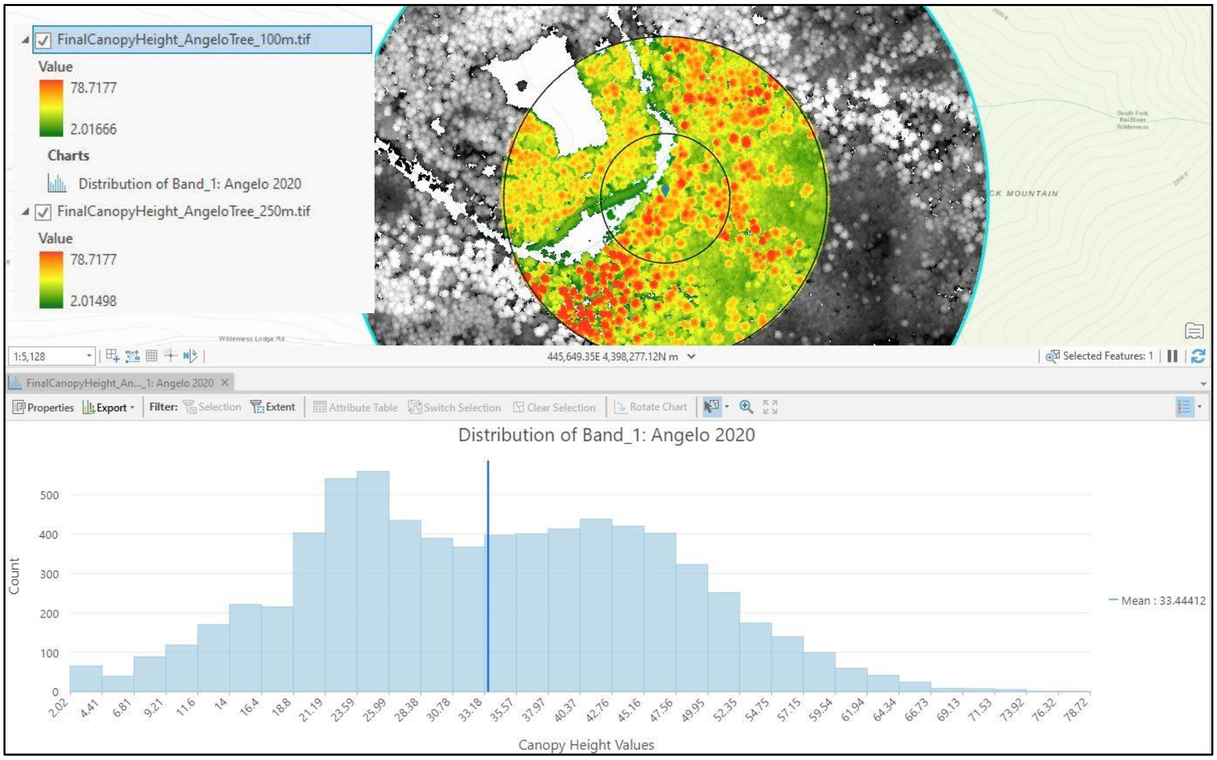


Figure 1: Plots comparing canopy height statistics (maximum, minimum and standard deviation) between sites based on results of raster analysis of LiDAR data in ArcGIS Pro. Sites are ordered by increasing values of 100m radius buffer results. Measurements are all in meters.



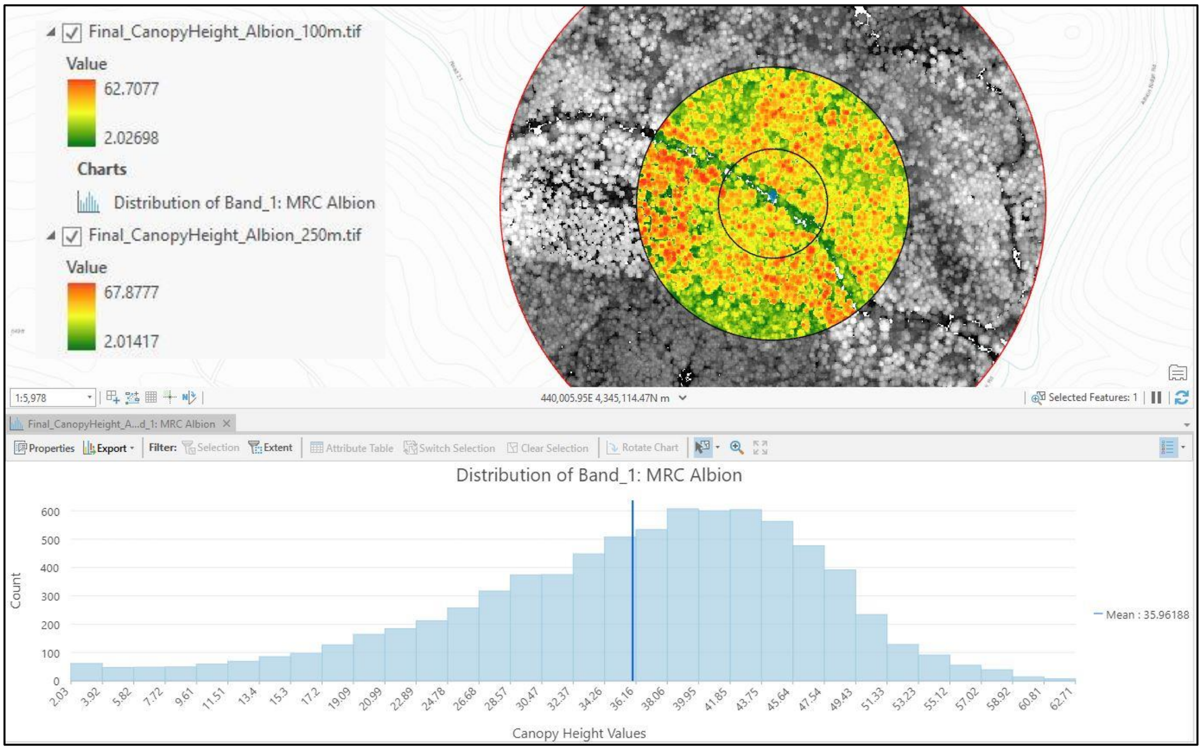


Figure 2: Examples of how canopy height within 100 m and 250 m radius of monitoring location were calculated from LiDAR data using ArcGIS Pro. Note how height < 2.0 m is filtered out to exclude bare earth or stream, as well as vegetation that is not trees. Histograms show how mean canopy height of sites might be similar even when distribution of canopy height is different.

Appendix S4: Results of stream area analysis with example rasters.

Site	Height Cutoff	Stream Corridor Area
Angelo 2019	1	2590
Angelo 2020	0.75	2011
Armstrong	1	1440
JDSF_Caspar	0.5	1071
JDSF_Hare	1	1042
JDSF_James	1	582
Lyme_NF10Mile	1	1720
Lyme_Pudding	0.5	837
Lyme_Redwood	0.5	674
Lyme_SF10Mile	1	1257
Mailliard Ranch	1	1083
Mailliard SNR	1	881
McApin (Richardson Reserve)	1	449
MontgomeryWoods	0.75	1126
MRC_Albion	0.75	1228
MRC_MalloPass 2020	0.5	796
MRC_MalloPass 2019	0.5	888
MRC_Masonite	0.5	899
RussianGulch	0.5	502
TCF Big River New	1	1671
TCF_BigRiver Original	1	1957
TCF_Salmon Creek	0.5	790
VanDamme	0.5	549

Table shows results of stream area analysis conducted using ArcGIS Pro. We ultimately calculated the stream area within a 50 m radius of each monitoring location.

For each study site, we added one-meter resolution digital elevation model data (USGS, 2020) to a map in ArcGIS Pro. We created a new point layer for ‘monitoring point’ at the point in the stream closest to where the detector was deployed. We also created a point layer upstream for where the stream would start. Using the DEM and point layers, we applied a flow accumulation model to produce rasters within various buffer distances (30m, 50m, and 100m) of the monitoring point that represented the relative height and width from the defined stream. We evaluated the resulting rasters to identify the appropriate height cutoff for the stream channel based on the stream topography modeled in ArcGIS Pro and our knowledge from being on the ground at the study site. Height cutoffs ranged from 0.5 to 1.0 m.

We then re-ran the model with the final height cutoff and a buffer distance of 50 m from the monitoring point. This created a monitoring zone raster representing the desired stream channel and an associated attribute table with the raster area calculated. We used this area value as our measurement for stream area.

The following figures show examples of how stream area was calculated in ArcGIS Pro.

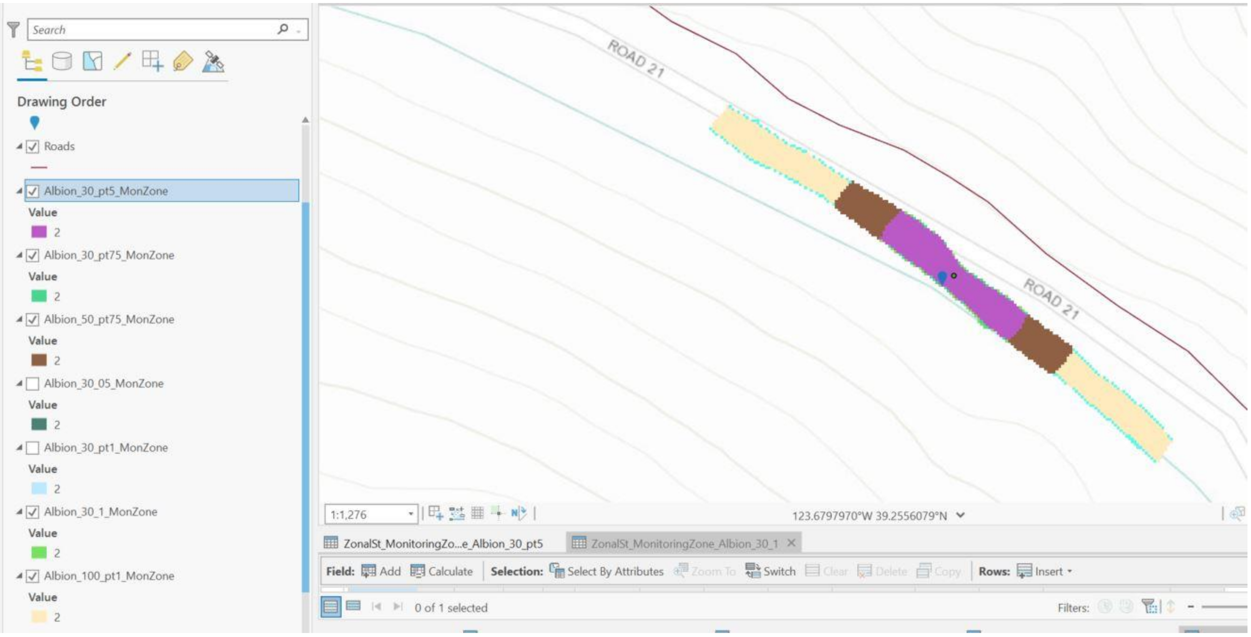


Figure 3: MRC Albion stream area. This is an example of a relatively straightforward stream where changing the height cutoff had minimal impact on the stream area raster. Buffer distances of 30m, 50m and 100m were viewed to assess changes in stream topography before the final buffer distance of 50m was decided on for use in the models.

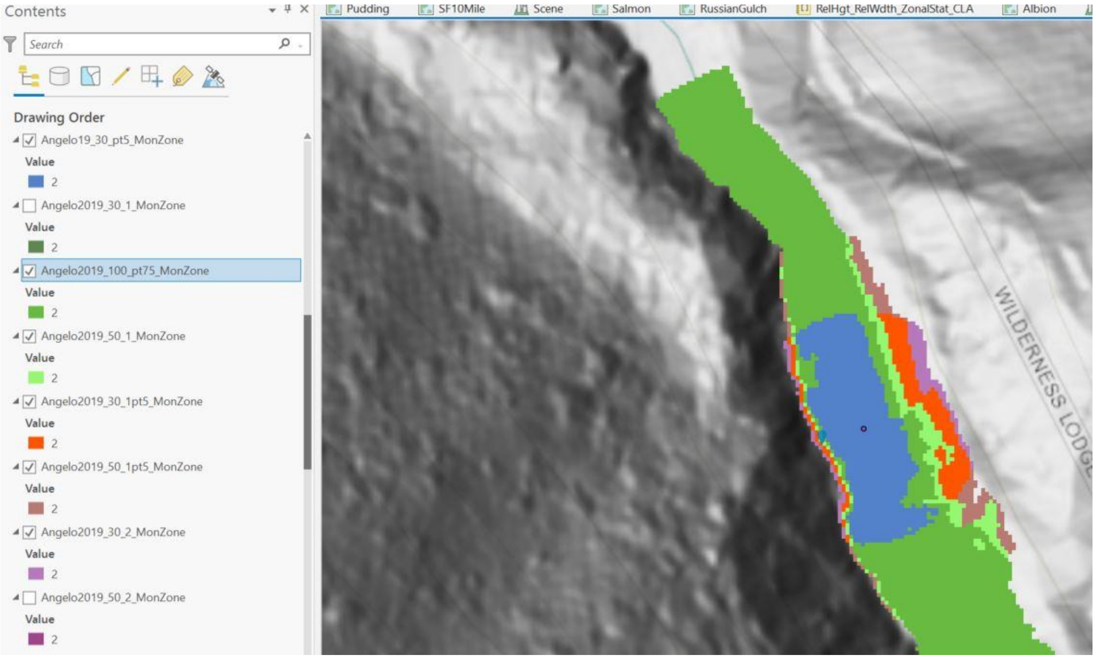


Figure 4: Angelo 2019 monitoring location. Different height cutoff values were viewed to determine the best value for representing the stream area based on bank topography.

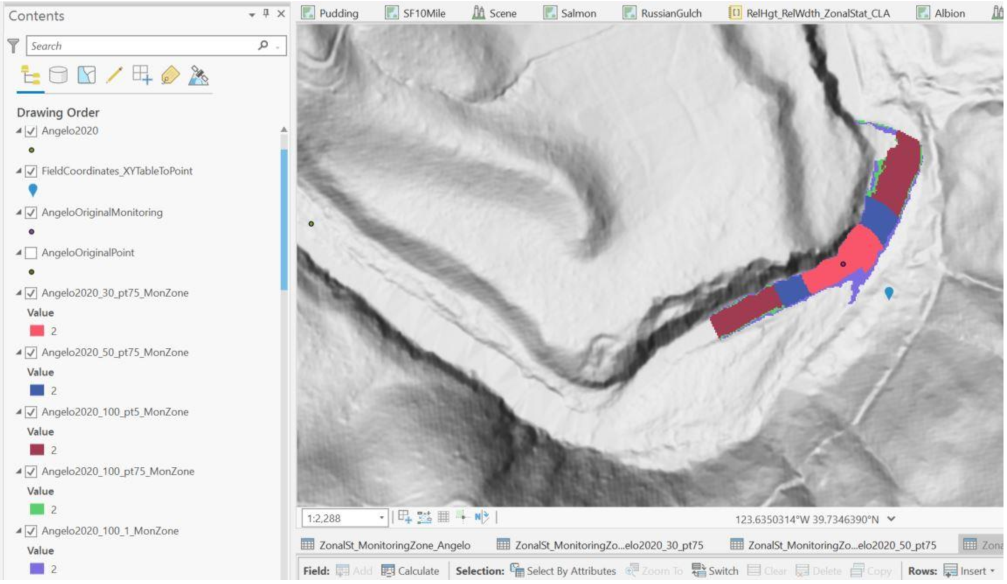


Figure 5: Angelo 2020 monitoring location. The 2020 monitoring location was shifted upstream from the original monitoring location and habitat covariates were also calculated for these monitoring coordinates.

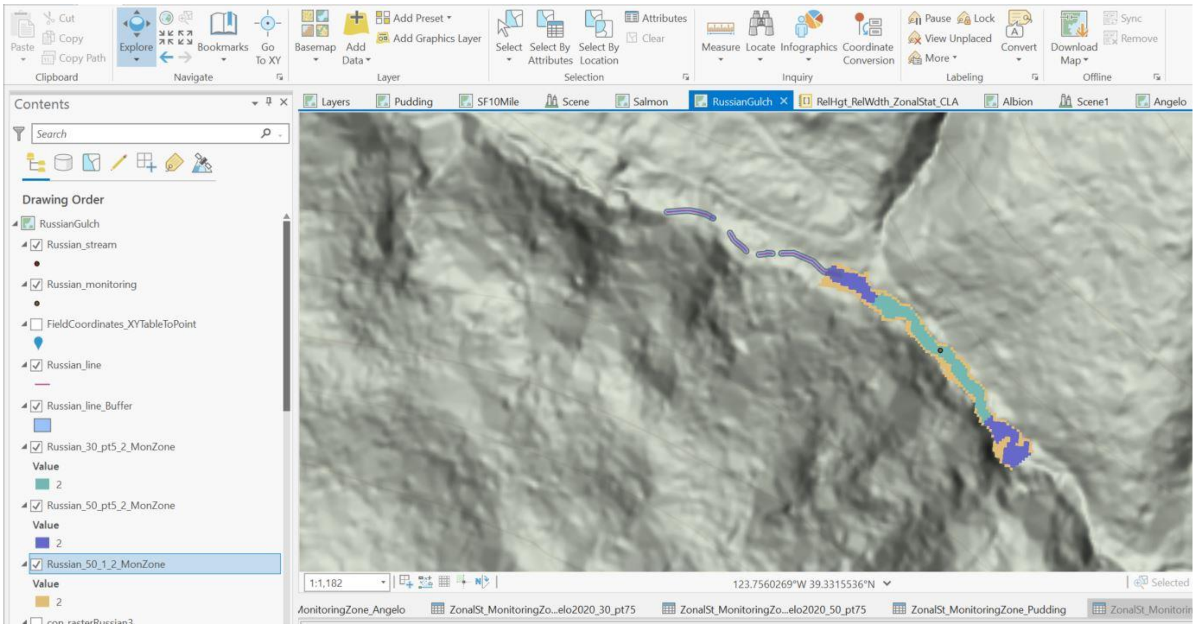


Figure 6: In some cases, issues occurred in the initial analysis of stream area due to errors in the downloaded Digital Elevation Model data. This was generally due to a road crossing or another anomaly causing the DEM value at that point to be calculated to be higher than actual. To correct this for the flow accumulation model, we created polygons to act as “breaches,” converted these features to rasters, and reclassified the rasters to have a value of 0. This value was substituted for the original DEM value at those points, and the resulting modified DEM raster was used in the analysis of stream error.

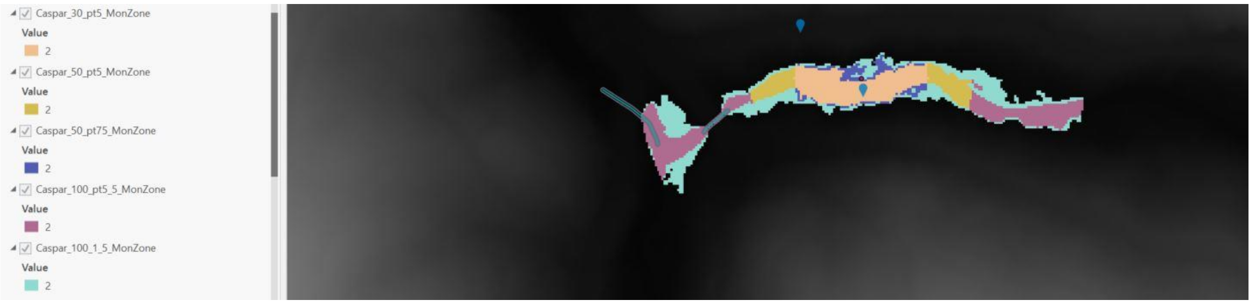


Figure 7: JDSF Caspar is another example of a site which required modification of the DEM raster due to road crossings causing errors in the flow accumulation model. The model flowed correctly once "breaches" were applied in the correct locations. Difference height cutoffs were also viewed before settling on a lower height cutoff value (0.5 m) as best representing the stream area.

Appendix S5: Plots comparing microclimate between sites and monitoring rounds.

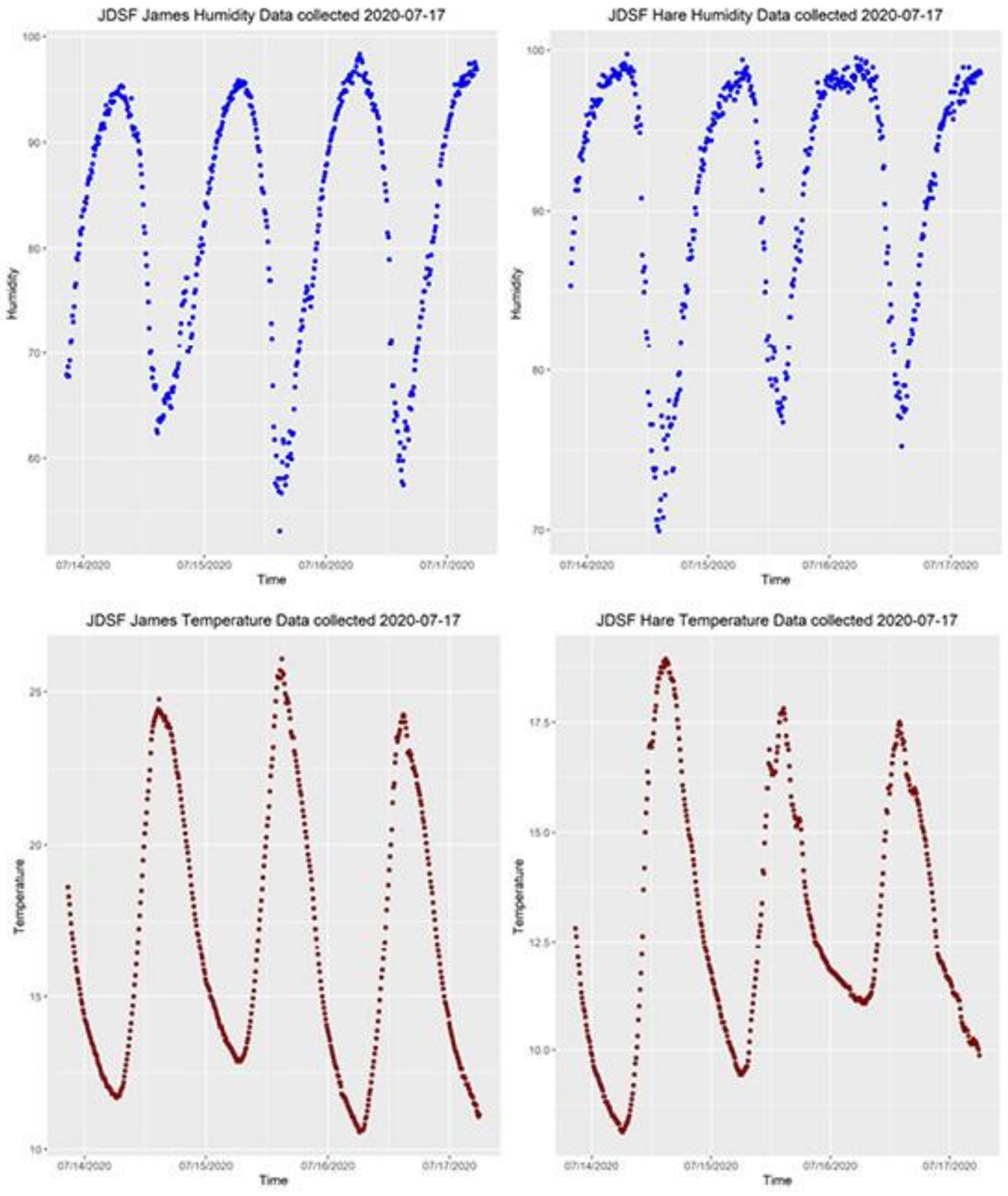


Figure 8: Example of differences in relative humidity and temperature between coastal and inland sites using data logged at JDSF James and JDSF Hare during the same monitoring dates. Note y-axes are on different scales. More variability between site microclimate is expressed by minimum humidity than other humidity statistics so this value for nighttime (sunset to sunrise) was used in our statistical models.

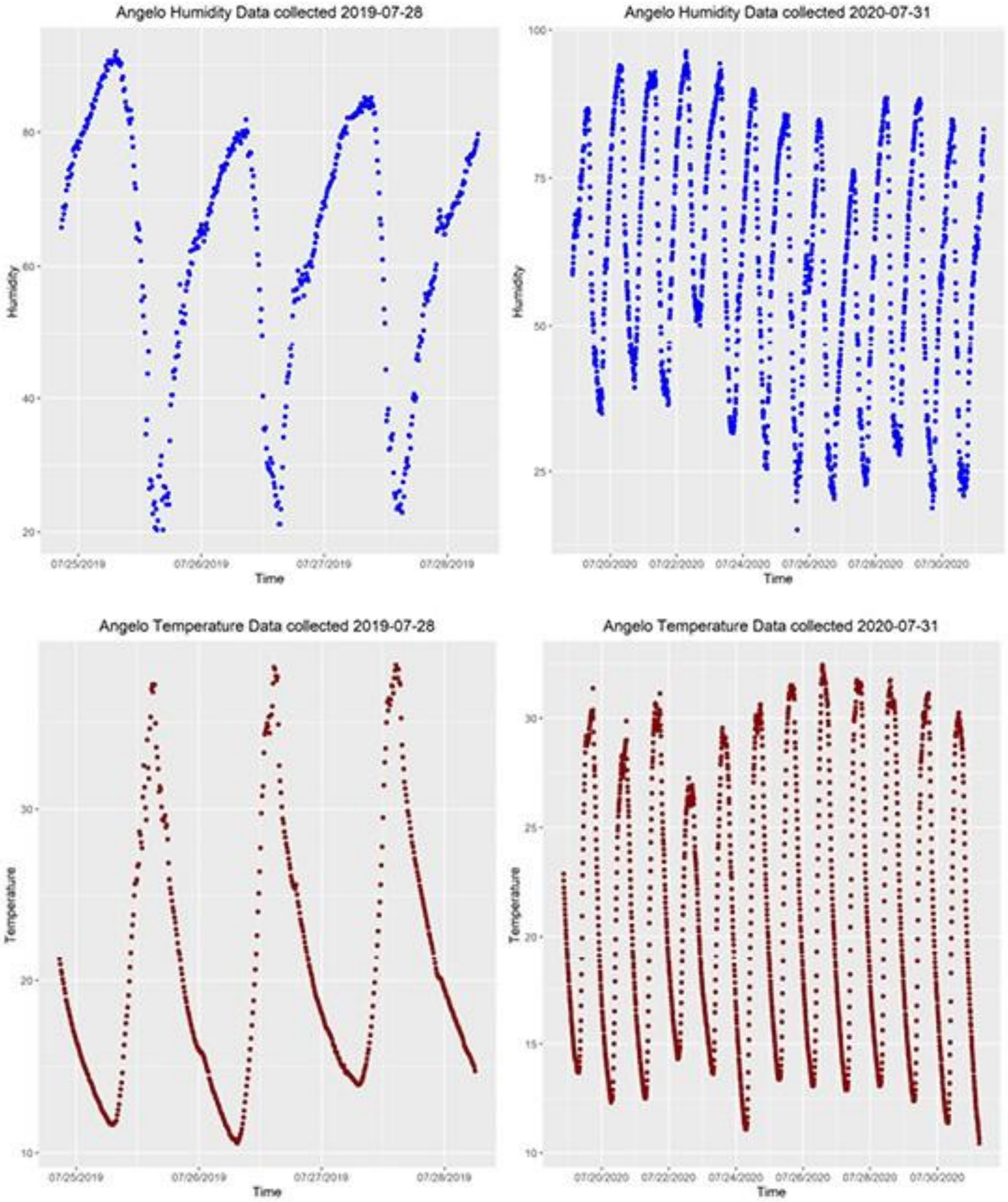
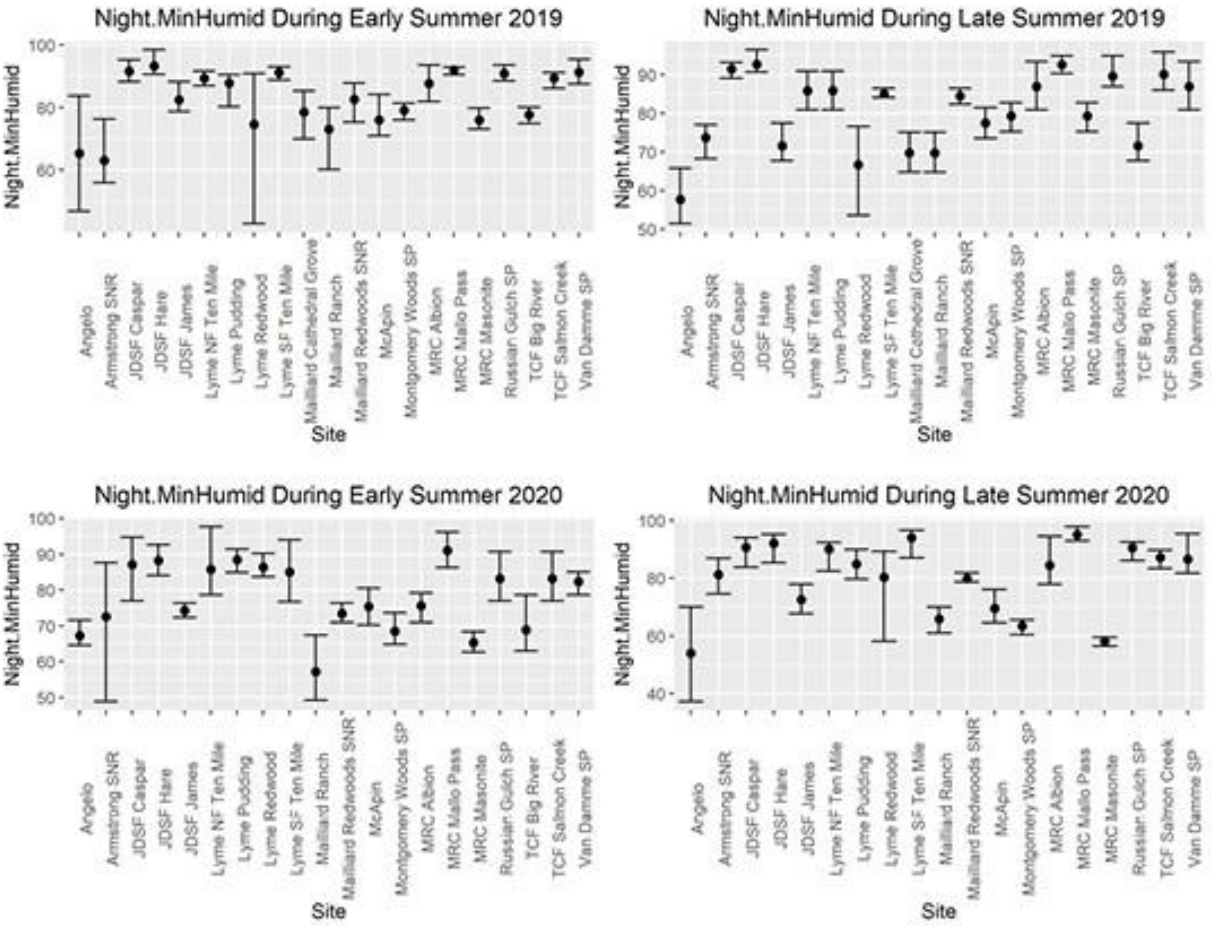


Figure 9: Example of how humidity and temperature vary at a site between similar Julian monitoring periods of different years and even between individual monitoring nights. Note y-axes of 2019 and 2020 data are on different scales.



Night.MinHumid During Early Summer 2019

Night.MinHumid During Late Summer 2019

Night.MinHumid During Early Summer 2020

Night.MinHumid During Late Summer 2020

Figure 10: Boxplots comparing relative humidity statistics of sites for each monitoring round. Boxplot points indicate means and whiskers show minimum and maximum relative humidity of that monitoring round.

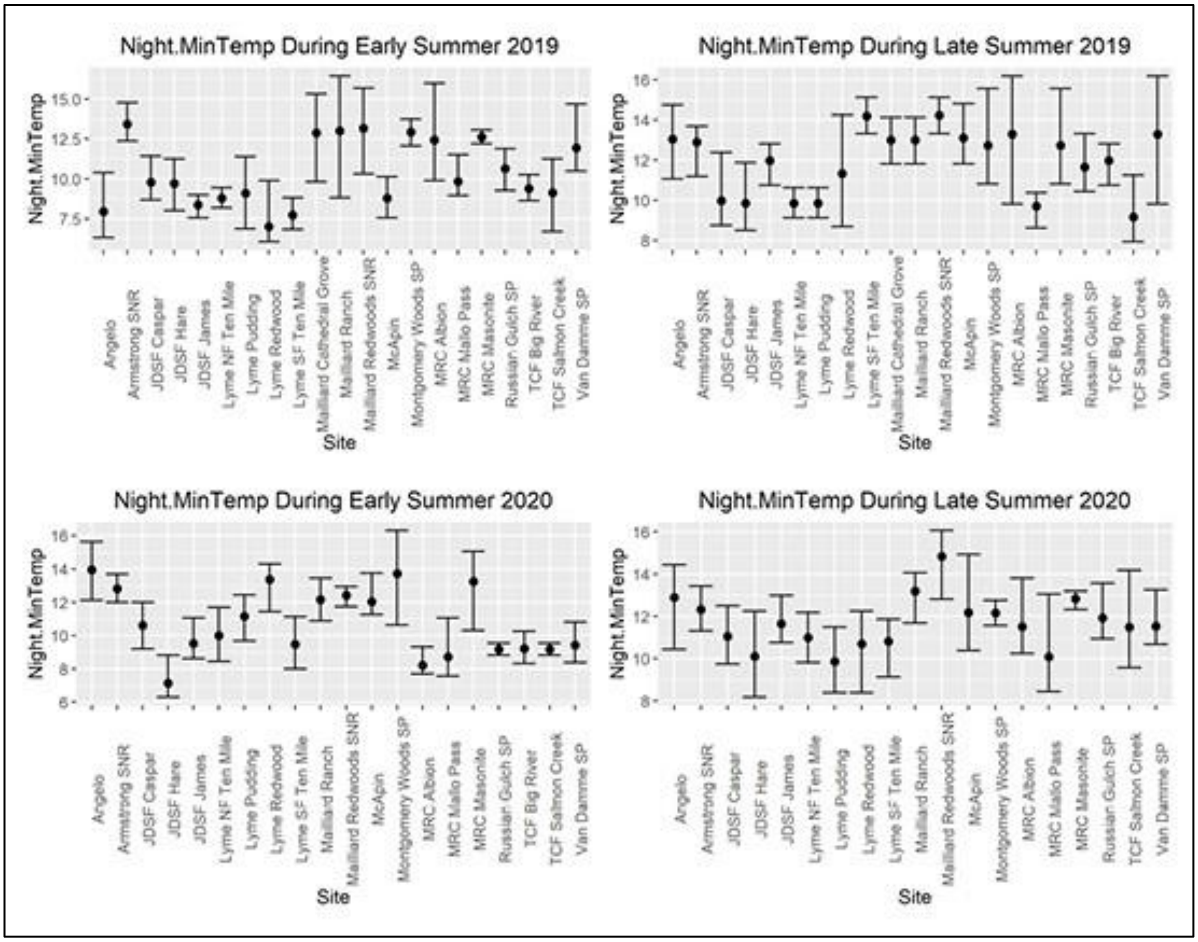


Figure 11: Boxplots comparing temperature statistics of sites for each monitoring round. Boxplot points indicate means and whiskers show minimum and maximum temperature of that monitoring round.

Appendix S6: GLMM species activity model summary results.

Antrozous pallidus (Anpa)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.8819)  ( log )
Formula: Anpa ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
   439.2    483.3   -208.6    417.2      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.8711 -0.2050 -0.0804 -0.0443  7.9112

Random effects:
 Groups Name        Variance  Std.Dev.
 Julian (Intercept) 2.439e-07 0.0004939
 Site.x (Intercept) 3.885e+00 1.9709552
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        -3.7914     0.8677  -4.370 1.24e-05 ***
s.Canopy_MEAN_100   1.1119     0.5389   2.063  0.03909 *
s.sqrtStream        0.7465     0.5377   1.388  0.16504
s.CMD               1.4667     0.6100   2.405  0.01619 *
s.Night.MinHumid   -0.1445     0.2049  -0.705  0.48080
s.Night.MinTemp     0.2140     0.2103   1.017  0.30894
Year1               0.1032     0.1684   0.613  0.53984
Model1             -0.6457     0.2460  -2.624  0.00868 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10 -0.219
s.sqrtStrem  0.056  0.147
s.CMD       -0.477  0.096  0.080
s.Nght.MnHm  0.015  0.249  0.189  0.163
s.Nght.MnTm -0.042 -0.184 -0.006 -0.121 -0.138
Year1        0.062 -0.220 -0.063 -0.006 -0.052 -0.039
Model1      -0.045  0.121 -0.198 -0.051 -0.148  0.012 -0.490
```

Eptesicus fuscus (Epfu)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.741)  ( log )
Formula: Epfu ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
  2100.8   2144.9  -1039.4   2078.8      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.8369 -0.6226 -0.3588  0.2630  5.4287

Random effects:
 Groups Name        Variance Std.Dev.
 Julian (Intercept) 0.1933   0.4396
 Site.x (Intercept) 0.6077   0.7796
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        1.22820    0.20297   6.051 1.44e-09 ***
s.Canopy_MEAN_100  0.27341    0.19046   1.436    0.151
s.sqrtStream      -0.30918    0.19334  -1.599    0.110
s.CMD              0.09753    0.20099   0.485    0.628
s.Night.MinHumid  -0.62903    0.12400  -5.073 3.92e-07 ***
s.Night.MinTemp    0.54929    0.10076   5.452 4.99e-08 ***
Year1              0.05643    0.09423   0.599    0.549
Model1            -0.12633    0.10189  -1.240    0.215
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10  0.003
s.sqrtStrem  0.073  0.214
s.CMD       -0.051 -0.020  0.027
s.Nght.MnHm  0.022  0.075  0.171  0.342
s.Nght.MnTm -0.053 -0.145 -0.043 -0.253 -0.171
Year1        0.043 -0.077 -0.086 -0.088 -0.150  0.146
Model1      -0.063  0.065  0.047 -0.017  0.055  0.010 -0.511
```

Lasiurus blossevillii (Labl)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.9042)  ( log )
Formula: Labl ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData

     AIC      BIC   logLik deviance df.resid
   807.8    851.9   -392.9    785.8      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.8944 -0.4132 -0.2100 -0.0790  8.7227

Random effects:
 Groups Name        Variance Std.Dev.
 Julian (Intercept) 0.1061   0.3257
 Site.x (Intercept) 2.3642   1.5376
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        -1.7169     0.4209  -4.079 4.51e-05 ***
s.Canopy_MEAN_100   0.1479     0.3819   0.387 0.698622
s.sqrtStream        0.3202     0.3752   0.853 0.393401
s.CMD               0.5852     0.3935   1.487 0.137015
s.Night.MinHumid   -0.6658     0.1807  -3.684 0.000230 ***
s.Night.MinTemp     0.6351     0.1304   4.868 1.13e-06 ***
Year1              -0.4589     0.1365  -3.361 0.000777 ***
Model1             -0.3400     0.1422  -2.391 0.016787 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10 -0.033
s.sqrtStrem -0.002  0.239
s.CMD       -0.179 -0.003  0.025
s.Nght.MnHm  0.049  0.086  0.128  0.267
s.Nght.MnTm -0.087 -0.104  0.040 -0.162 -0.219
Year1        0.097 -0.051 -0.122 -0.061 -0.266 -0.002
Model1       0.020  0.049 -0.066 -0.042  0.037 -0.113 -0.419
```

Lasiurus cinereus (Laci)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.5187)  ( log )
Formula: Laci ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
   456.2    500.3   -217.1    434.2      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.6925 -0.2644 -0.1015 -0.0490  5.5759

Random effects:
 Groups Name        Variance  Std.Dev.
 Julian (Intercept) 2.696e-08 0.0001642
 Site.x (Intercept) 6.889e+00 2.6246755
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)       -3.67174    0.91929  -3.994 6.49e-05 ***
s.Canopy_MEAN_100  0.09781    0.69948   0.140 0.888799
s.sqrtStream       0.80954    0.66166   1.223 0.221146
s.CMD              1.08417    0.70482   1.538 0.123996
s.Night.MinHumid   0.26259    0.26271   1.000 0.317525
s.Night.MinTemp    0.68081    0.17583   3.872 0.000108 ***
Year1             -0.57718    0.21520  -2.682 0.007316 **
Model1            -0.23881    0.20389  -1.171 0.241490
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10 -0.148
s.sqrtStrem -0.225  0.361
s.CMD       -0.311  0.071  0.113
s.Nght.MnHm -0.138  0.058  0.191  0.268
s.Nght.MnTm -0.070 -0.092  0.063 -0.099 -0.182
Year1        0.193  0.010 -0.207 -0.085 -0.234 -0.108
Model1      -0.052  0.030 -0.021  0.007  0.049 -0.025 -0.541
```

Lasionycteris noctivagans (Lano)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.8884)  ( log )
Formula: Lano ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData

     AIC      BIC   logLik deviance df.resid
  1725.5   1769.6   -851.7   1703.5      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.9194 -0.5821 -0.3824  0.2500  4.4264

Random effects:
 Groups Name        Variance Std.Dev.
 Julian (Intercept) 0.5443   0.7378
 Site.x (Intercept) 1.9359   1.3914
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        0.42899    0.34226   1.253 0.210059
s.Canopy_MEAN_100 -0.33799    0.32667  -1.035 0.300839
s.sqrtStream       0.88298    0.32071   2.753 0.005901 **
s.CMD              0.31592    0.32589   0.969 0.332353
s.Night.MinHumid   0.17943    0.15474   1.160 0.246244
s.Night.MinTemp    0.37443    0.11268   3.323 0.000891 ***
Year1             -0.23587    0.10624  -2.220 0.026402 *
Model1             0.08781    0.10276   0.855 0.392815
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10  0.028
s.sqrtStrem  0.045  0.320
s.CMD       -0.064 -0.031  0.060
s.Nght.MnHm -0.028  0.077  0.149  0.249
s.Nght.MnTm -0.041 -0.113 -0.026 -0.158 -0.154
Year1        0.047 -0.022 -0.232 -0.105 -0.249  0.129
Model1      -0.039  0.016  0.065  0.051  0.083 -0.045 -0.526
```

Myotis evotis (Myev)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(2.0437)  ( log )
Formula: Myev ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
  1405.4   1449.5   -691.7   1383.4      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2380 -0.6262 -0.3830  0.3848  7.7496

Random effects:
 Groups Name        Variance  Std.Dev.
 Julian (Intercept) 2.325e-08 0.0001525
 Site.x (Intercept) 1.755e+00 1.3247494
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        0.05519    0.30872   0.179   0.8581
s.Canopy_MEAN_100  0.72180    0.33386   2.162   0.0306 *
s.sqrtStream      -0.04181    0.27886  -0.150   0.8808
s.CMD              0.27746    0.30193   0.919   0.3581
s.Night.MinHumid   0.05300    0.09021   0.588   0.5569
s.Night.MinTemp    0.11914    0.06657   1.790   0.0735 .
Year1             -0.03222    0.07859  -0.410   0.6818
Model1            -0.09077    0.08912  -1.018   0.3085
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10 -0.029
s.sqrtStrem  0.066  0.344
s.CMD       -0.078  0.003  0.018
s.Nght.MnHm -0.017  0.151  0.104  0.166
s.Nght.MnTm  0.006 -0.157  0.025 -0.111 -0.114
Year1        0.036 -0.120 -0.115 -0.004 -0.117 -0.024
Model1      -0.048  0.173 -0.029  0.001  0.018  0.010 -0.639
```

Myotis thysanodes (Myth)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(1.6181)  ( log )
Formula: Myth ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
  1301.4   1345.5   -639.7   1279.4      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2187 -0.5652 -0.2964  0.2355  7.3864

Random effects:
 Groups Name        Variance  Std.Dev.
 Julian (Intercept) 5.640e-08 0.0002375
 Site.x (Intercept) 2.013e+00 1.4186595
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)       -0.39474    0.34394  -1.148  0.25109
s.Canopy_MEAN_100  0.89767    0.32569   2.756  0.00585 **
s.sqrtStream       0.47499    0.33133   1.434  0.15169
s.CMD              0.96084    0.32893   2.921  0.00349 **
s.Night.MinHumid  -0.12720    0.09411  -1.352  0.17652
s.Night.MinTemp    0.12713    0.07891   1.611  0.10715
Year1             -0.12107    0.08596  -1.408  0.15900
Model1             0.18344    0.09890   1.855  0.06363 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10 -0.065
s.sqrtStrem -0.008  0.469
s.CMD       -0.123 -0.014  0.054
s.Nght.MnHm -0.008  0.201  0.175  0.140
s.Nght.MnTm -0.006 -0.120 -0.038 -0.105 -0.132
Year1        0.060 -0.226 -0.211  0.018 -0.049 -0.076
Model1      -0.078  0.186 -0.025 -0.043 -0.096  0.147 -0.607
```

Myotis volans (Myvo)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(1.2578)  ( log )
Formula: Myvo ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
  1755.1   1799.2   -866.6   1733.1      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.1165 -0.5955 -0.3138  0.3822  6.0908

Random effects:
 Groups Name        Variance  Std.Dev.
 Julian (Intercept) 1.003e-08 0.0001002
 Site.x (Intercept) 2.748e+00 1.6575737
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        0.58864    0.38172   1.542  0.12306
s.Canopy_MEAN_100  0.43331    0.38277   1.132  0.25762
s.sqrtStream       1.11351    0.35217   3.162  0.00157 **
s.CMD              0.20181    0.37222   0.542  0.58769
s.Night.MinHumid  -0.10747    0.11407  -0.942  0.34609
s.Night.MinTemp    0.24976    0.08058   3.100  0.00194 **
Year1              0.15645    0.08911   1.756  0.07915 .
Model1            -0.74372    0.10267  -7.244 4.36e-13 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10  0.011
s.sqrtStrem  0.037  0.455
s.CMD       -0.062 -0.055  0.007
s.Nght.MnHm -0.008  0.207  0.144  0.152
s.Nght.MnTm -0.002 -0.134  0.044 -0.103 -0.143
Year1        0.014 -0.153 -0.186 -0.039 -0.197 -0.016
Model1       0.000  0.077 -0.031 -0.003  0.022  0.126 -0.607
```

Myotis yumanensis (Myyu)

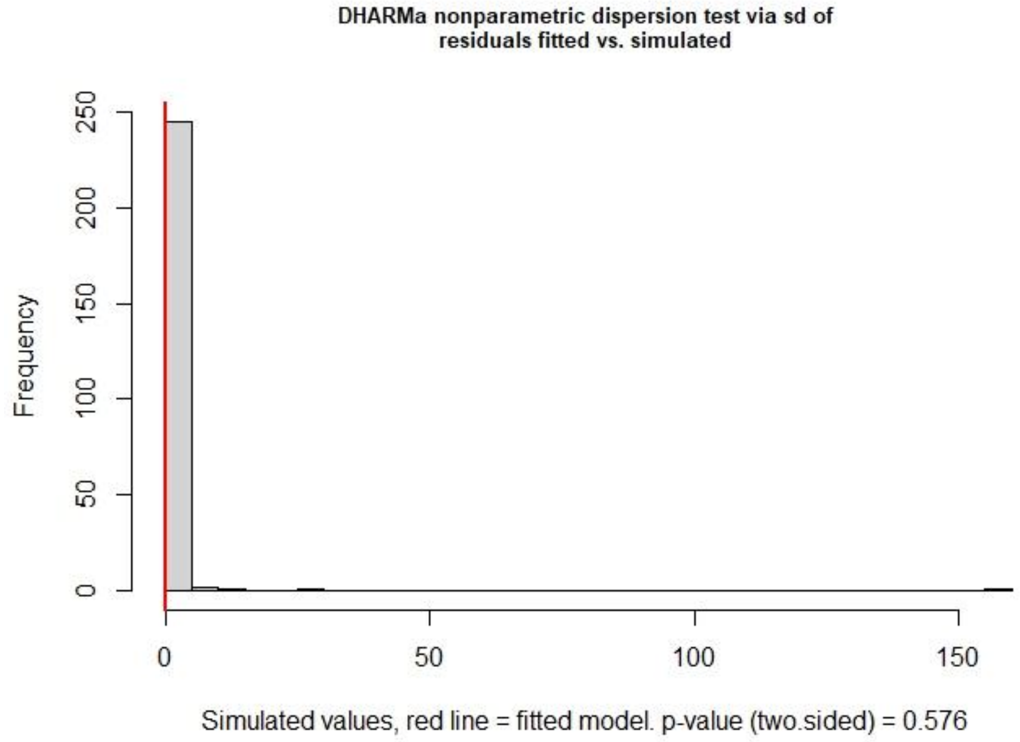
```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(1.1051)  ( log )
Formula: Myyu ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData

     AIC      BIC   logLik deviance df.resid
  4198.9   4242.9  -2088.4   4176.9      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.0378 -0.7222 -0.2090  0.3978  4.8511

Random effects:
 Groups Name        Variance Std.Dev.
 Julian (Intercept) 0.1707   0.4131
 Site.x (Intercept) 2.7359   1.6541
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)        4.07638    0.37969  10.736   <2e-16 ***
s.Canopy_MEAN_100  0.57129    0.46099   1.239   0.2152
s.sqrtStream       0.21762    0.33204   0.655   0.5122
s.CMD             -0.45259    0.36804  -1.230   0.2188
s.Night.MinHumid  -0.17027    0.10578  -1.610   0.1075
s.Night.MinTemp    0.03960    0.07511   0.527   0.5981
Year1              0.15368    0.08152   1.885   0.0594 .
Model1             0.01423    0.09044   0.157   0.8750
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10  0.014
s.sqrtStrem  0.077  0.270
s.CMD       -0.051 -0.110  0.014
s.Nght.MnHm -0.010  0.051  0.080  0.153
s.Nght.MnTm -0.003 -0.073 -0.013 -0.085 -0.145
Year1        0.020 -0.260 -0.146  0.010 -0.179  0.080
Model1      -0.027  0.251 -0.007 -0.034  0.022 -0.016 -0.631
```

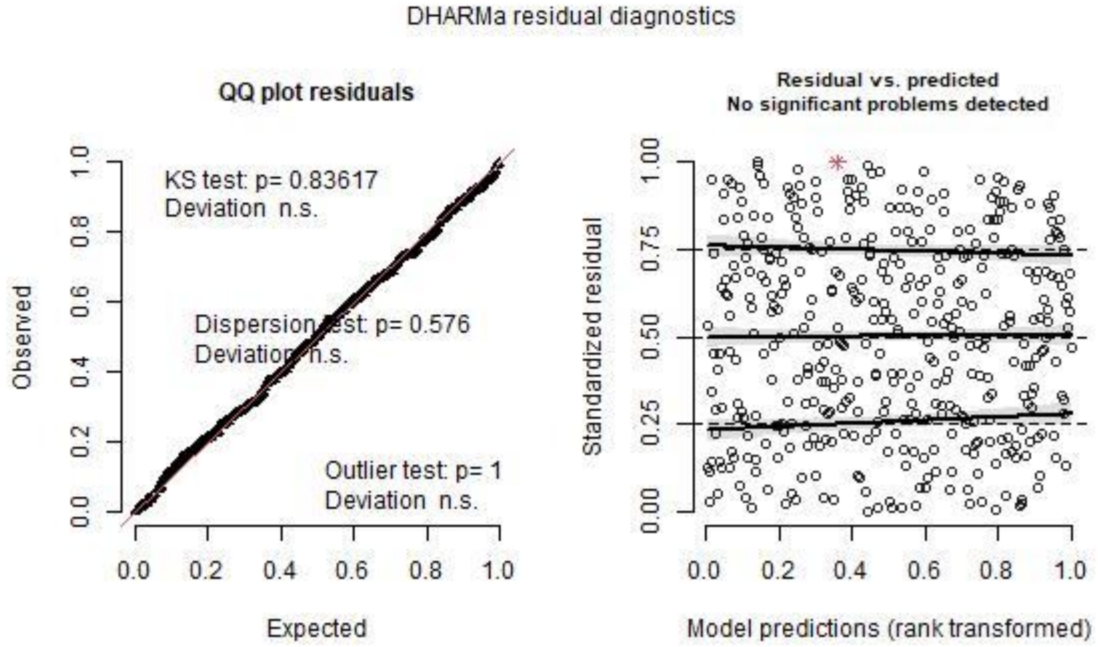
Tadarida brasiliensis (Tabr)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
['glmerMod']
 Family: Negative Binomial(0.7069)  ( log )
Formula: Tabr ~ s.Canopy_MEAN_100 + s.sqrtStream + s.CMD + s.Night.MinHumid +
    s.Night.MinTemp + Year + Model + (1 | Site.x) + (1 | Julian)
   Data: ModelData
Control: ctrl

     AIC      BIC   logLik deviance df.resid
   789.8    833.9   -383.9    767.8      396

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.7696 -0.4719 -0.2801 -0.1436  7.7239

Random effects:
 Groups Name        Variance Std.Dev.
 Julian (Intercept) 0.0438   0.2093
 Site.x (Intercept) 1.2271   1.1077
Number of obs: 407, groups:  Julian, 62; Site.x, 20

Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)       -1.37575    0.30640  -4.490 7.12e-06 ***
s.Canopy_MEAN_100 -0.21882    0.29079  -0.752  0.45176
s.sqrtStream       1.12394    0.28619   3.927 8.59e-05 ***
s.CMD              0.62885    0.30326   2.074  0.03811 *
s.Night.MinHumid   0.03649    0.16857   0.216  0.82862
s.Night.MinTemp    0.34691    0.12919   2.685  0.00725 **
Year1             -0.43687    0.13396  -3.261  0.00111 **
Model1             0.11963    0.14099   0.848  0.39618
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s.C_ME s.sqrS s.CMD  s.N.MH s.N.MT Year1
s.C_MEAN_10  0.074
s.sqrtStrem -0.126  0.179
s.CMD       -0.192 -0.088  0.155
s.Nght.MnHm -0.035  0.027  0.200  0.340
s.Nght.MnTm -0.088 -0.103  0.030 -0.157 -0.116
Year1        0.154  0.026 -0.236 -0.102 -0.212 -0.094
Model1      -0.039  0.022 -0.020  0.012  0.077 -0.018 -0.482
```

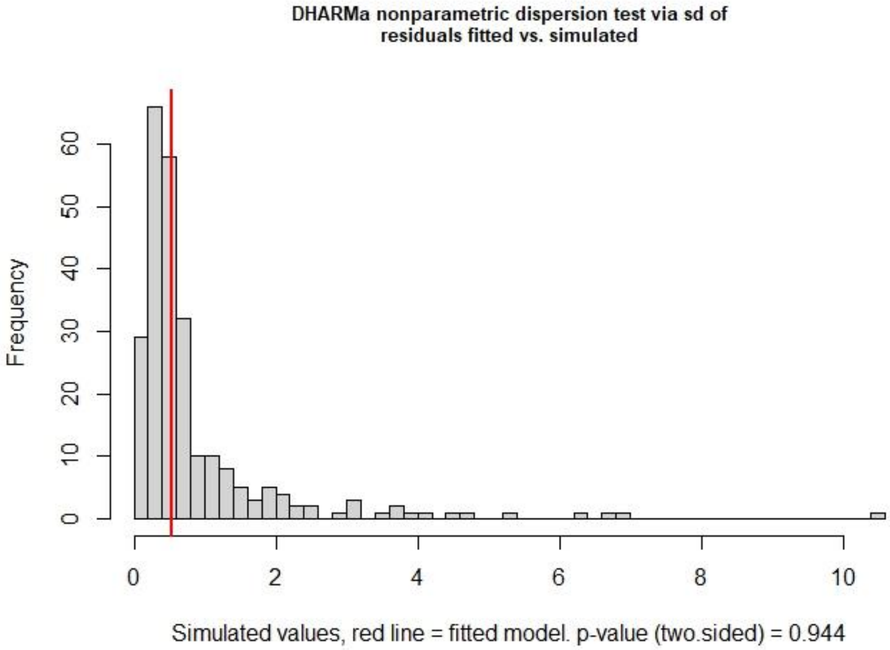
Appendix S7: Residual diagnostics for GLMM species activity model results.

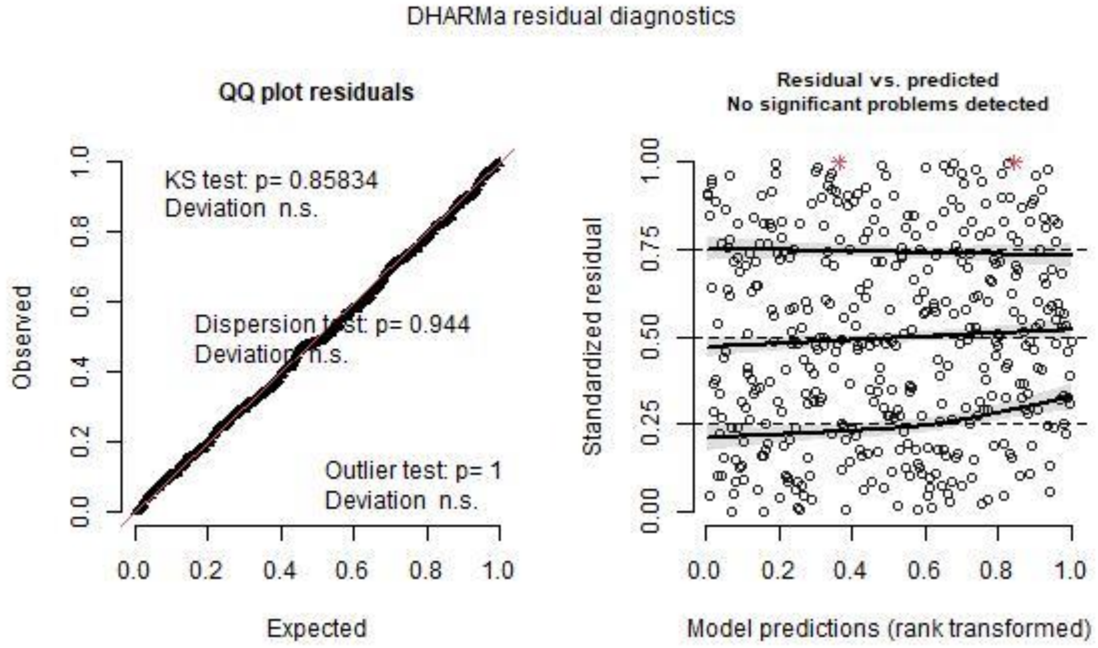
Antrozous pallidus (Anpa)



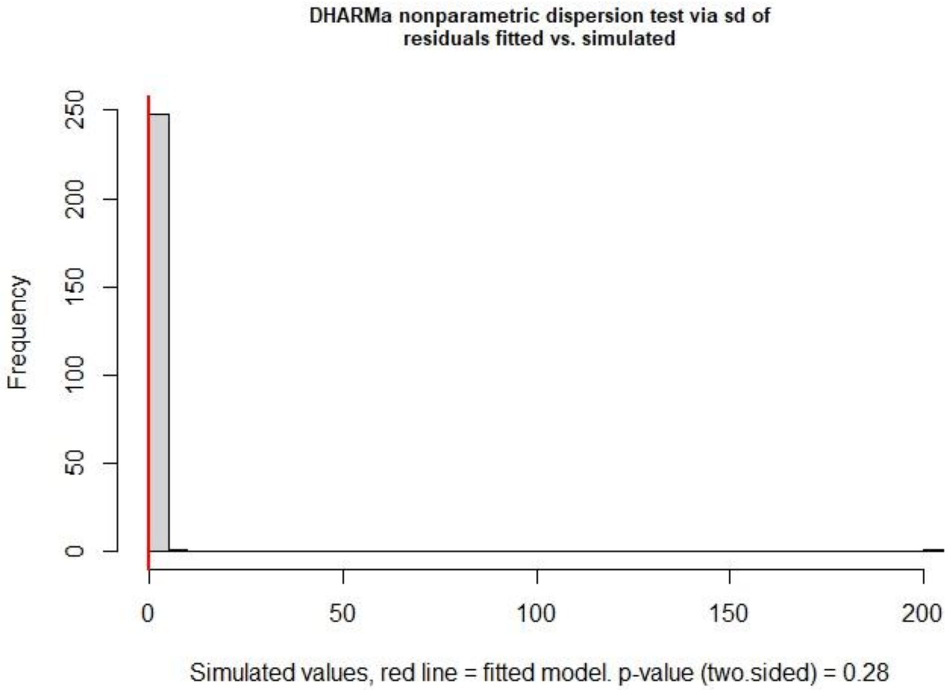


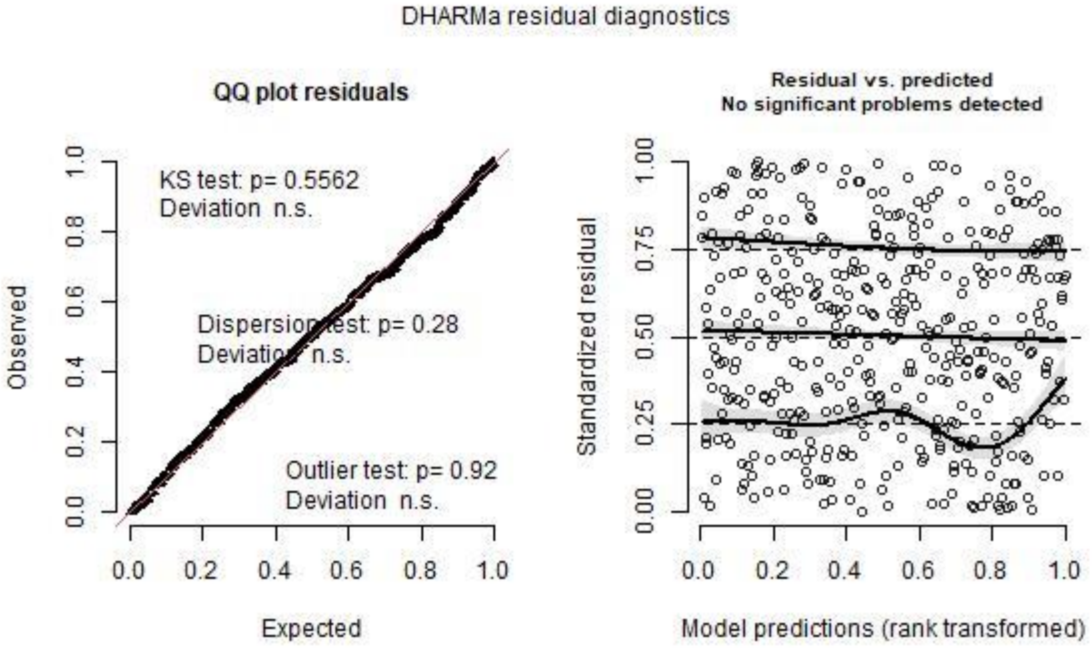
Eptesicus fuscus (Epfu)



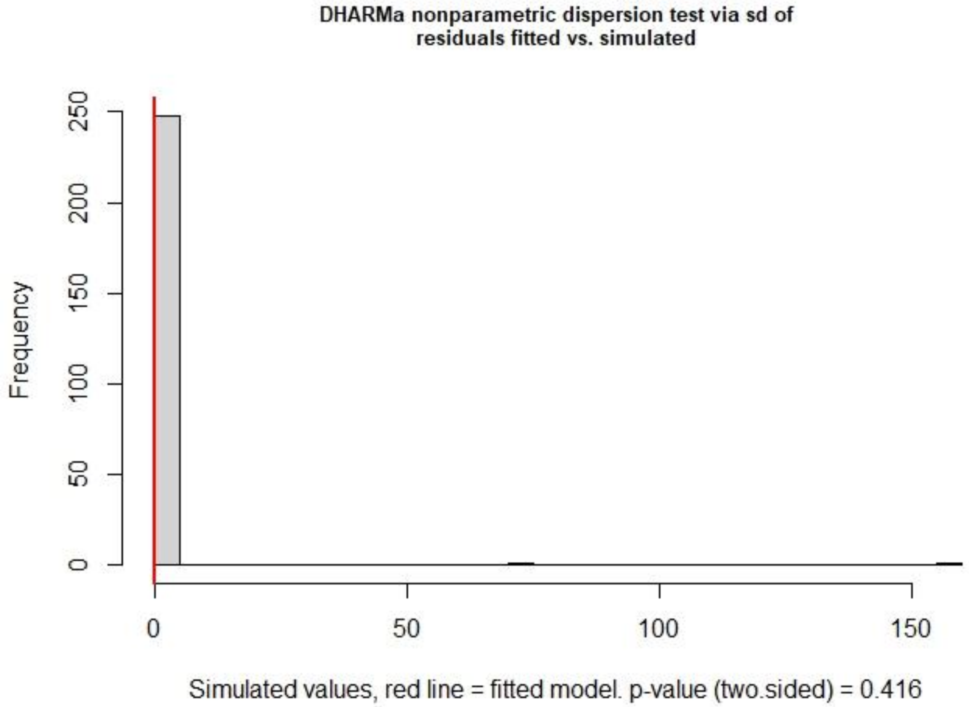


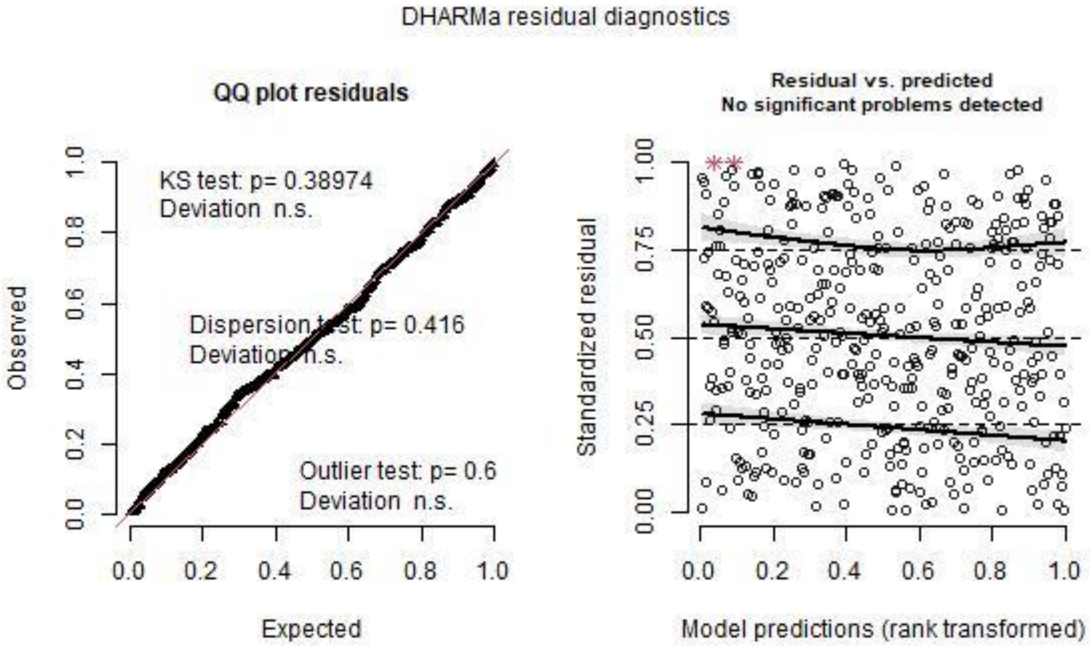
Lasiurus blossevillii (Labl)



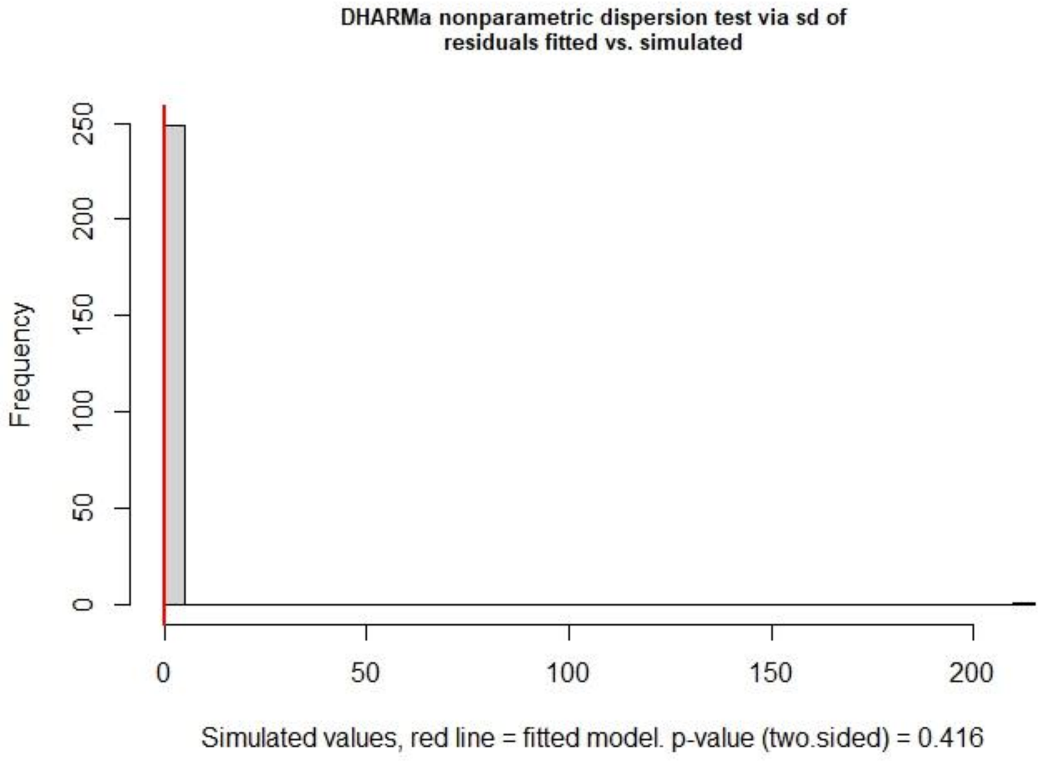


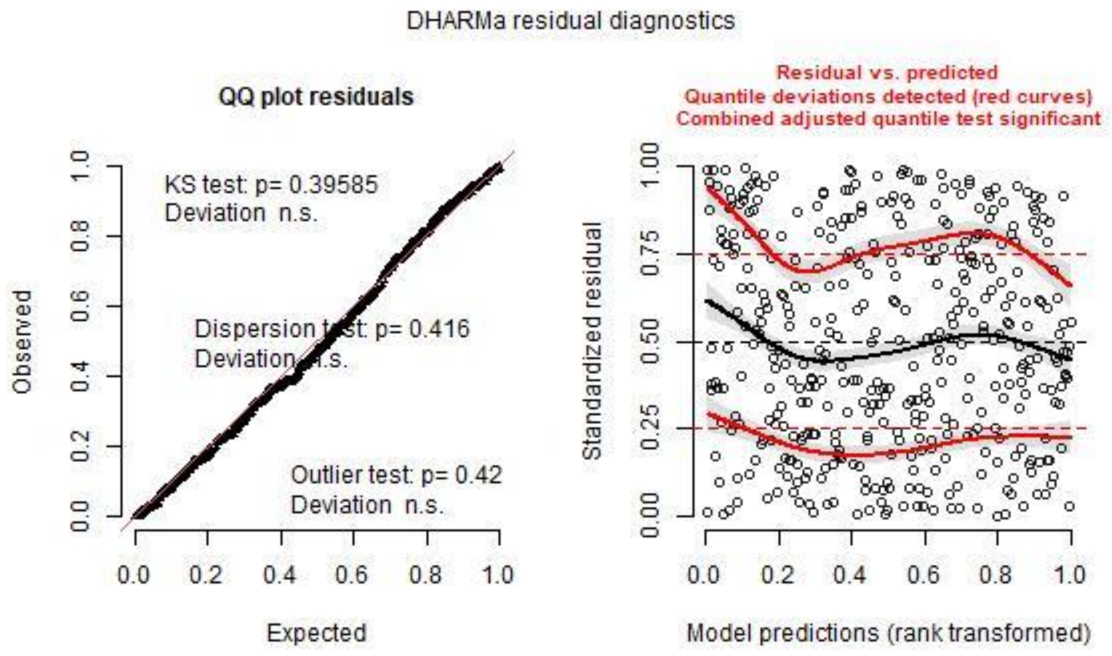
Lasiurus cinereus (Laci)



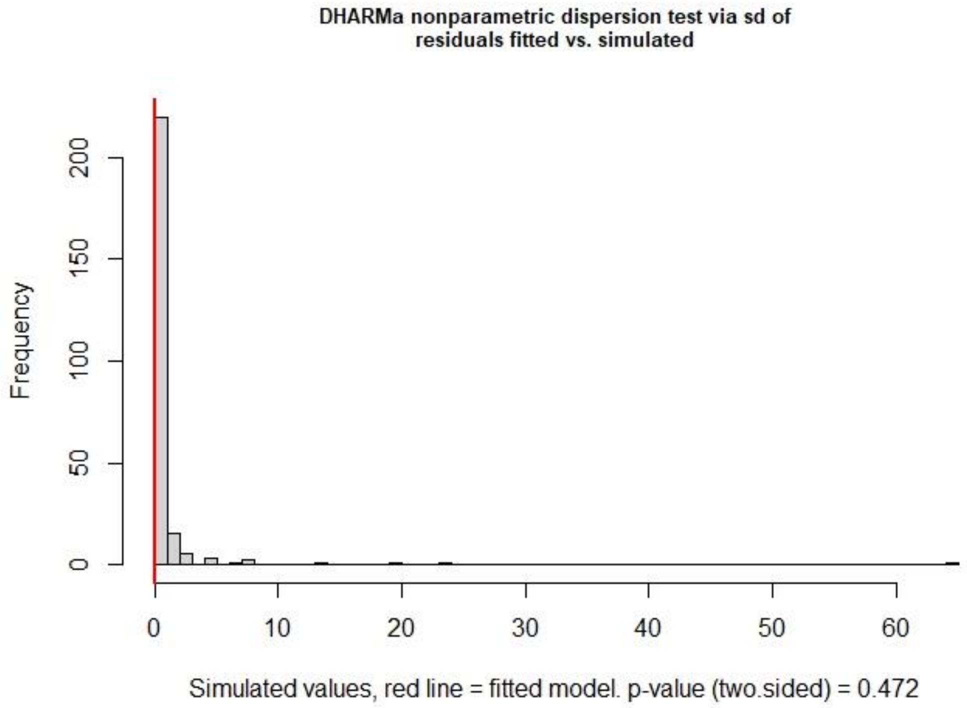


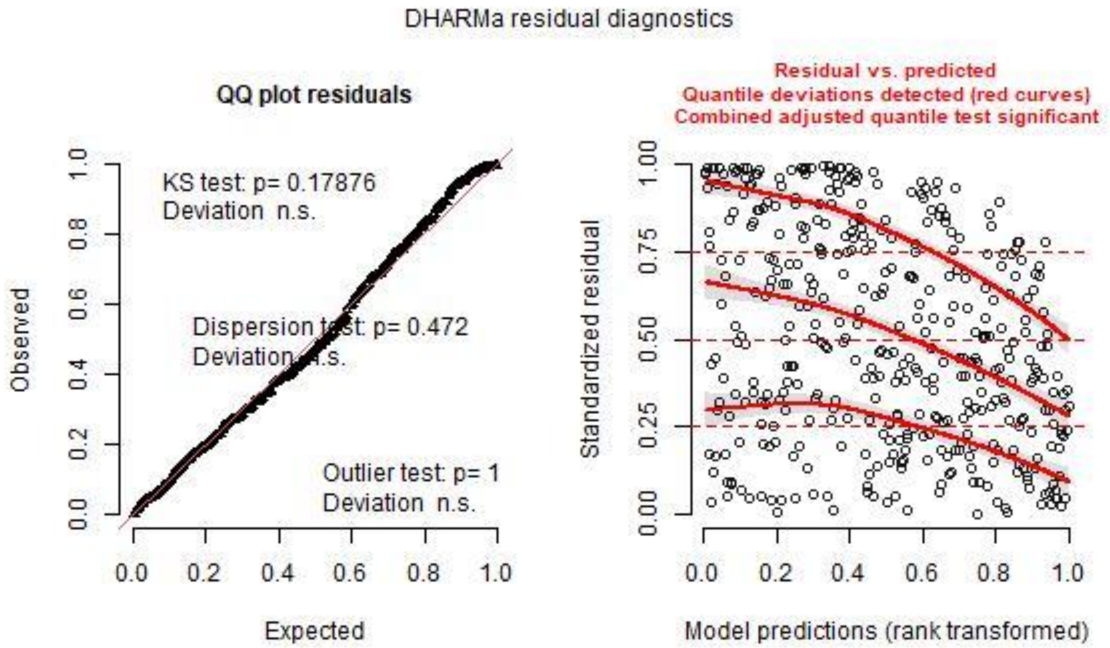
Lasioncyteris noctivagans (Lano)



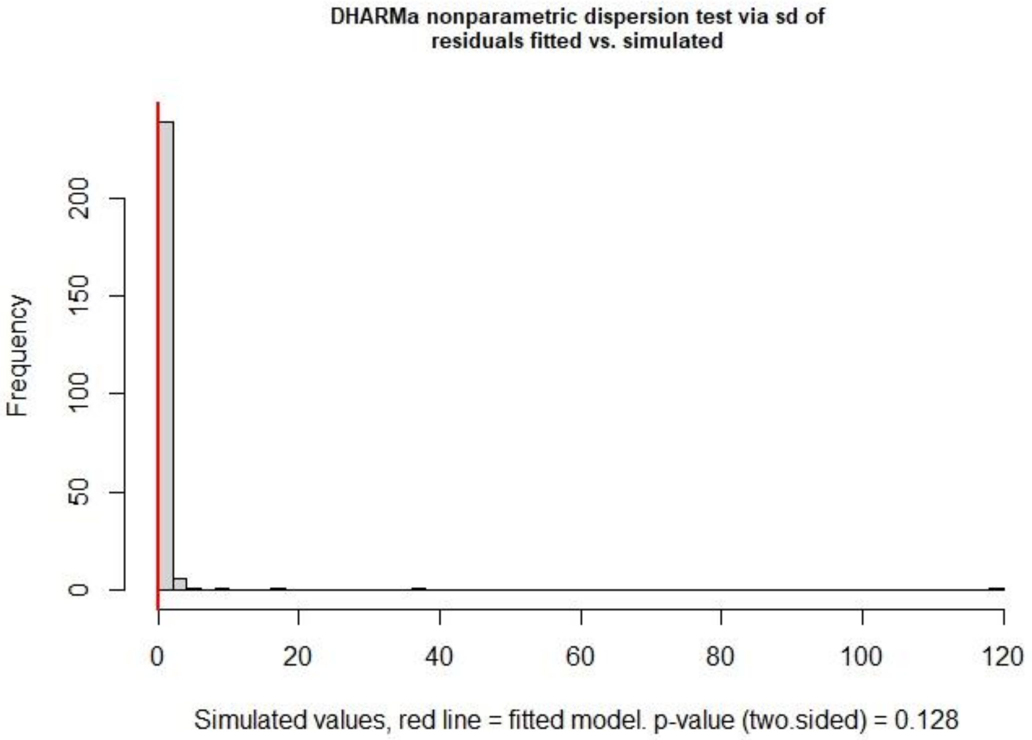


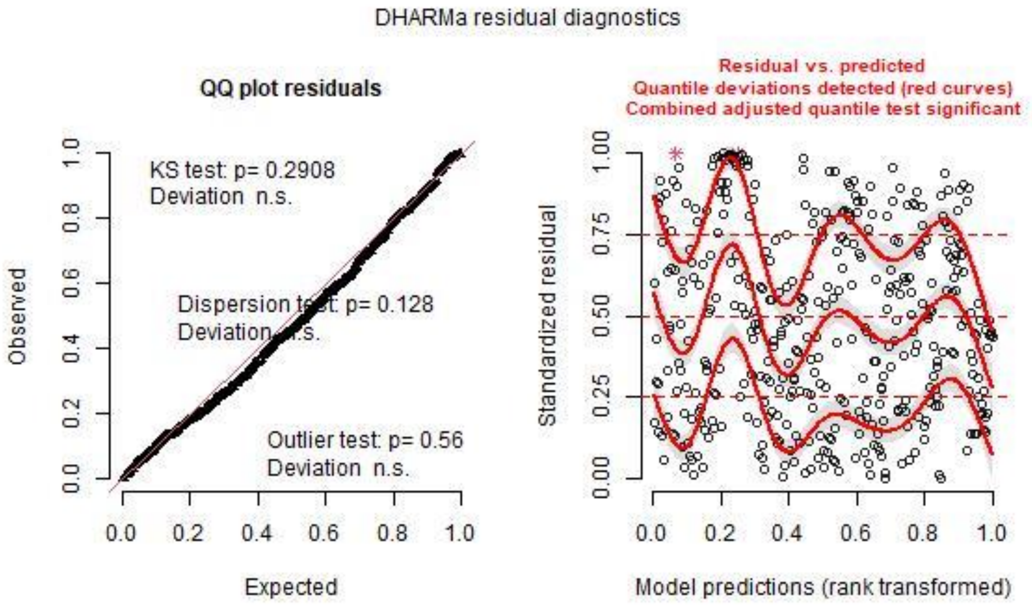
Myotis evotis (Myev)



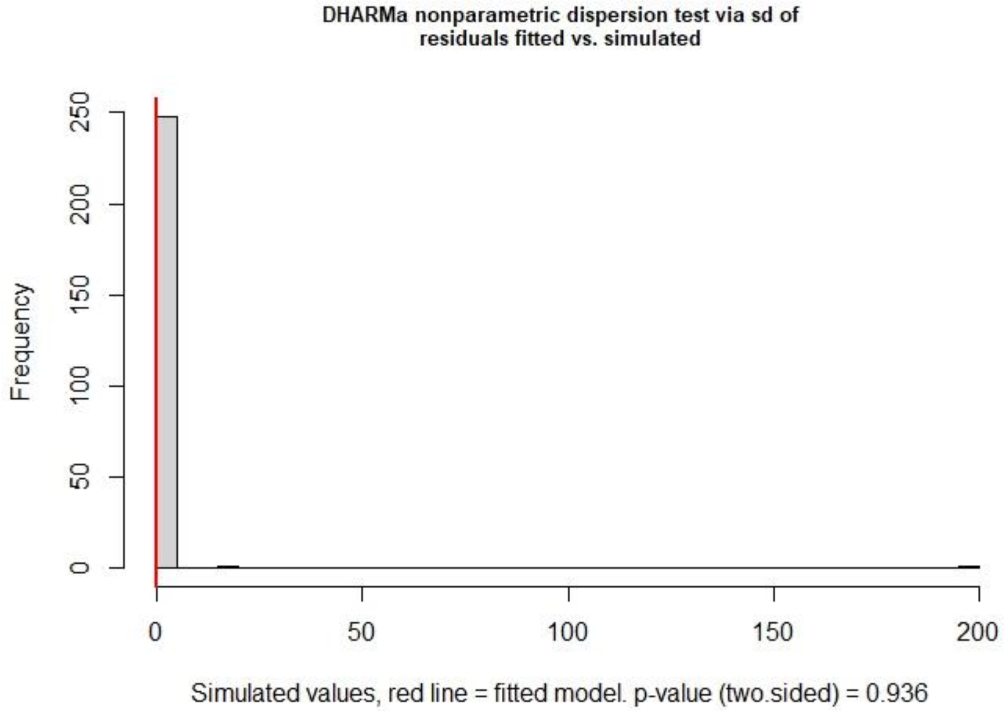


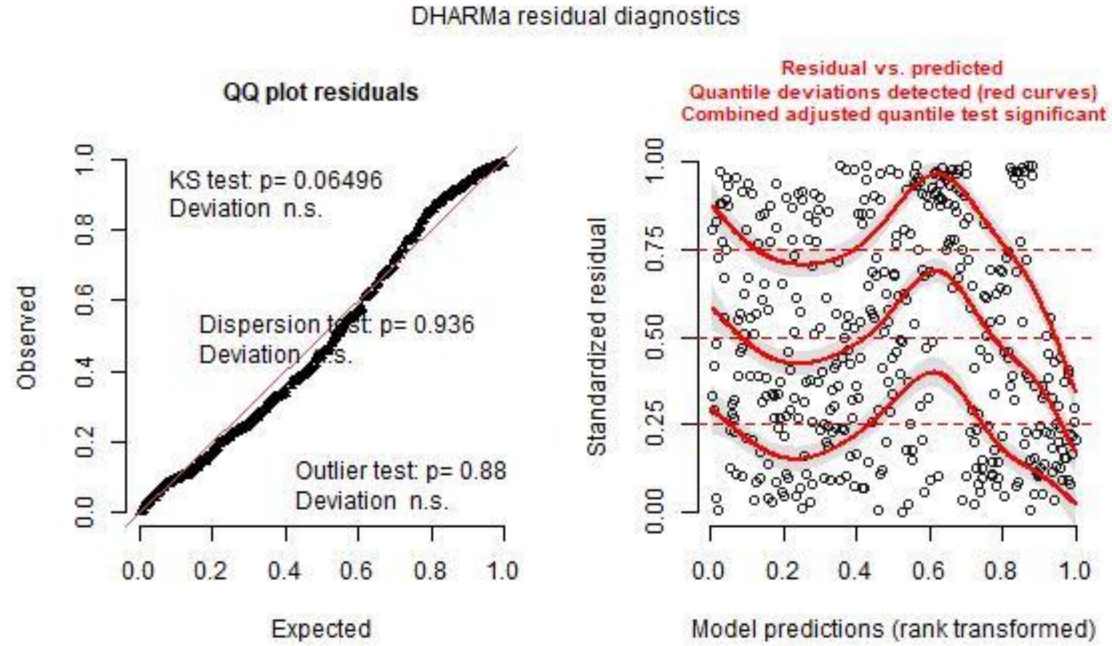
Myotis thysanodes (Myth)



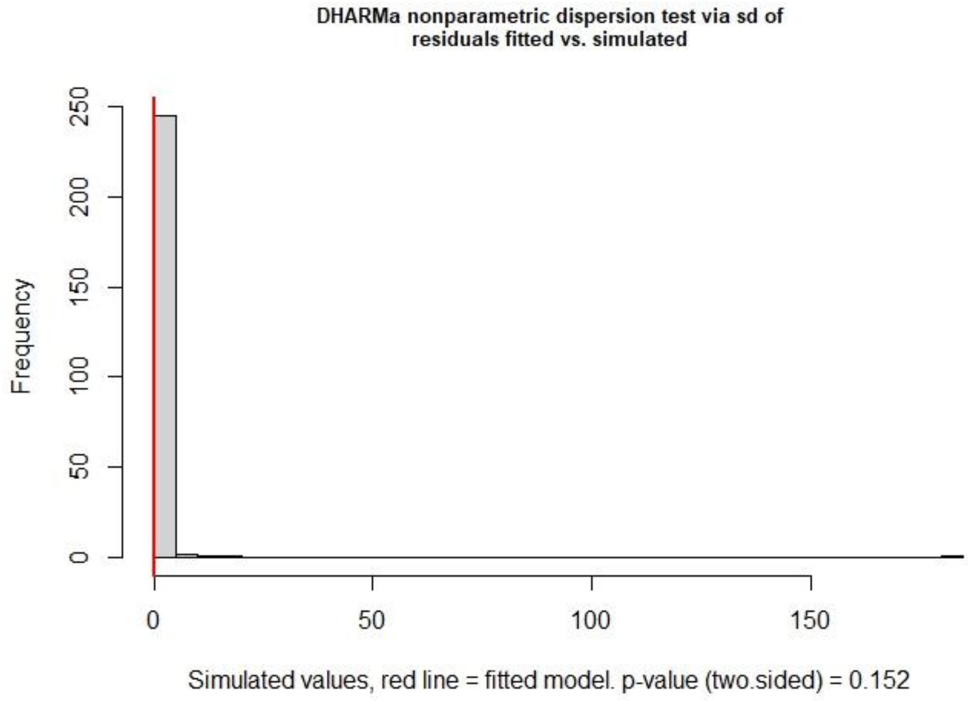


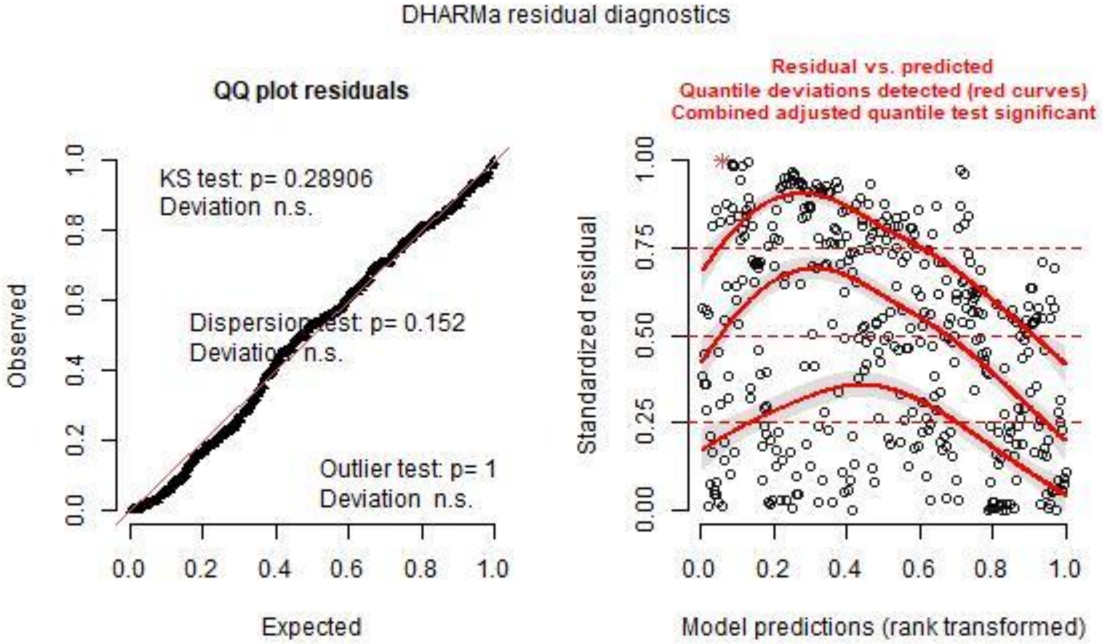
Myotis volans (Myvo)



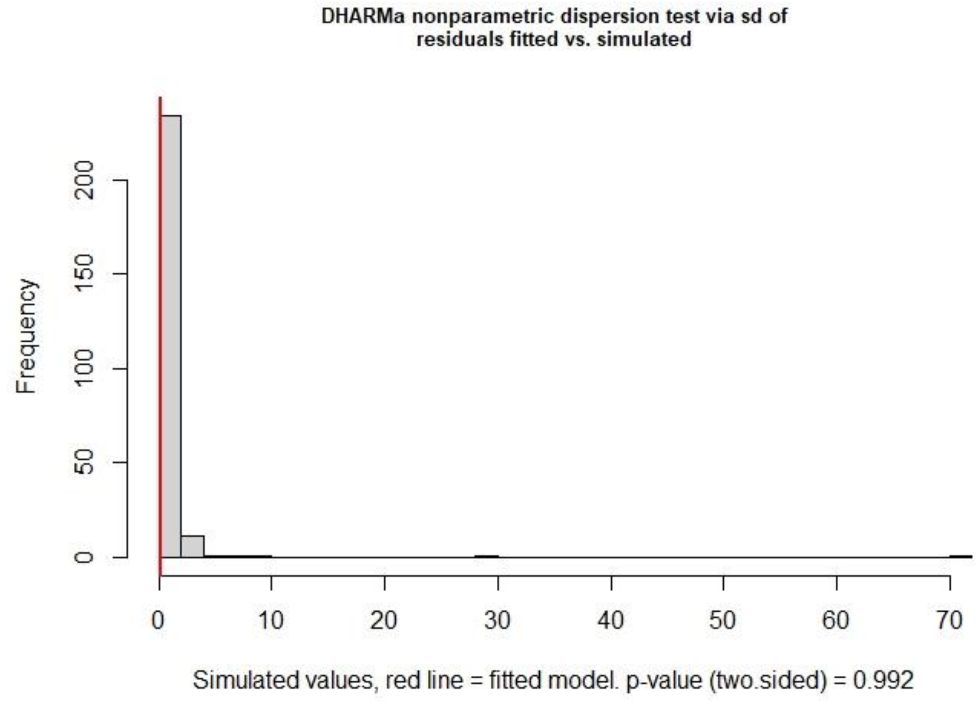


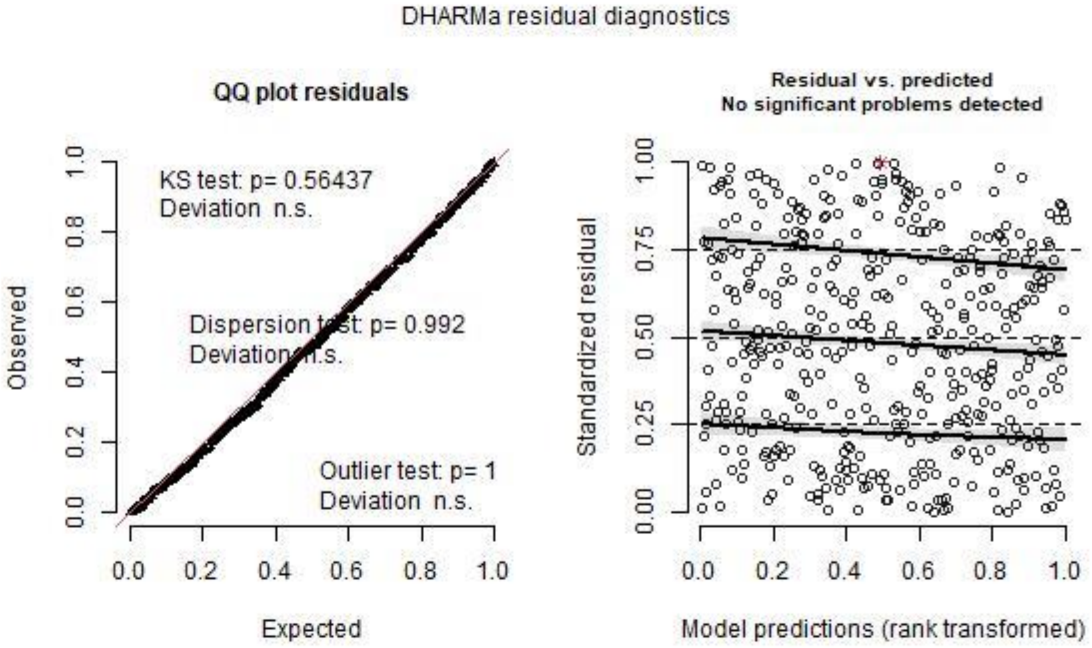
Myotis yumanensis (Myyu)





Tadarida brasiliensis (Tabr)





Chapter 2 Supporting Information

for

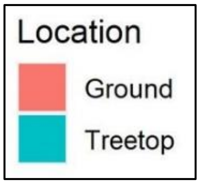
Forest canopy acoustic surveys reveal year-round bat activity

Contents

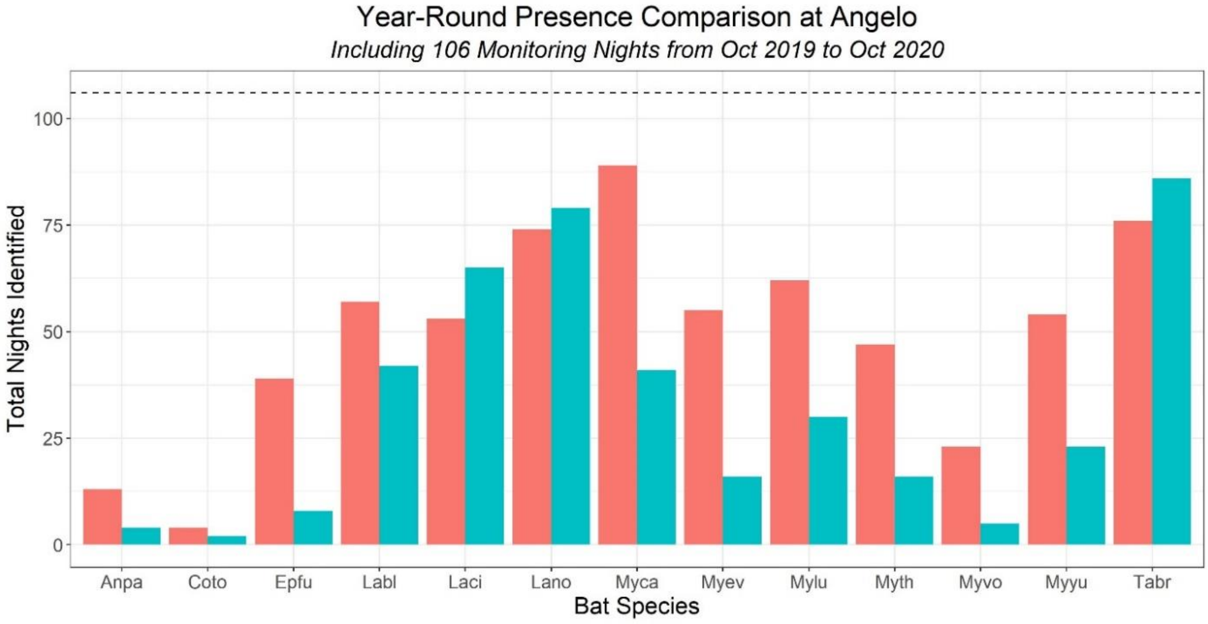
Appendices S1-S7

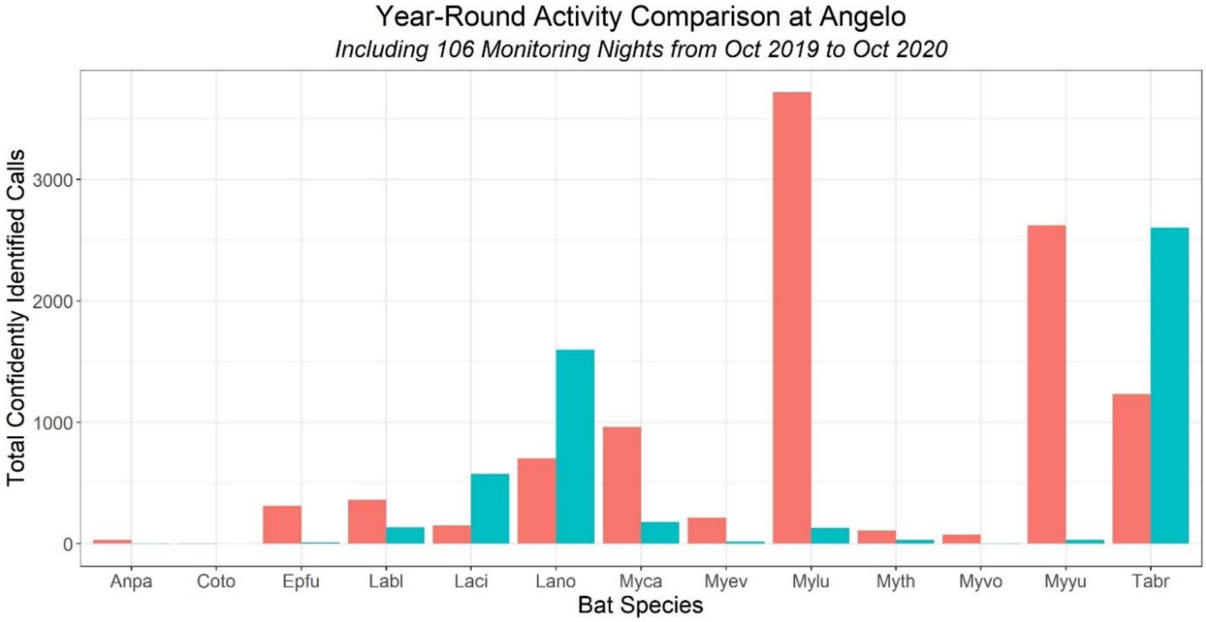
Appendix S1: Plots of species presence and activity data by site.

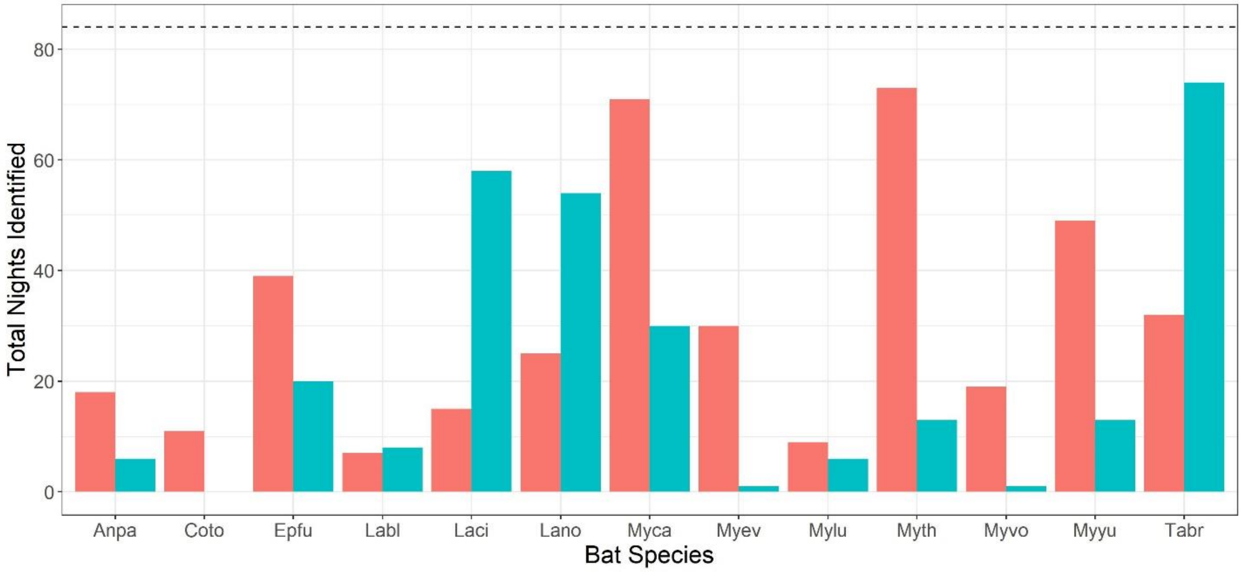
Acoustic data from all detector locations was first auto-classified using SonoBat call classification software then manually vetted to species. The resulting ‘confidently identified call’ data was used to calculate species presence and activity. Species presence is calculated as the total number of nights that at least one call was identified. Activity is the total number of identified calls.



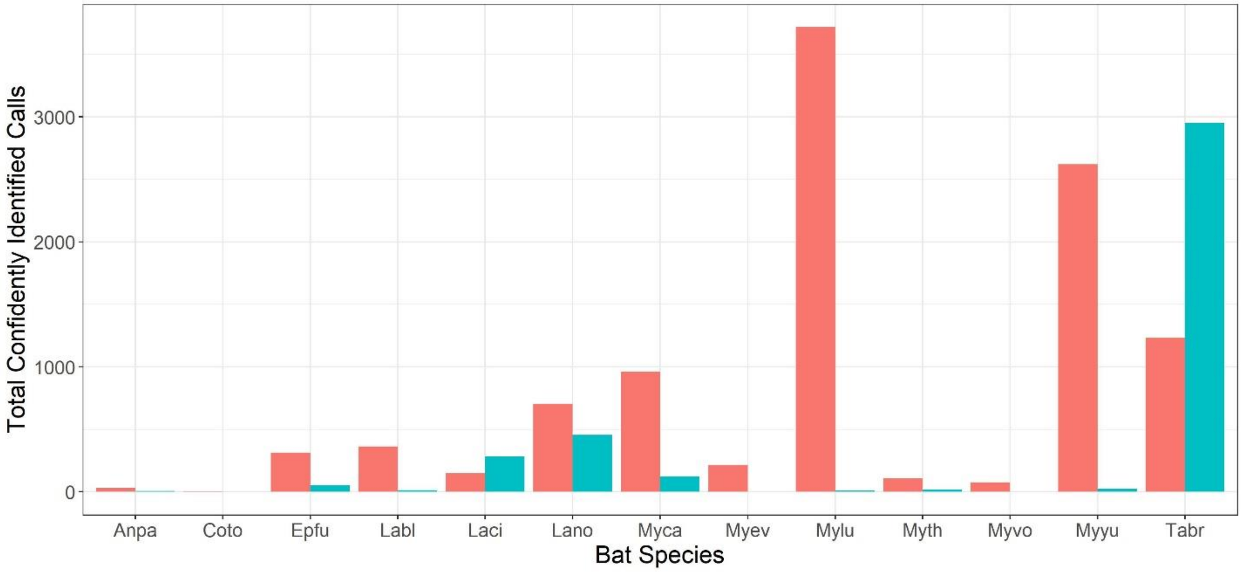
In all of the following plots, red bars represent ‘ground’ detector locations and blue bars represent ‘treetop’ detector locations.



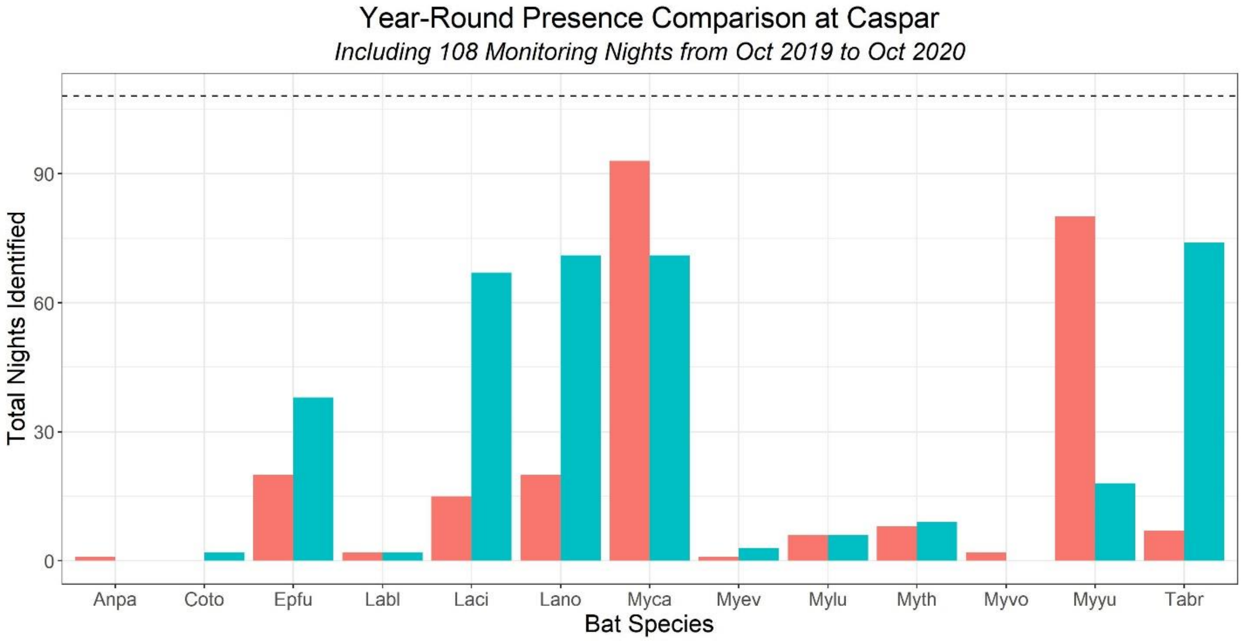



Year-Round Presence Comparison at Armstrong

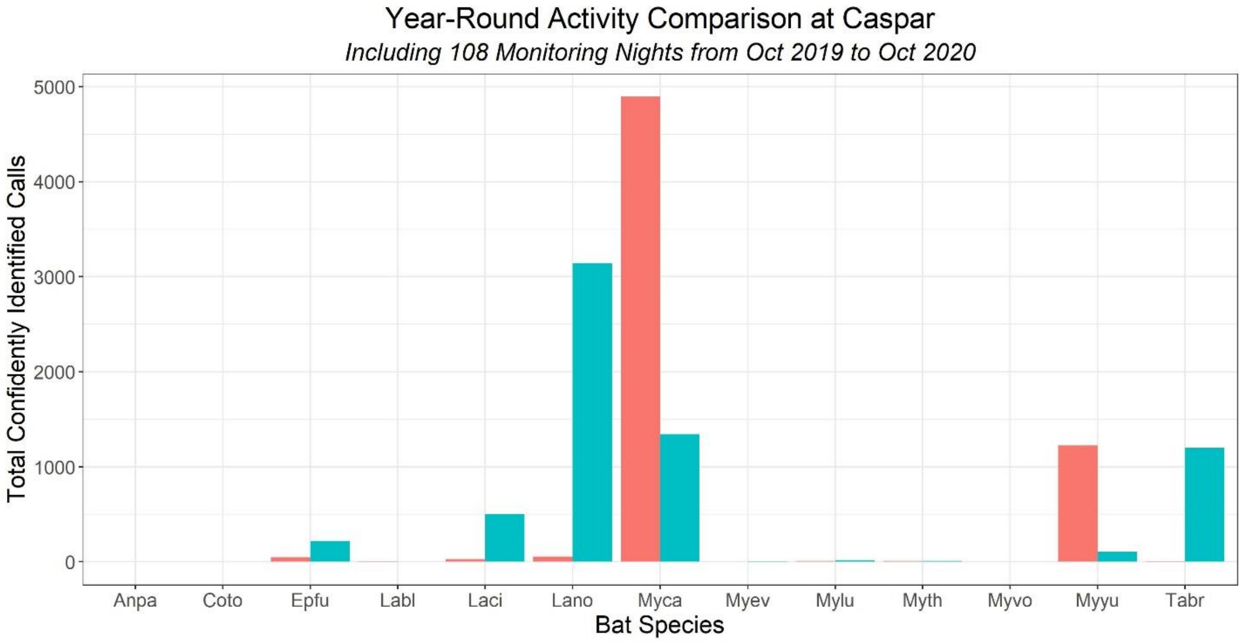
Including 84 Monitoring Nights from Oct 2019 to Aug 2020


Year-Round Activity Comparison at Armstrong

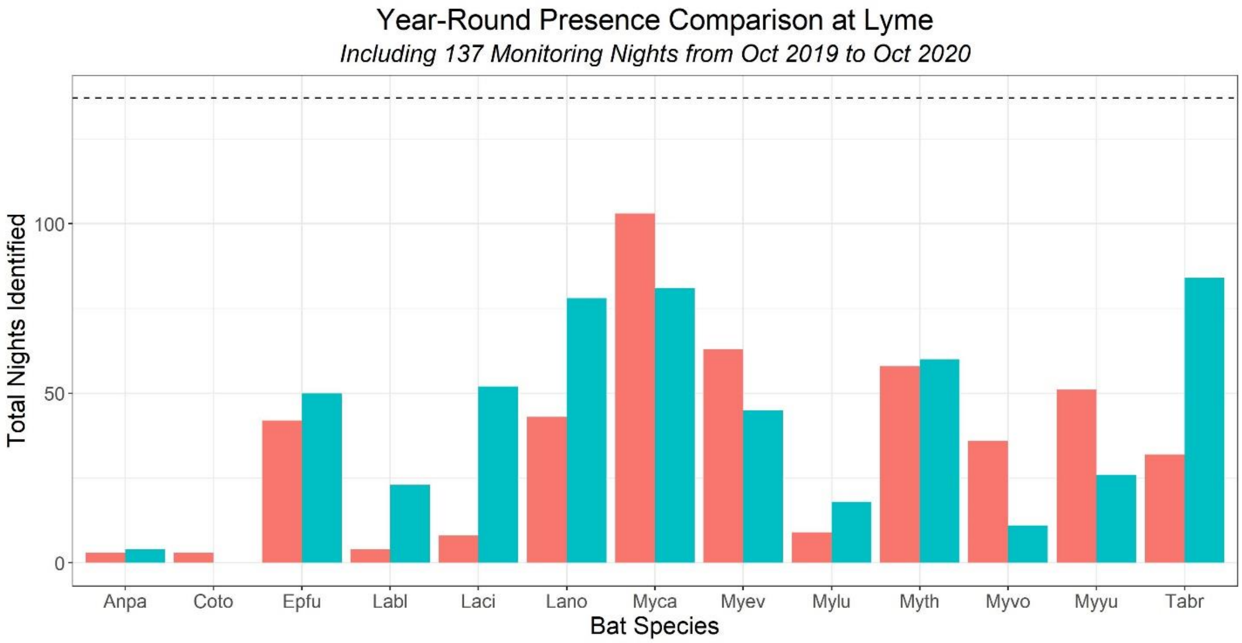
Including 84 Monitoring Nights from Oct 2019 to Aug 2020

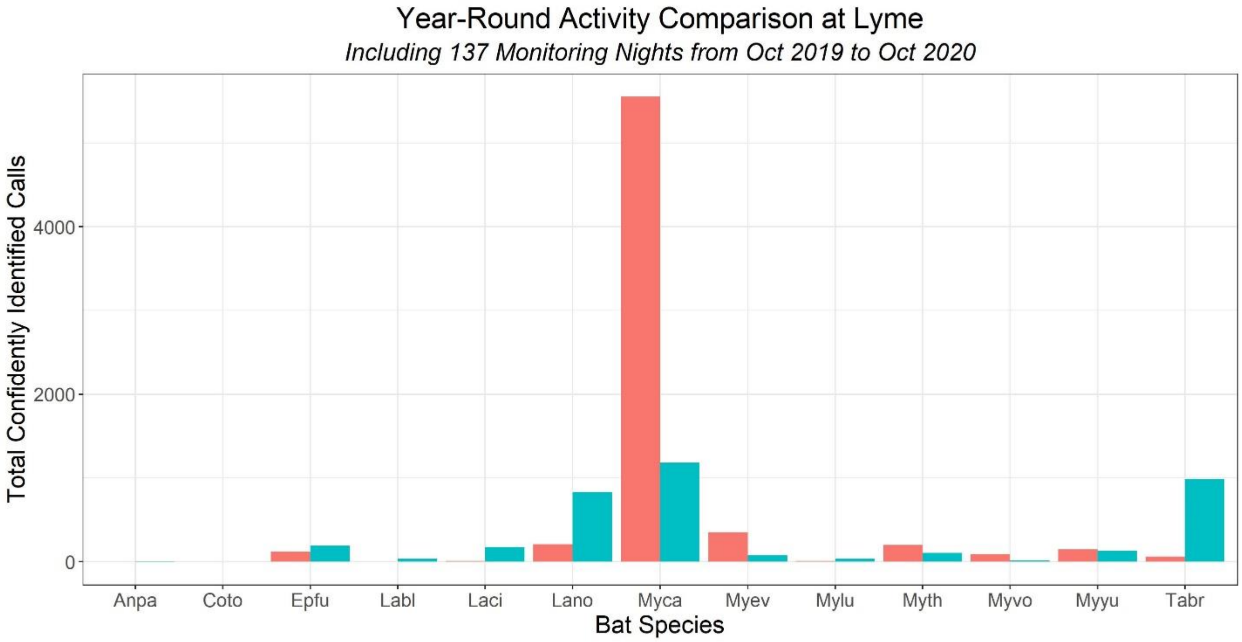

Year-Round Presence Comparison at Caspar

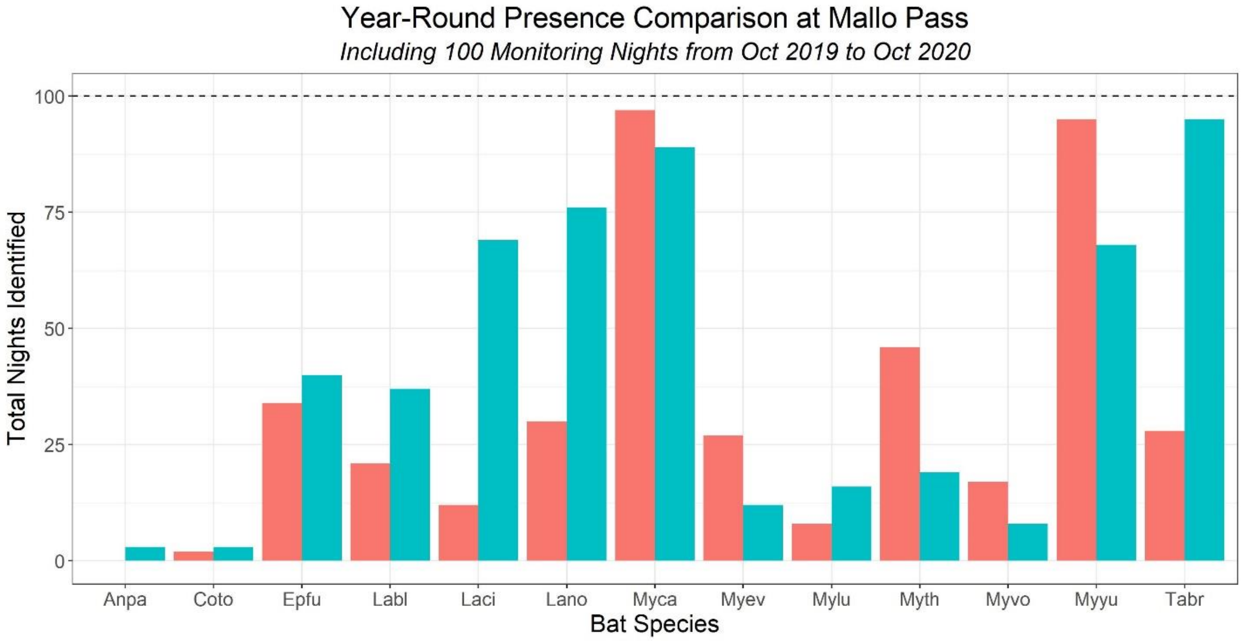
Including 108 Monitoring Nights from Oct 2019 to Oct 2020

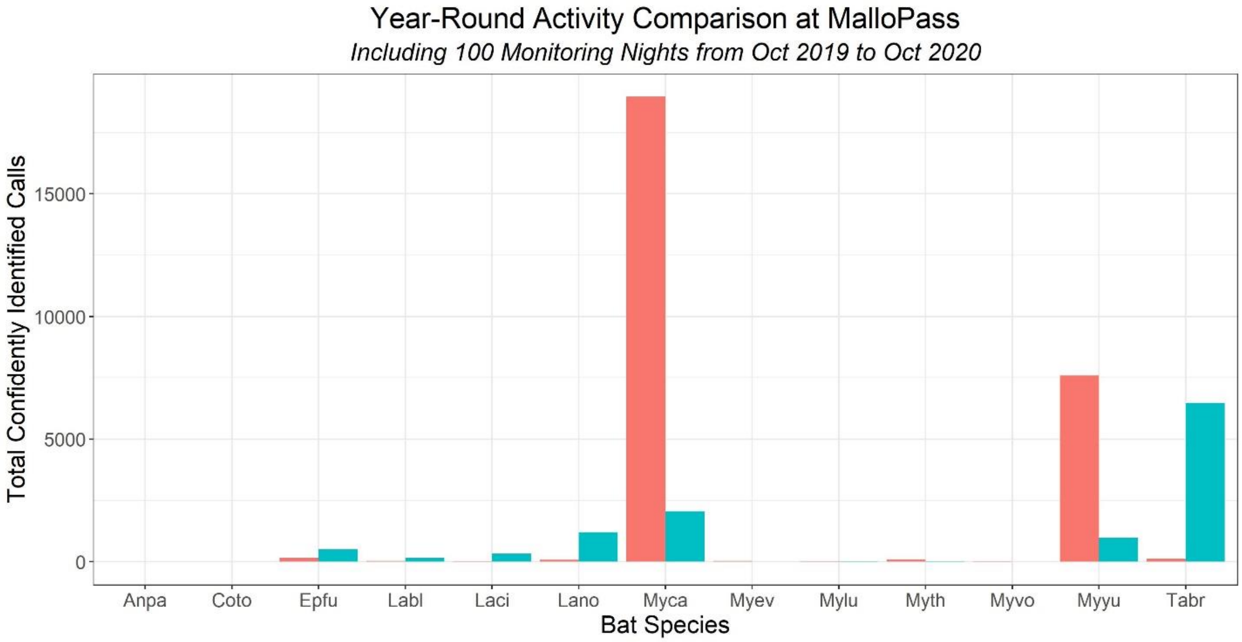

Year-Round Activity Comparison at Caspar

Including 108 Monitoring Nights from Oct 2019 to Oct 2020


Year-Round Presence Comparison at Lyme
Including 137 Monitoring Nights from Oct 2019 to Oct 2020
Total Nights Identified
0
50
100
Anpa
Coto
Epfu
Labl
Laci
Lano
Myca
Myev
Mylu
Myth
Myvo
Myyu
Tabr
Bat Species


Year-Round Activity Comparison at Lyme
Including 137 Monitoring Nights from Oct 2019 to Oct 2020
Total Confidently Identified Calls
0
2000
4000
Anpa
Coto
Epfu
Labl
Laci
Lano
Myca
Myev
Mylu
Myth
Myvo
Myyu
Tabr
Bat Species

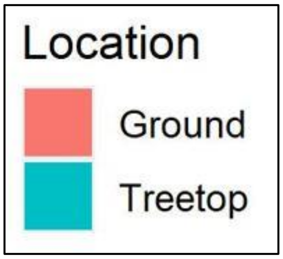

Year-Round Presence Comparison at Mallo Pass
Including 100 Monitoring Nights from Oct 2019 to Oct 2020
Total Nights Identified
100
75
50
25
0
Anpa
Coto
Epfu
Labl
Laci
Lano
Myca
Myev
Mylu
Myth
Myvo
Myyu
Tabr
Bat Species


Year-Round Activity Comparison at MalloPass
Including 100 Monitoring Nights from Oct 2019 to Oct 2020
Total Confidently Identified Calls
15000
10000
5000
0
Anpa
Coto
Epfu
Labl
Laci
Lano
Myca
Myev
Mylu
Myth
Myvo
Myyu
Tabr
Bat Species

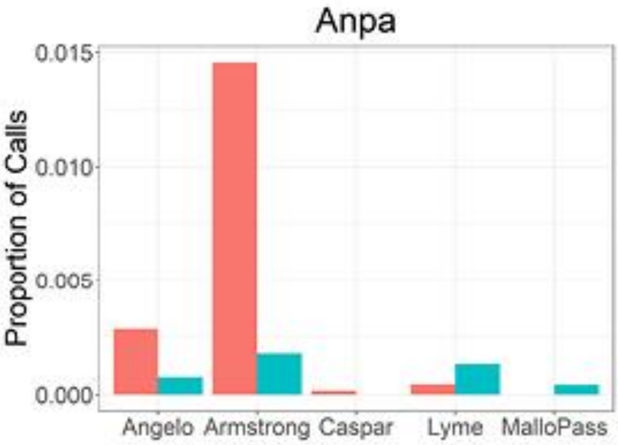
Appendix S2: Species calls as proportion of total calls at detector location

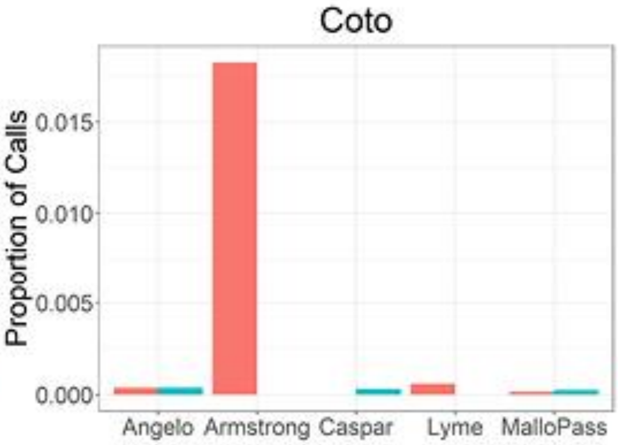
I calculated the total number of calls at each of the ten detector locations, then I computed the proportion of each species calls relative to all calls identified at that detector location. The result is presented in the following table and plots.

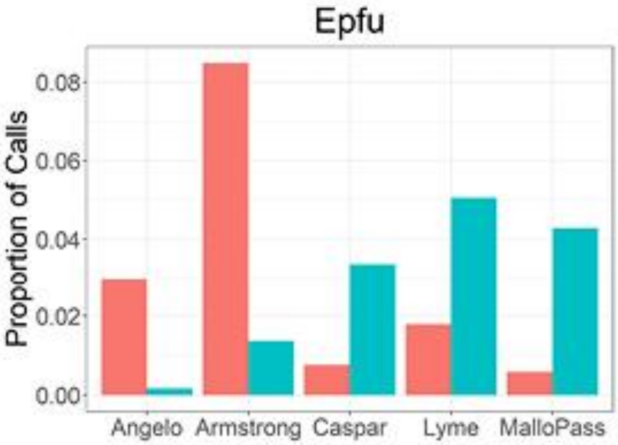
	Angelo		Armstrong		Caspar		Lyme		Mallo Pass	
Species	**G**	**T**	**G**	**T**	**G**	**T**	**G**	**T**	**G**	**T**
Anpa	0.3%	0.1%	1.5%	0.2%	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%
Coto	0.0%	0.0%	1.8%	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%	0.0%
Epfu	3.0%	0.2%	8.5%	1.4%	0.8%	3.4%	1.8%	5.1%	0.6%	4.3%
Labl	3.5%	2.5%	0.3%	0.3%	0.1%	0.0%	0.1%	1.0%	0.2%	1.4%
Laci	1.4%	10.8%	0.5%	7.1%	0.4%	7.7%	0.1%	4.7%	0.1%	2.8%
Lano	6.7%	30.1%	1.9%	11.5%	0.9%	48.0%	3.1%	22.1%	0.3%	10.2%
Myca	9.2%	3.3%	27.5%	3.1%	77.9%	20.5%	82.1%	31.3%	69.8%	17.4%
Myev	2.1%	0.4%	1.5%	0.0%	0.0%	0.1%	5.2%	2.1%	0.1%	0.1%
Mylu	35.4%	2.4%	0.3%	0.2%	0.1%	0.3%	0.1%	1.0%	0.1%	0.2%
Myth	1.0%	0.6%	39.3%	0.5%	0.1%	0.1%	3.0%	2.8%	0.3%	0.2%
Myvo	0.7%	0.1%	0.9%	0.0%	0.0%	0.0%	1.4%	0.3%	0.1%	0.1%
Myyu	25.0%	0.6%	14.0%	0.7%	19.5%	1.6%	2.2%	3.5%	28.0%	8.3%
Tabr	11.7%	48.9%	2.0%	74.9%	0.1%	18.3%	0.9%	26.2%	0.4%	55.0%

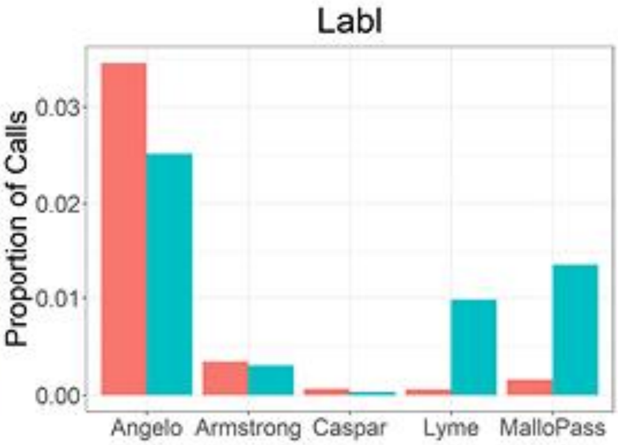


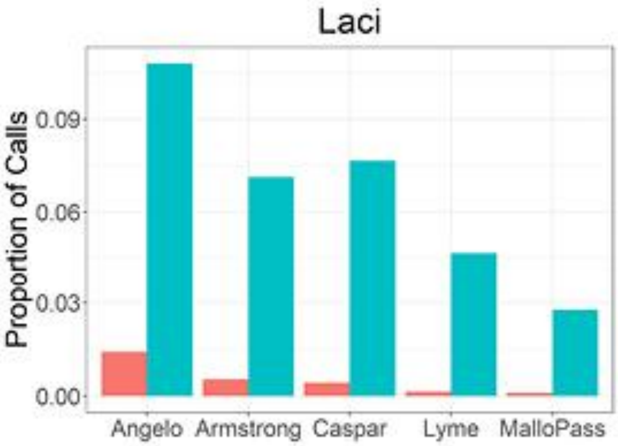
In all of the following plots, red bars represent ‘ground’ detector locations and blue bars represent ‘treetop’ detector locations.

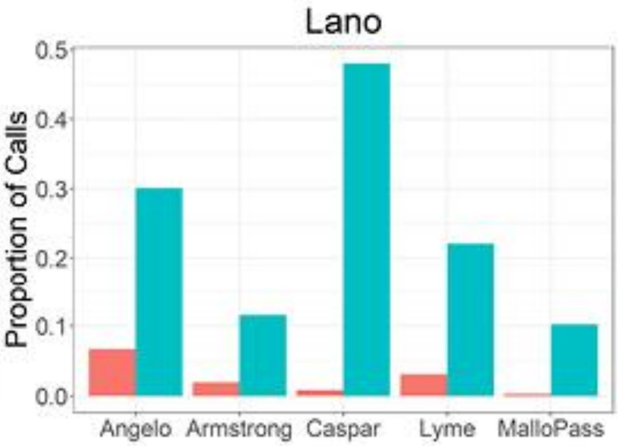

Anpa
Proportion of Calls
0.015
0.010
0.005
0.000
Angelo
Armstrong
Caspar
Lyme
MalloPass

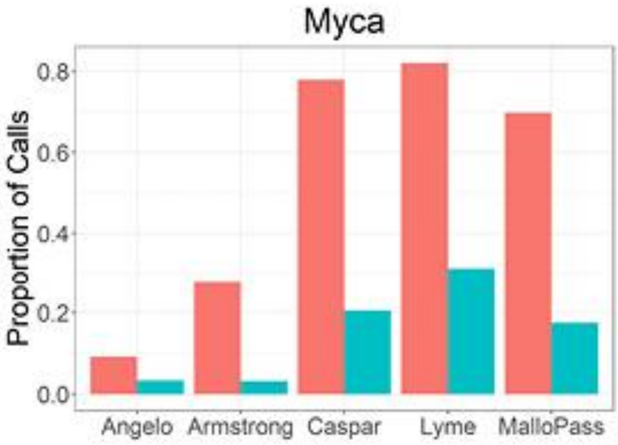

Coto
Proportion of Calls
0.015
0.010
0.005
0.000
Angelo
Armstrong
Caspar
Lyme
MalloPass

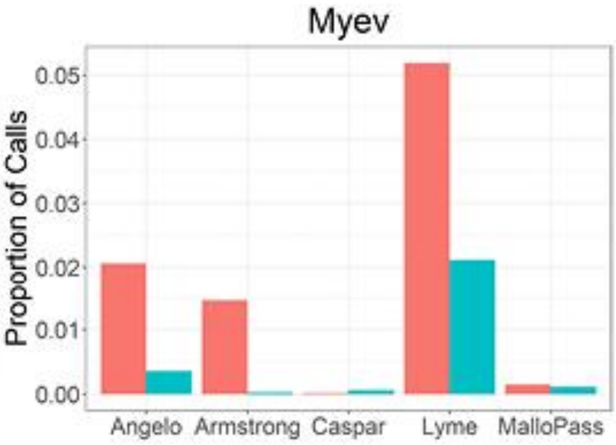

Epfu
Proportion of Calls
0.08
0.06
0.04
0.02
0.00
Angelo
Armstrong
Caspar
Lyme
MalloPass

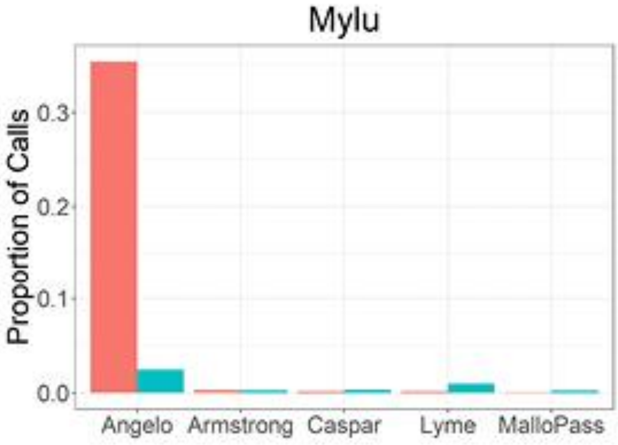

Labl
Proportion of Calls
0.03
0.02
0.01
0.00
Angelo
Armstrong
Caspar
Lyme
MalloPass

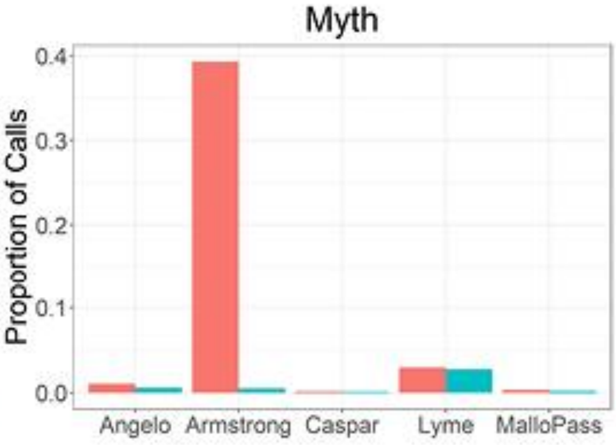

Laci
Proportion of Calls
0.09
0.06
0.03
0.00
Angelo
Armstrong
Caspar
Lyme
MalloPass

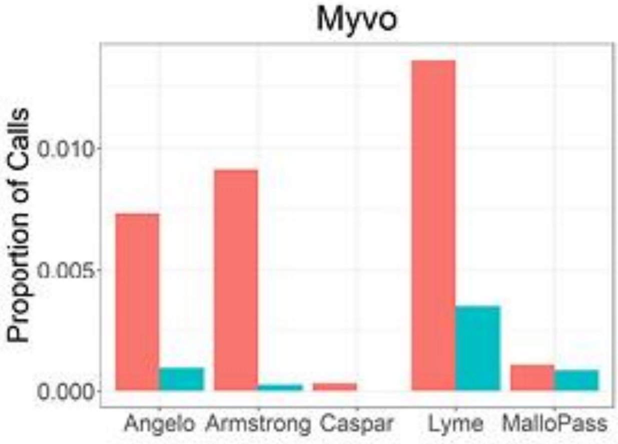

Lano
Proportion of Calls
0.5
0.4
0.3
0.2
0.1
0.0
Angelo
Armstrong
Caspar
Lyme
MalloPass

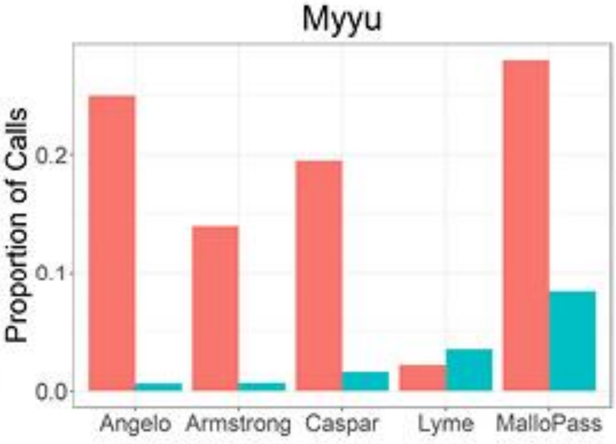

Myca
Proportion of Calls
0.8
0.6
0.4
0.2
0.0
Angelo
Armstrong
Caspar
Lyme
MalloPass

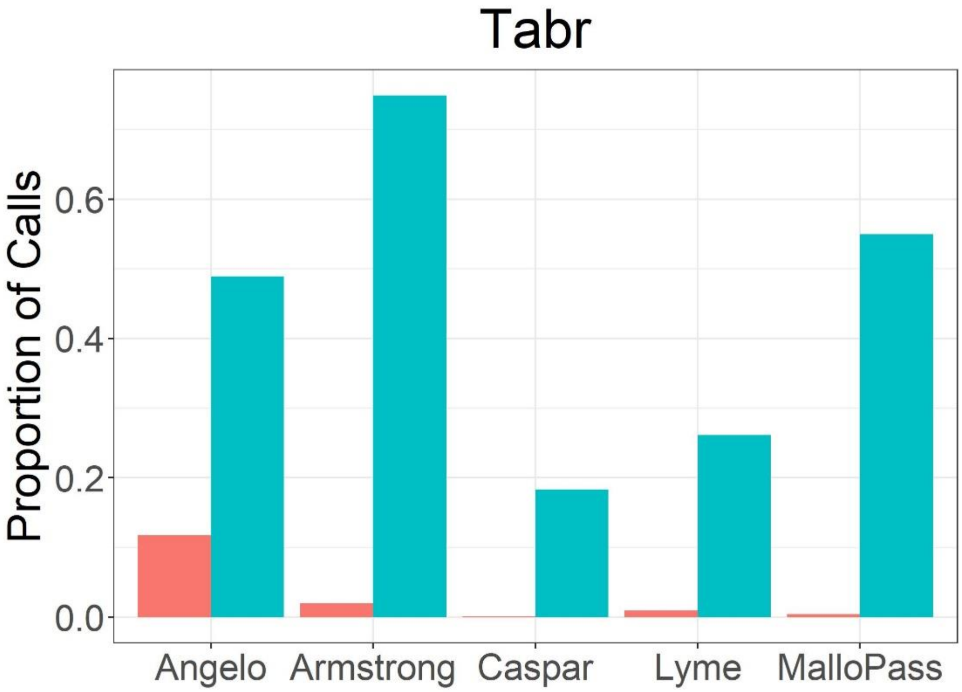

Myev
Proportion of Calls
0.05
0.04
0.03
0.02
0.01
0.00
Angelo
Armstrong
Caspar
Lyme
MalloPass


Mylu
Proportion of Calls
0.3
0.2
0.1
0.0
Angelo
Armstrong
Caspar
Lyme
MalloPass


Myth
Proportion of Calls
0.4
0.3
0.2
0.1
0.0
Angelo
Armstrong
Caspar
Lyme
MalloPass

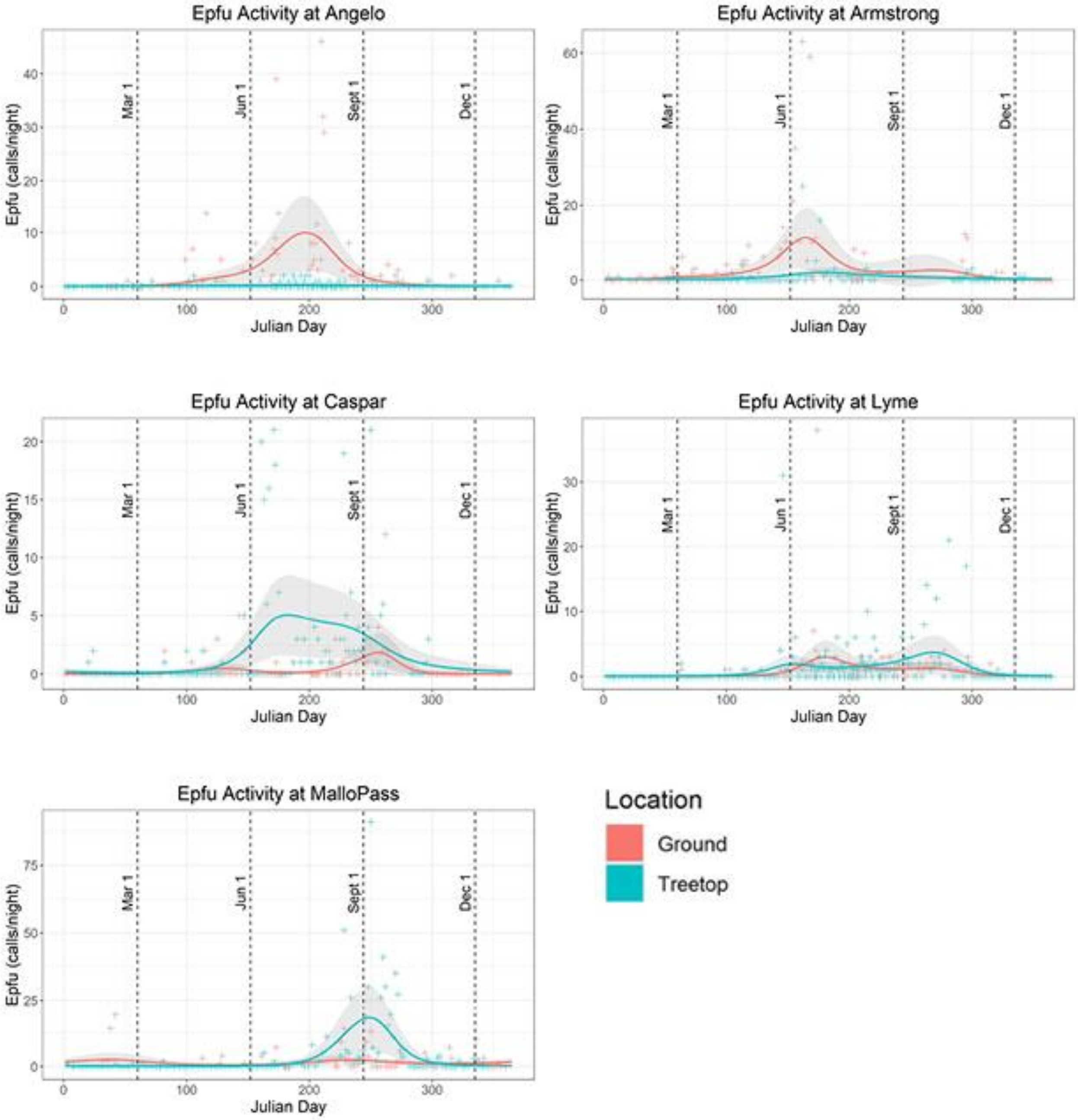

Myvo
Proportion of Calls
0.010
0.005
0.000
Angelo
Armstrong
Caspar
Lyme
MalloPass

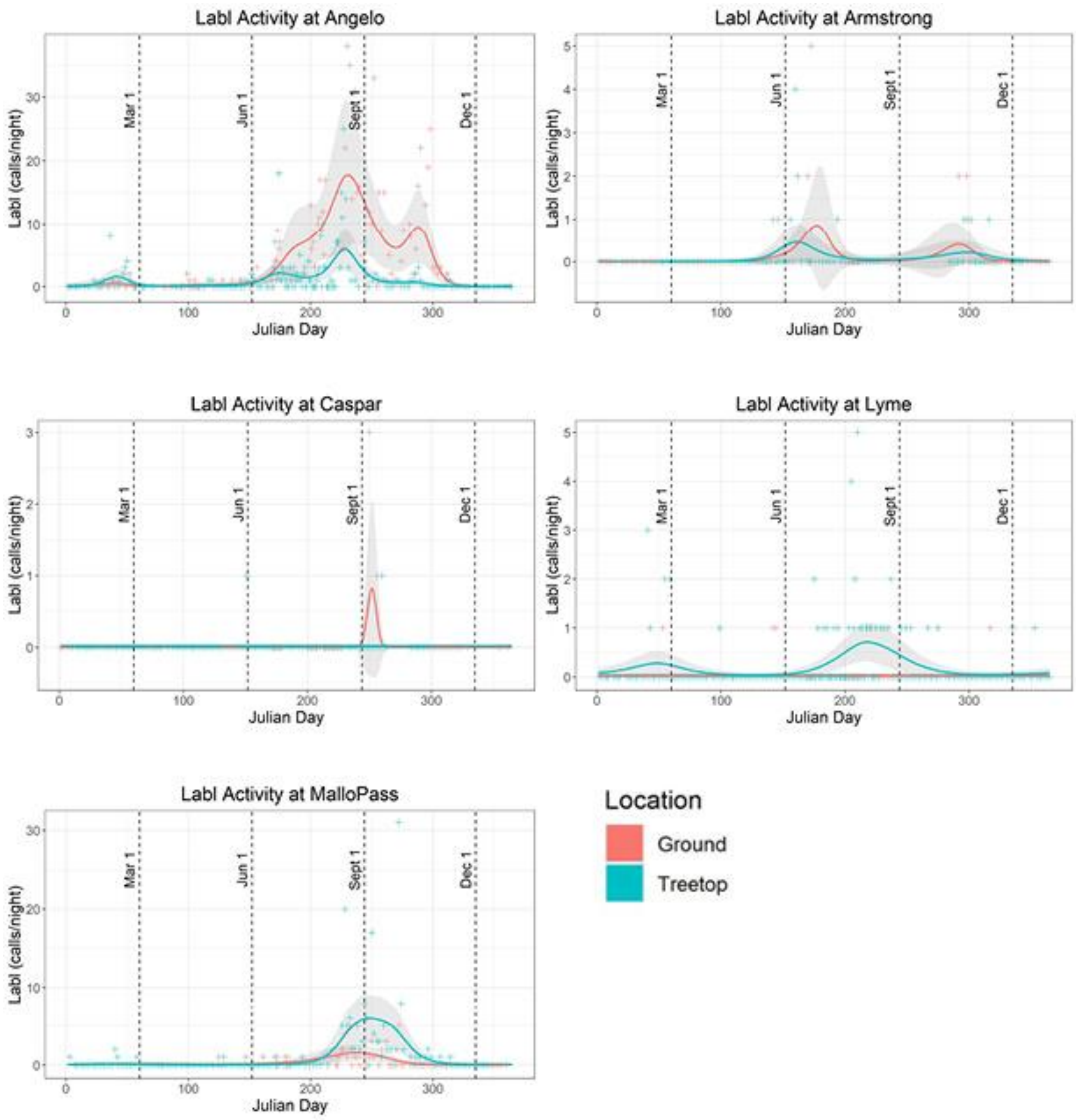

Myyu
Proportion of Calls
0.2
0.1
0.0
Angelo
Armstrong
Caspar
Lyme
MalloPass

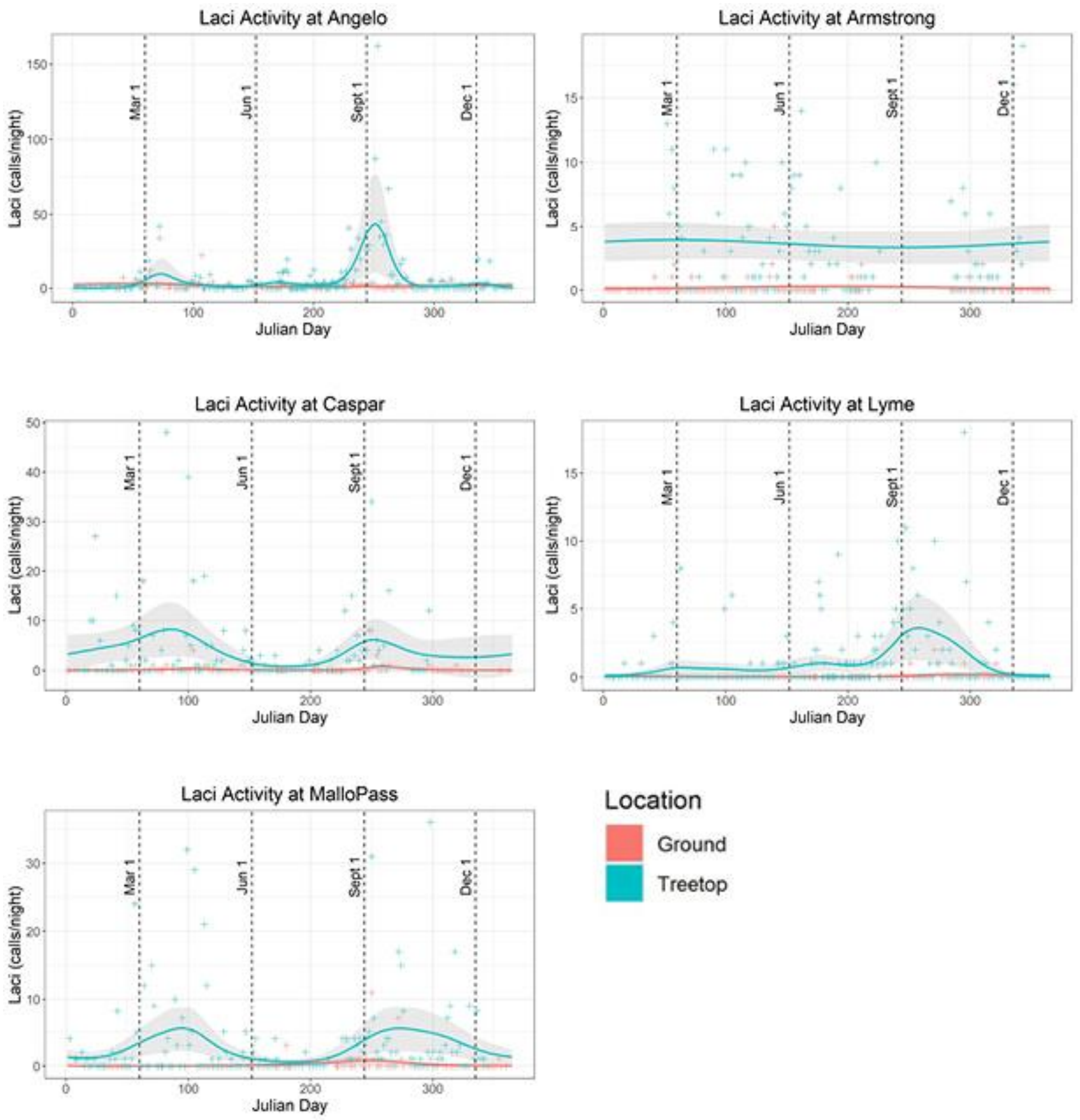

Tabr
Proportion of Calls
0.0
0.2
0.4
0.6
Angelo
Armstrong
Caspar
Lyme
MalloPass

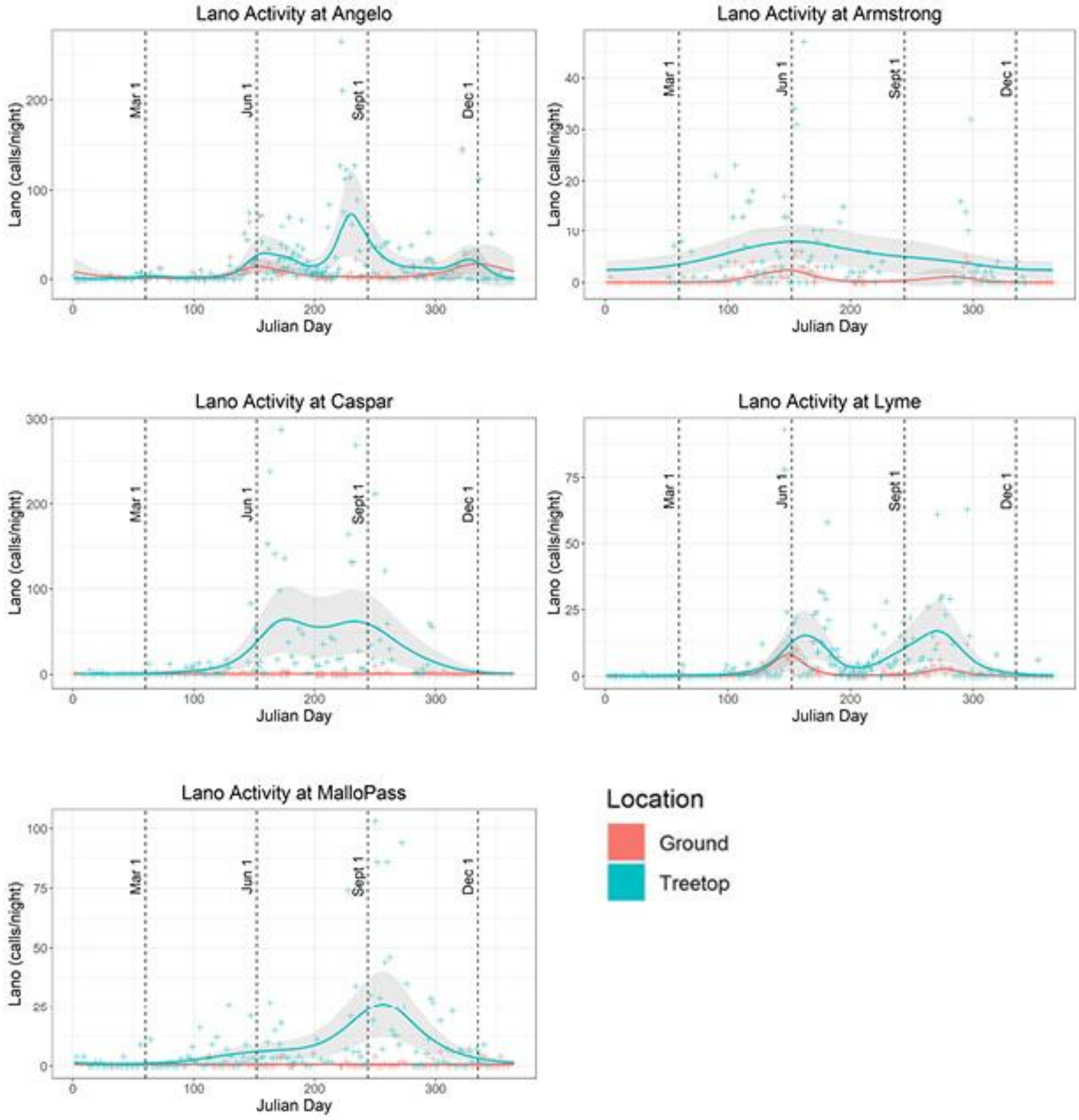
Appendix S3: GAM species activity model prediction plots

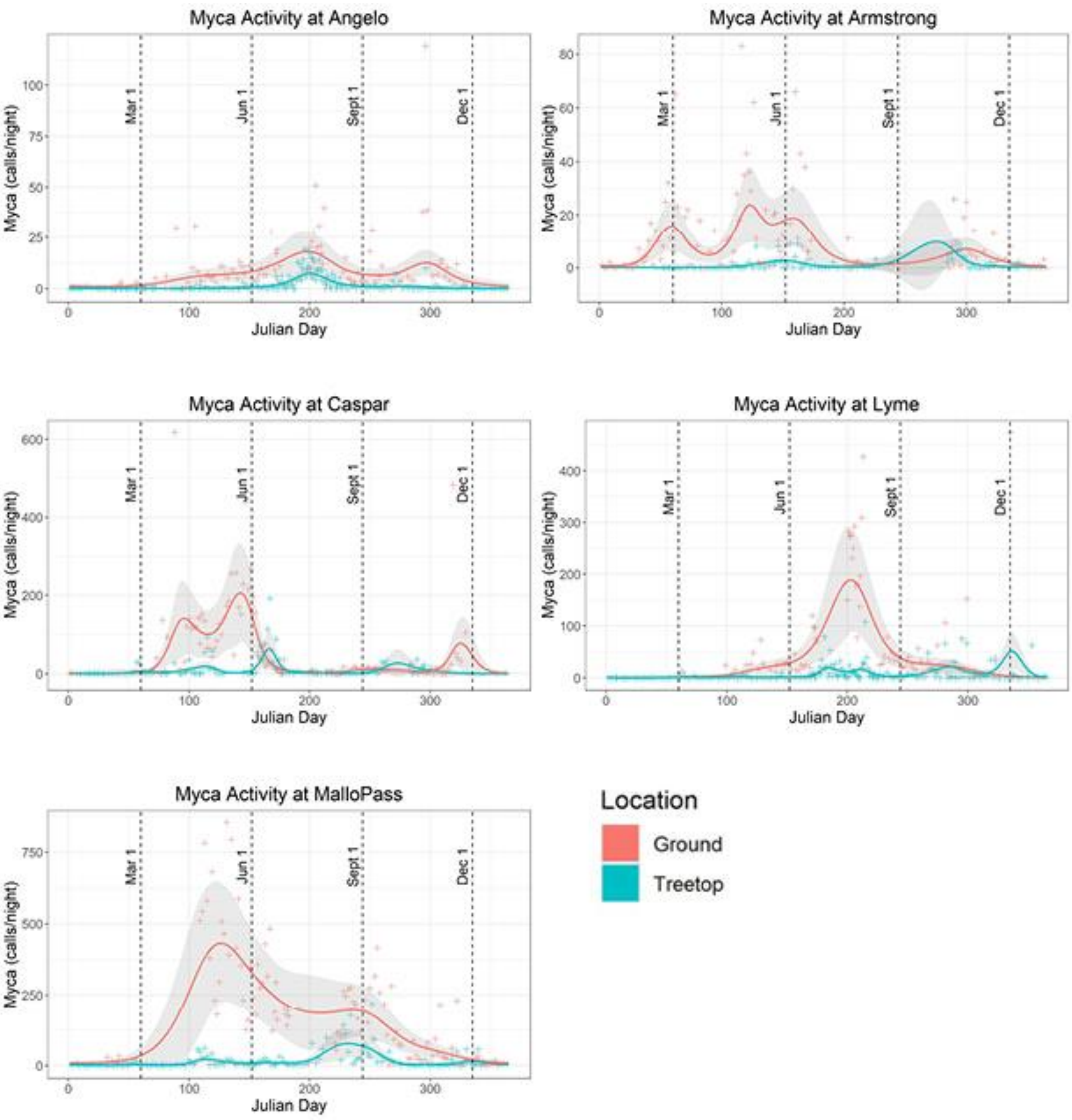
After fitting each GAM species activity model in R, I used function predict.gam( ) to generate new model predictions. I then plotted model predictions as fitted splines with 95-percent confidence intervals alongside actual detection activity indicated by point data.

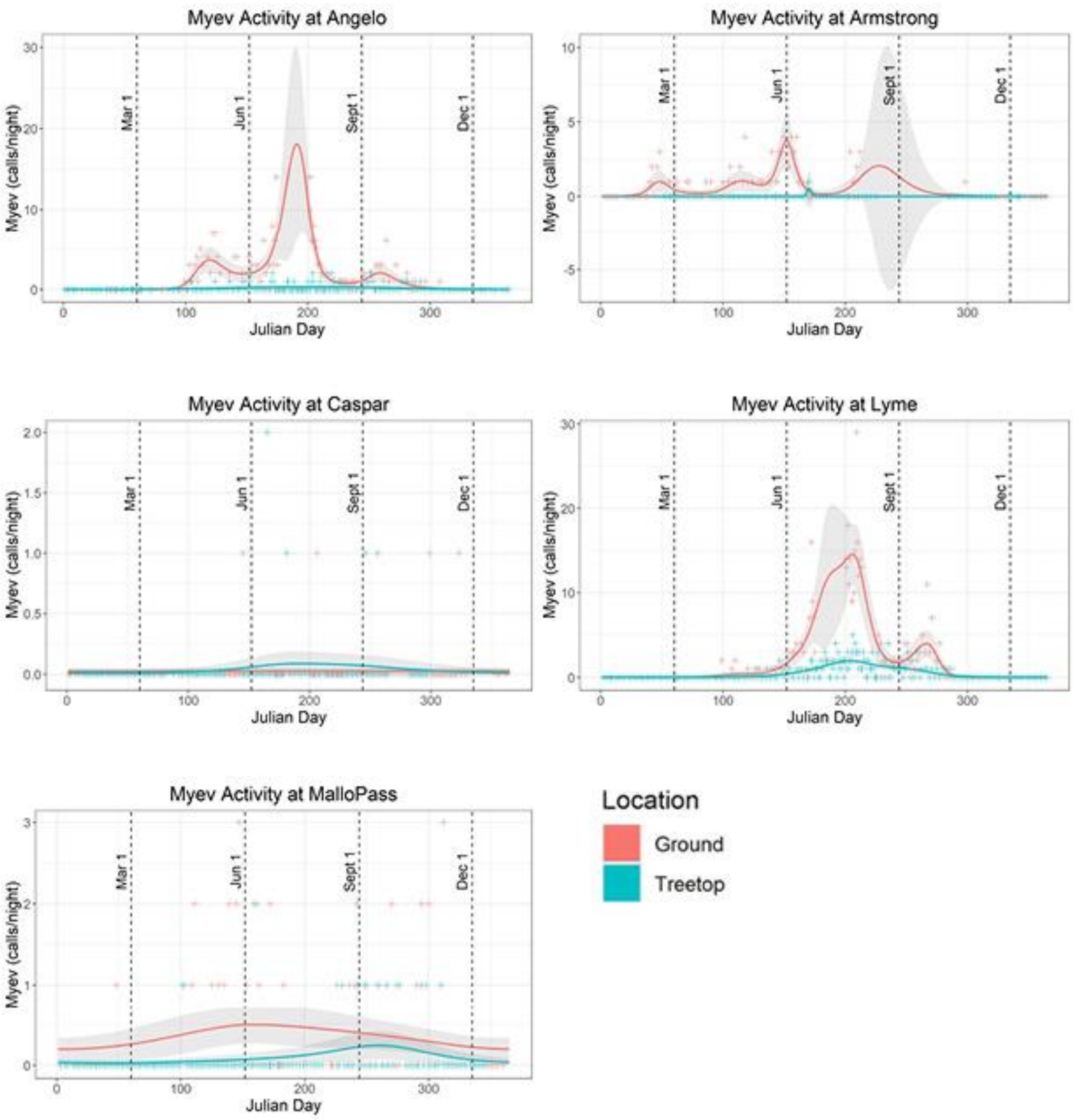


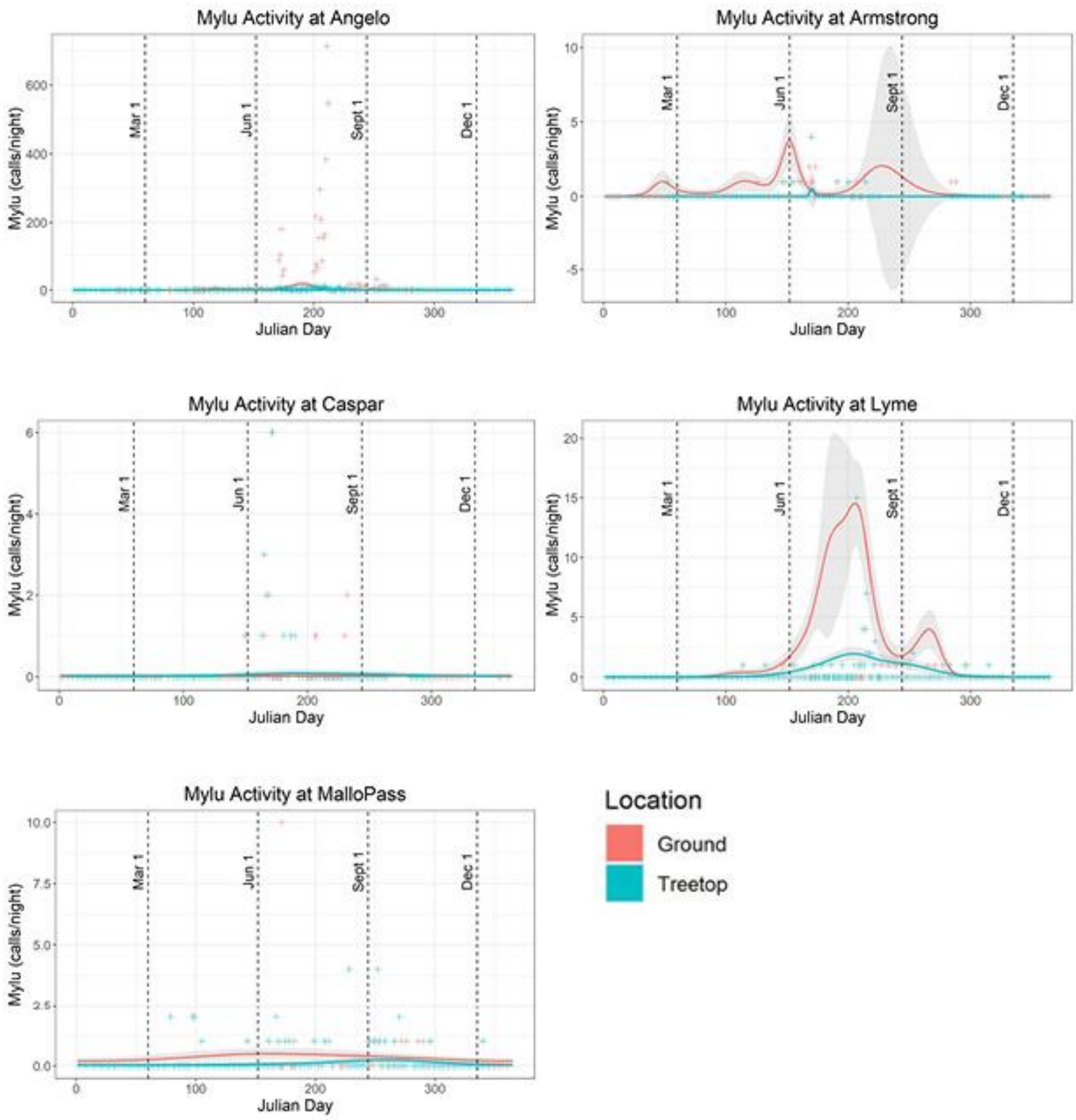

Labl Activity at Angelo
Labl Activity at Armstrong
Labl Activity at Caspar
Labl Activity at Lyme
Labl Activity at MalloPass
Labl (calls/night)
Julian Day
0
100
200
300
Mar 1
Jun 1
Sept 1
Dec 1
0
10
20
30
1
2
3
4
5
Location
Ground
Treetop

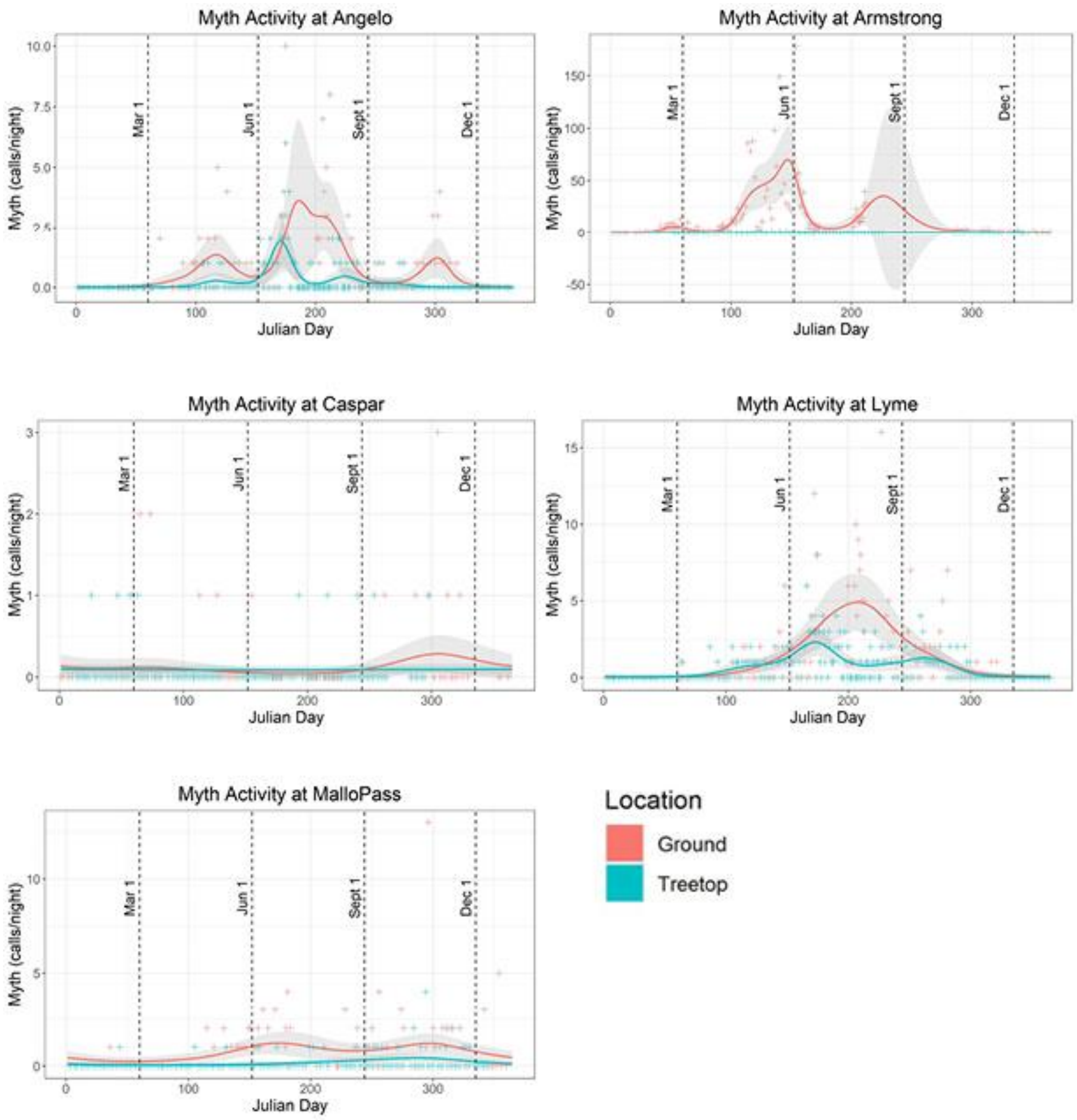

Laci Activity at Angelo
Laci Activity at Armstrong
Laci Activity at Caspar
Laci Activity at Lyme
Laci Activity at MalloPass
Laci (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
0
50
100
150
0
5
10
15
0
10
20
30
40
50
Location
🟥 Ground
🟦 Treetop

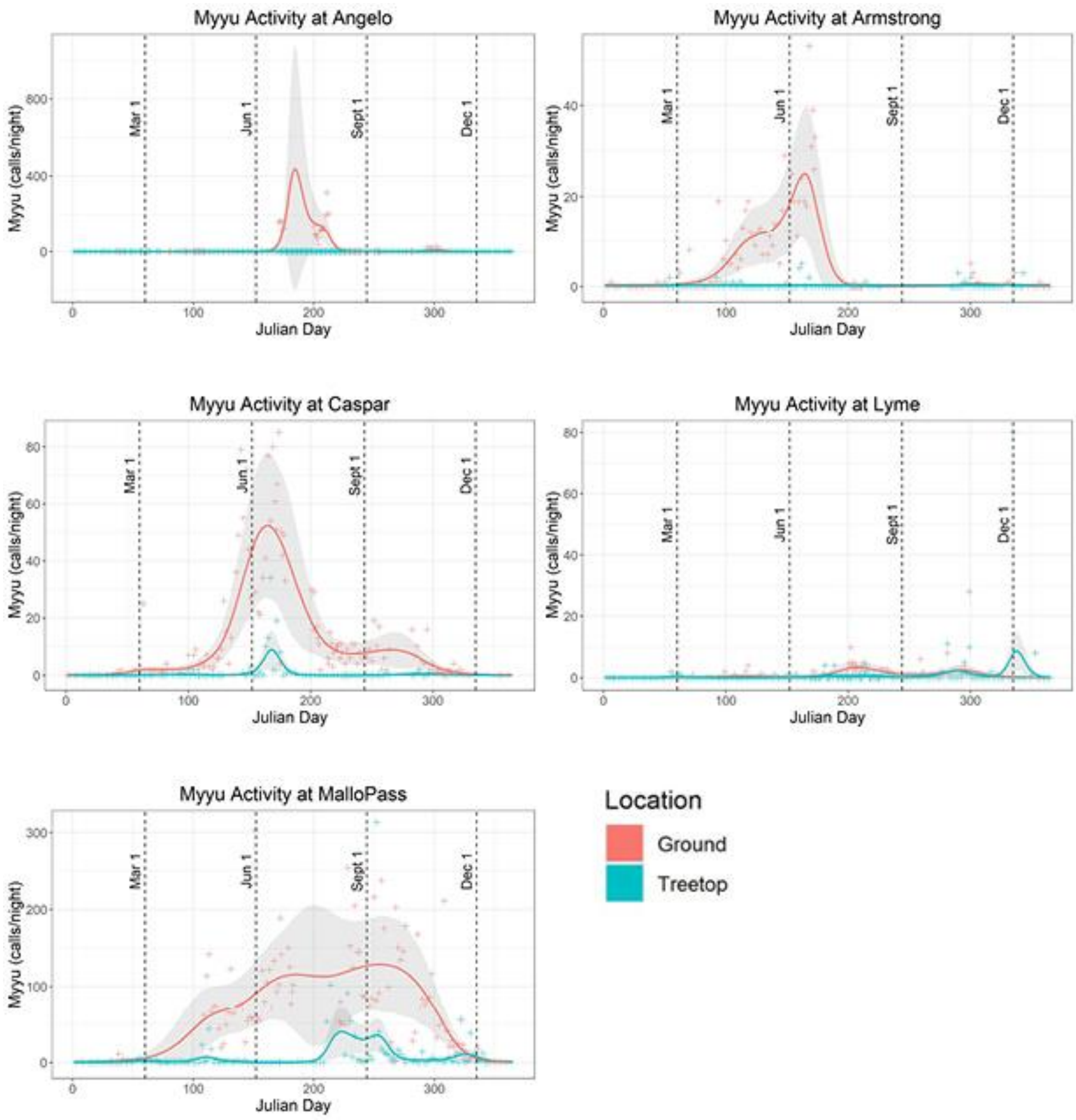

Lano Activity at Angelo
Lano Activity at Armstrong
Lano Activity at Caspar
Lano Activity at Lyme
Lano Activity at MalloPass
Lano (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
0
10
20
30
40
25
50
75
Location
Ground
Treetop

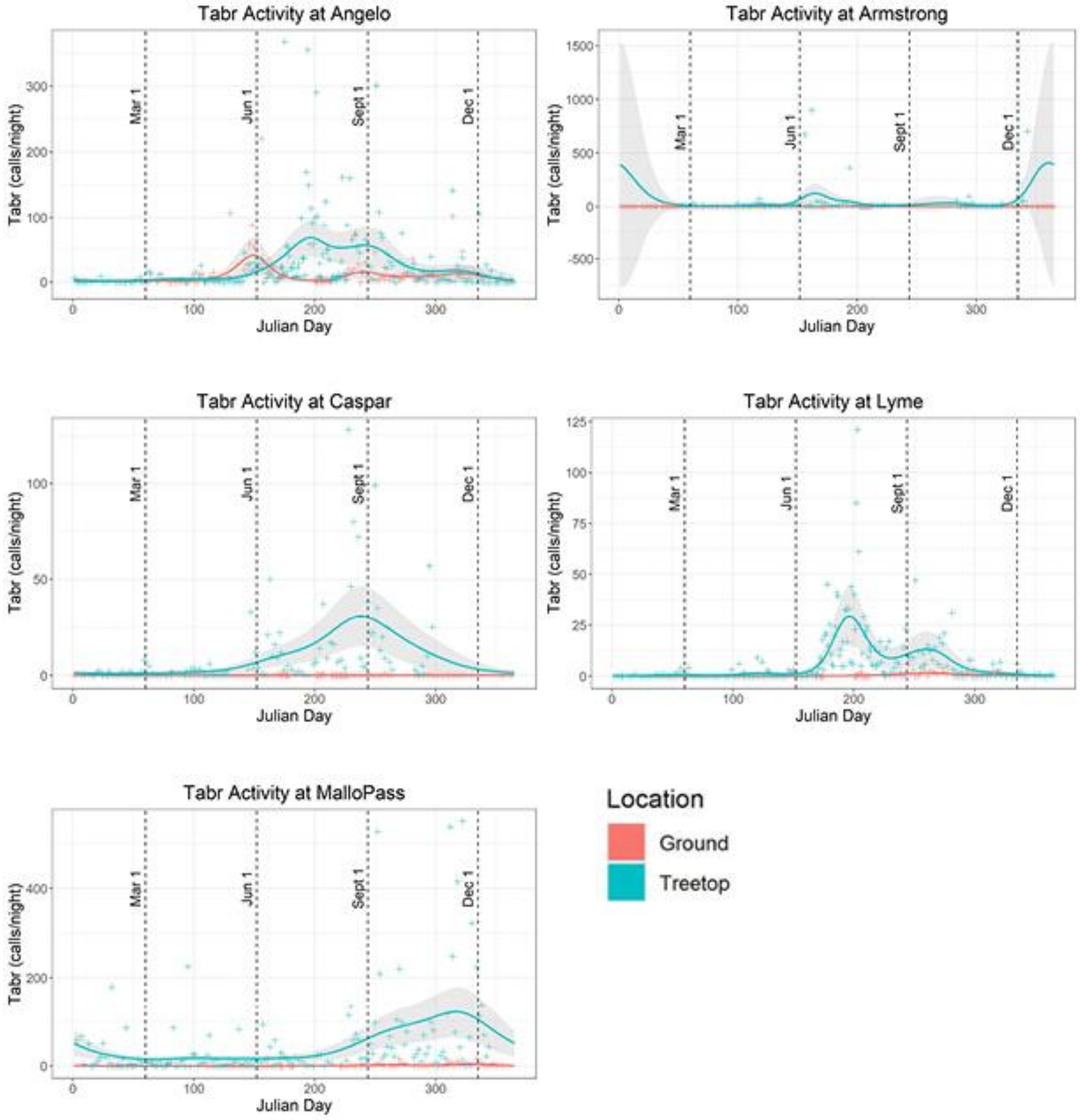

Myca Activity at Angelo
Myca Activity at Armstrong
Myca Activity at Caspar
Myca Activity at Lyme
Myca Activity at MalloPass
Myca (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Location
🟥 Ground
🟦 Treetop


Myev Activity at Angelo
Myev Activity at Armstrong
Myev Activity at Caspar
Myev Activity at Lyme
Myev Activity at MalloPass
Myev (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
10
20
30
5
-5
0.0
0.5
1.0
1.5
2.0
1
2
3
Location
Ground
Treetop


Mylu Activity at Angelo
Mylu (calls/night)
0
200
400
600
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Julian Day
Mylu Activity at Armstrong
Mylu (calls/night)
-5
0
5
10
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Julian Day
Mylu Activity at Caspar
Mylu (calls/night)
0
2
4
6
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Julian Day
Mylu Activity at Lyme
Mylu (calls/night)
0
5
10
15
20
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Julian Day
Mylu Activity at MalloPass
Mylu (calls/night)
0.0
2.5
5.0
7.5
10.0
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
Julian Day
Location
Ground
Treetop


Myth Activity at Angelo
Myth Activity at Armstrong
Myth Activity at Caspar
Myth Activity at Lyme
Myth Activity at MalloPass
Myth (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
0.0
2.5
5.0
7.5
10.0
-50
50
150
1
2
3
5
10
15
Location
Ground
Treetop


Myyu Activity at Angelo
Myyu Activity at Armstrong
Myyu Activity at Caspar
Myyu Activity at Lyme
Myyu Activity at MalloPass
Myyu (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
400
800
20
40
60
80
Location
Ground
Treetop



Tabr Activity at Angelo
Tabr Activity at Armstrong
Tabr Activity at Caspar
Tabr Activity at Lyme
Tabr Activity at MalloPass
Tabr (calls/night)
Julian Day
Mar 1
Jun 1
Sept 1
Dec 1
0
100
200
300
1500
1000
500
-500
50
25
75
125
400
Location
Ground
Treetop

Appendix S4: ANOVA results for GAM species activity models.

For each species model that converged, I applied analysis of variance (ANOVA) to test whether model terms (Site, Location, and Site:Location interaction) were significant. This was computed using function anova( ) from package 'car.' The output is presented below with significant model terms (p-value < 0.05) indicated in red font.

```
Family: Negative Binomial(0.394)

Link function: log


Formula:

Epfu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +

   Site * Location


Parametric Terms:

           df Chi.sq  p-value

Site          4 43.784 7.11e-09

Location      1  2.024    0.155

Site:Location  4 53.678 6.15e-11


Approximate significance of smooth terms:

                                          edf Ref.df  Chi.sq  p-value

s(Julian):SiteByLocationAngelo_Ground     4.366 22.000  57.730  < 2e-16

s(Julian):SiteByLocationAngelo_Treetop    2.061 23.000   7.482  0.01171

s(Julian):SiteByLocationArmstrong_Ground   5.511 22.000  55.876  < 2e-16

s(Julian):SiteByLocationArmstrong_Treetop  2.793 22.000  14.636  0.00062

s(Julian):SiteByLocationCaspar_Ground     5.488 23.000  25.230 5.35e-05

s(Julian):SiteByLocationCaspar_Treetop    3.883 22.000  46.148  < 2e-16

s(Julian):SiteByLocationLyme_Ground       4.722 23.000  29.683 3.64e-06

s(Julian):SiteByLocationLyme_Treetop      5.692 23.000  50.287  < 2e-16

s(Julian):SiteByLocationMalloPass_Ground   3.835 23.000  12.520  0.00600

s(Julian):SiteByLocationMalloPass_Treetop  5.135 23.000 108.567  < 2e-16
```

```
Family: Negative Binomial(0.938)
Link function: log

Formula:
Labl ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric Terms:
            df Chi.sq p-value
Site          4  84.97 < 2e-16
Location      1   0.27 0.60364
Site:Location  4  17.75 0.00138

Approximate significance of smooth terms:
                                              edf    Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     8.868e+00 2.200e+01 137.185  < 2e-16
s(Julian):SiteByLocationAngelo_Treetop    1.056e+01 2.300e+01  83.881  < 2e-16
s(Julian):SiteByLocationArmstrong_Ground  4.867e+00 2.200e+01  12.138   0.0195
s(Julian):SiteByLocationArmstrong_Treetop 4.194e+00 2.200e+01   8.744   0.0540
s(Julian):SiteByLocationCaspar_Ground     1.828e+00 1.400e+01   2.410   0.2600
s(Julian):SiteByLocationCaspar_Treetop    9.535e-04 2.200e+01   0.001   0.5900
s(Julian):SiteByLocationLyme_Ground       1.073e-03 2.300e+01   0.001   0.5716
s(Julian):SiteByLocationLyme_Treetop      5.256e+00 2.300e+01  27.601 1.21e-05
s(Julian):SiteByLocationMalloPass_Ground  4.418e+00 2.300e+01  33.761  < 2e-16
s(Julian):SiteByLocationMalloPass_Treetop 6.015e+00 2.300e+01 103.972  < 2e-16
```

```
Family: Negative Binomial(0.495)
Link function: log

Formula:
Laci ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric Terms:
             df Chi.sq p-value
Site          4 113.30  <2e-16
Location      1 215.36  <2e-16
Site:Location  4  84.58  <2e-16

Approximate significance of smooth terms:
                                          edf  Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground      2.2138 22.0000  8.693  0.00748
s(Julian):SiteByLocationAngelo_Treetop    11.5617 23.0000 97.311  < 2e-16
s(Julian):SiteByLocationArmstrong_Ground   1.1772 22.0000  2.359  0.11685
s(Julian):SiteByLocationArmstrong_Treetop  0.4713 22.0000  0.571  0.29028
s(Julian):SiteByLocationCaspar_Ground      5.5926 23.0000 17.472  0.00250
s(Julian):SiteByLocationCaspar_Treetop     5.1388 22.0000 26.919 1.83e-05
s(Julian):SiteByLocationLyme_Ground        2.1445 23.0000  7.216  0.01645
s(Julian):SiteByLocationLyme_Treetop       6.8583 23.0000 42.960  < 2e-16
s(Julian):SiteByLocationMalloPass_Ground   2.8367 23.0000 16.369  0.00024
s(Julian):SiteByLocationMalloPass_Treetop  5.8432 23.0000 32.513 3.52e-06
```

```
Family: Negative Binomial(0.502)

Link function: log


Formula:

Lano ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +

   Site * Location


Parametric Terms:

            df Chi.sq  p-value

Site         4 141.98  < 2e-16

Location     1 280.04  < 2e-16

Site:Location  4  73.59 3.96e-15


Approximate significance of smooth terms:

                                          edf    Ref.df  Chi.sq  p-value

s(Julian):SiteByLocationAngelo_Ground     6.198e+00 2.200e+01  36.150 2.08e-06

s(Julian):SiteByLocationAngelo_Treetop    1.095e+01 2.300e+01 138.307  < 2e-16

s(Julian):SiteByLocationArmstrong_Ground  5.533e+00 2.200e+01  37.997  < 2e-16

s(Julian):SiteByLocationArmstrong_Treetop 2.213e+00 2.200e+01   7.850    0.013

s(Julian):SiteByLocationCaspar_Ground     2.979e-03 2.300e+01   0.001    0.825

s(Julian):SiteByLocationCaspar_Treetop    4.973e+00 2.200e+01 135.605  < 2e-16

s(Julian):SiteByLocationLyme_Ground       6.986e+00 2.300e+01  57.069  < 2e-16

s(Julian):SiteByLocationLyme_Treetop      8.065e+00 2.300e+01 127.937  < 2e-16

s(Julian):SiteByLocationMalloPass_Ground  5.355e-04 2.300e+01   0.000    0.675

s(Julian):SiteByLocationMalloPass_Treetop 4.782e+00 2.300e+01  76.352  < 2e-16
```

```
Family: Negative Binomial(0.835)
Link function: log

Formula:
Myca ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric Terms:
            df Chi.sq p-value
Site         4 541.57 < 2e-16
Location     1 226.31 < 2e-16
Site:Location  4  28.72 8.9e-06

Approximate significance of smooth terms:
                                       edf Ref.df Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground     6.452 22.000  41.50  <2e-16
s(Julian):SiteByLocationAngelo_Treetop    6.895 23.000 112.79  <2e-16
s(Julian):SiteByLocationArmstrong_Ground   9.538 22.000  99.54  <2e-16
s(Julian):SiteByLocationArmstrong_Treetop  6.454 22.000  42.18  <2e-16
s(Julian):SiteByLocationCaspar_Ground     12.698 23.000 289.56  <2e-16
s(Julian):SiteByLocationCaspar_Treetop    12.644 22.000 119.93  <2e-16
s(Julian):SiteByLocationLyme_Ground       7.291 23.000 193.34  <2e-16
s(Julian):SiteByLocationLyme_Treetop     15.007 23.000 222.69  <2e-16
s(Julian):SiteByLocationMalloPass_Ground   5.609 23.000 136.23  <2e-16
s(Julian):SiteByLocationMalloPass_Treetop 11.824 23.000 142.75  <2e-16
```

```
Family: Negative Binomial(7.454)

Link function: log


Formula:

Myev ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +

   Site * Location


Parametric Terms:

            df Chi.sq p-value

Site         4 17.892  0.0013

Location     1  0.122  0.7265

Site:Location  4  4.908  0.2969


Approximate significance of smooth terms:

                                          edf    Ref.df  Chi.sq p-value

s(Julian):SiteByLocationAngelo_Ground      9.861683 22.000000 112.227 < 2e-16

s(Julian):SiteByLocationAngelo_Treetop     3.001695 23.000000  13.525 0.00132

s(Julian):SiteByLocationArmstrong_Ground   9.983409 22.000000  58.457 < 2e-16

s(Julian):SiteByLocationArmstrong_Treetop  1.516746 16.000000   0.988 0.51066

s(Julian):SiteByLocationCaspar_Ground      0.002608 23.000000   0.002 0.54385

s(Julian):SiteByLocationCaspar_Treetop     1.592154 22.000000   2.997 0.12824

s(Julian):SiteByLocationLyme_Ground        9.200876 23.000000 205.462 < 2e-16

s(Julian):SiteByLocationLyme_Treetop       4.890580 23.000000  54.854 < 2e-16

s(Julian):SiteByLocationMalloPass_Ground   1.850878 23.000000   4.925 0.04705

s(Julian):SiteByLocationMalloPass_Treetop  2.359304 23.000000   8.705 0.00884
```

```
Family: Negative Binomial(0.954)
Link function: log

Formula:
Mylu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric Terms:
             df Chi.sq p-value
Site          4 17.189 0.00178
Location      1  0.019 0.89159
Site:Location  4  7.735 0.10178

Approximate significance of smooth terms:
                                        edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground      8.641 22.000 279.960  < 2e-16
s(Julian):SiteByLocationAngelo_Treetop     5.050 23.000  85.100  < 2e-16
s(Julian):SiteByLocationArmstrong_Ground   3.883 22.000  12.562 0.006633
s(Julian):SiteByLocationArmstrong_Treetop  2.488 22.000   7.972 0.016387
s(Julian):SiteByLocationCaspar_Ground      2.455 23.000   6.554 0.035204
s(Julian):SiteByLocationCaspar_Treetop     2.749 22.000  10.434 0.006346
s(Julian):SiteByLocationLyme_Ground        2.114 23.000   5.485 0.045929
s(Julian):SiteByLocationLyme_Treetop       7.284 23.000  46.598  < 2e-16
s(Julian):SiteByLocationMalloPass_Ground   5.256 22.000  12.862 0.018935
s(Julian):SiteByLocationMalloPass_Treetop  3.360 23.000  16.314 0.000459
```

```
Family: Negative Binomial(1.909)
Link function: log

Formula:
Myth ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric Terms:
              df Chi.sq  p-value
Site           4  56.07 1.94e-11
Location       1  43.61 4.01e-11
Site:Location  4  56.28 1.75e-11

Approximate significance of smooth terms:
                                          edf  Ref.df  Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground      8.9789 22.0000  52.528 < 2e-16
s(Julian):SiteByLocationAngelo_Treetop     8.1791 23.0000  42.729 < 2e-16
s(Julian):SiteByLocationArmstrong_Ground  12.0239 22.0000 346.168 < 2e-16
s(Julian):SiteByLocationArmstrong_Treetop  3.7153 22.0000   8.230 0.04737
s(Julian):SiteByLocationCaspar_Ground      2.8523 23.0000   8.161 0.02206
s(Julian):SiteByLocationCaspar_Treetop     0.1581 22.0000   0.165 0.34525
s(Julian):SiteByLocationLyme_Ground        4.3904 23.0000  78.361 < 2e-16
s(Julian):SiteByLocationLyme_Treetop       6.9207 23.0000  51.650 < 2e-16
s(Julian):SiteByLocationMalloPass_Ground   3.8169 23.0000  10.756 0.01421
s(Julian):SiteByLocationMalloPass_Treetop  2.5482 23.0000  13.856 0.00058
```

```
Family: Negative Binomial(0.951)
Link function: log

Formula:
Myyu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric Terms:
            df Chi.sq  p-value
Site          4 455.32  < 2e-16
Location      1  84.86  < 2e-16
Site:Location  4  31.93 1.97e-06

Approximate significance of smooth terms:
                                          edf    Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     12.697502 22.000000 322.19  < 2e-16
s(Julian):SiteByLocationAngelo_Treetop     4.170296 23.000000  22.40 4.87e-05
s(Julian):SiteByLocationArmstrong_Ground   8.324374 22.000000 181.58  < 2e-16
s(Julian):SiteByLocationArmstrong_Treetop  0.001452 22.000000   0.00    0.959
s(Julian):SiteByLocationCaspar_Ground      8.360795 23.000000 180.21  < 2e-16
s(Julian):SiteByLocationCaspar_Treetop     7.959832 22.000000  62.18  < 2e-16
s(Julian):SiteByLocationLyme_Ground        7.207267 23.000000  49.61  < 2e-16
s(Julian):SiteByLocationLyme_Treetop      12.526689 23.000000  82.75  < 2e-16
s(Julian):SiteByLocationMalloPass_Ground   6.684637 23.000000 188.66  < 2e-16
s(Julian):SiteByLocationMalloPass_Treetop 13.476777 23.000000 189.40  < 2e-16
```

```
Family: Negative Binomial(0.627)

Link function: log


Formula:

Tabr ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +

   Site * Location


Parametric Terms:

            df Chi.sq p-value

Site          4  311.5  <2e-16

Location      1  297.1  <2e-16

Site:Location  4  157.2  <2e-16


Approximate significance of smooth terms:

                                          edf    Ref.df  Chi.sq  p-value

s(Julian):SiteByLocationAngelo_Ground      8.588468 22.000000  64.341  < 2e-16

s(Julian):SiteByLocationAngelo_Treetop     8.046312 23.000000 170.799  < 2e-16

s(Julian):SiteByLocationArmstrong_Ground   4.642589 22.000000  38.342  < 2e-16

s(Julian):SiteByLocationArmstrong_Treetop  9.246812 22.000000  60.093  < 2e-16

s(Julian):SiteByLocationCaspar_Ground      0.003856 23.000000   0.002    0.563

s(Julian):SiteByLocationCaspar_Treetop     4.172467 22.000000  98.421  < 2e-16

s(Julian):SiteByLocationLyme_Ground        3.398507 23.000000  29.778  < 2e-16

s(Julian):SiteByLocationLyme_Treetop      10.081585 23.000000 200.980  < 2e-16

s(Julian):SiteByLocationMalloPass_Ground   5.987727 23.000000  31.810 4.26e-06

s(Julian):SiteByLocationMalloPass_Treetop  4.714715 23.000000  64.136  < 2e-16
```

Appendix S5: GAM species activity model summary results.

I used generalized additive models (GAMs) to examine species activity in relation to study site and detector position over the 12-month study period. Summary results for all thirteen species models, including the three which did not converge, is included below.

```
Family: Negative Binomial(0.715)
Link function: log

Formula:
Anpa ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)       -35.18  634119.16      0       1
Site1            32.01  634119.16      0       1
Site2            32.81  634119.16      0       1
Site3           -108.60 2536476.66      0       1
Site4            30.02  634119.16      0       1
Location1         -13.18  634119.16      0       1
Site1:Location1     13.53  634119.16      0       1
Site2:Location1     13.26  634119.16      0       1
Site3:Location1    -60.57 2536476.66      0       1
Site4:Location1     13.11  634119.16      0       1

Approximate significance of smooth terms:
                                        edf Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     3.302e+00     22 24.504 7.33e-06 ***
s(Julian):SiteByLocationAngelo_Treetop    2.096e+00     23  5.295   0.0489 *
s(Julian):SiteByLocationArmstrong_Ground  5.838e+00     22 55.250  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 3.658e-05     22  0.000   0.8046
s(Julian):SiteByLocationCaspar_Ground     1.526e+00     22  0.926   0.5349
s(Julian):SiteByLocationCaspar_Treetop    1.175e-11     23  0.000   1.0000
s(Julian):SiteByLocationLyme_Ground       1.985e+00     23  2.997   0.1944
s(Julian):SiteByLocationLyme_Treetop      2.329e+00     23  4.867   0.0828 .
s(Julian):SiteByLocationMalloPass_Ground  1.869e+00     22  1.372   0.4959
s(Julian):SiteByLocationMalloPass_Treetop 1.888e+00     16  3.115   0.1807
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.365   Deviance explained = 64.3%
-REML = 258.47  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(2.212)
Link function: log

Formula:
Coto ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)       -84.65  547941.60       0        1
Site1             78.40  547941.60       0        1
Site2             60.32  547941.60       0        1
Site3             31.13 2191766.33       0        1
Site4           -248.32  547941.92       0        1
Location1         53.85  547941.60       0        1
Site1:Location1    -51.06  547941.60       0        1
Site2:Location1    -52.63  547941.60       0        1
Site3:Location1   -102.34 2191766.33       0        1
Site4:Location1    262.11  547941.92       0        1

Approximate significance of smooth terms:
                                      edf Ref.df Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground     3.339e-05     22  0.000   0.561
s(Julian):SiteByLocationAngelo_Treetop    2.567e+00     23  4.825   0.112
s(Julian):SiteByLocationArmstrong_Ground  2.557e+00     13 26.805 9.8e-07 ***
s(Julian):SiteByLocationArmstrong_Treetop 1.709e+00     16  1.229   0.487
s(Julian):SiteByLocationCaspar_Ground     1.033e-11     23  0.000   1.000
s(Julian):SiteByLocationCaspar_Treetop    1.747e+00     22  2.312   0.251
s(Julian):SiteByLocationLyme_Ground       4.092e+00     20  4.506   0.350
s(Julian):SiteByLocationLyme_Treetop      1.592e+00     23  1.493   0.385
s(Julian):SiteByLocationMalloPass_Ground  2.294e+00     22  3.520   0.187
s(Julian):SiteByLocationMalloPass_Treetop 7.432e-01     23  1.017   0.244
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.732   Deviance explained = 83.8%
-REML = 127.52  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.394)
Link function: log

Formula:
Epfu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)     -0.65415    0.08073  -8.102 5.38e-16 ***
Site1          -0.54018    0.15948  -3.387 0.000706 ***
Site2           0.63651    0.14668   4.340 1.43e-05 ***
Site3          -0.46810    0.19740  -2.371 0.017728 *
Site4          -0.19271    0.16102  -1.197 0.231364
Location1       0.11486    0.08073   1.423 0.154836
Site1:Location1  0.83565    0.15948   5.240 1.61e-07 ***
Site2:Location1  0.39682    0.14668   2.705 0.006823 **
Site3:Location1 -1.08700    0.19740  -5.506 3.66e-08 ***
Site4:Location1 -0.35670    0.16102  -2.215 0.026740 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
                                 edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     4.366     22  57.730  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    2.061     23   7.482  0.01171 *
s(Julian):SiteByLocationArmstrong_Ground  5.511     22  55.876  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 2.793     22  14.636  0.00062 ***
s(Julian):SiteByLocationCaspar_Ground     5.488     23  25.230 5.35e-05 ***
s(Julian):SiteByLocationCaspar_Treetop    3.883     22  46.148  < 2e-16 ***
s(Julian):SiteByLocationLyme_Ground       4.722     23  29.683 3.64e-06 ***
s(Julian):SiteByLocationLyme_Treetop      5.692     23  50.287  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  3.835     23  12.520  0.00600 **
s(Julian):SiteByLocationMalloPass_Treetop 5.135     23 108.567  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.287   Deviance explained = 50.2%
-REML = 1659.4  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.938)
Link function: log

Formula:
Labl ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric coefficients:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)      -7.133      9.252  -0.771    0.441
Site1             6.842      9.253   0.739    0.460
Site2             3.439      9.274   0.371    0.711
Site3           -20.149     37.003  -0.545    0.586
Site4             4.377      9.255   0.473    0.636
Location1        -4.804      9.252  -0.519    0.604
Site1:Location1   5.302      9.253   0.573    0.567
Site2:Location1   4.329      9.274   0.467    0.641
Site3:Location1 -18.453     37.003  -0.499    0.618
Site4:Location1   4.079      9.255   0.441    0.659

Approximate significance of smooth terms:
                                           edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground    8.868e+00     22 137.185  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop   1.056e+01     23  83.881  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  4.867e+00     22  12.138   0.0195 *
s(Julian):SiteByLocationArmstrong_Treetop 4.194e+00     22   8.744   0.0540 .
s(Julian):SiteByLocationCaspar_Ground    1.828e+00     14   2.410   0.2600
s(Julian):SiteByLocationCaspar_Treetop   9.535e-04     22   0.001   0.5900
s(Julian):SiteByLocationLyme_Ground      1.073e-03     23   0.001   0.5716
s(Julian):SiteByLocationLyme_Treetop     5.256e+00     23  27.601 1.21e-05 ***
s(Julian):SiteByLocationMalloPass_Ground  4.418e+00     23  33.761  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 6.015e+00     23 103.972  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.522   Deviance explained =   75%
-REML = 968.56  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.495)

Link function: log

Formula:
Laci ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)    -0.50019    0.08764  -5.708 1.15e-08 ***
Site1           1.20731    0.11527  10.474  < 2e-16 ***
Site2           0.33586    0.14279   2.352   0.0187 *
Site3          -0.06154    0.16625  -0.370   0.7112
Site4          -1.29663    0.23648  -5.483 4.18e-08 ***
Location1      -1.28606    0.08764 -14.675  < 2e-16 ***
Site1:Location1  0.99967    0.11527   8.673  < 2e-16 ***
Site2:Location1 -0.14174    0.14279  -0.993   0.3209
Site3:Location1 -0.40381    0.16625  -2.429   0.0151 *
Site4:Location1 -0.23790    0.23648  -1.006   0.3144
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                    edf Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground      2.2138     22  8.693  0.00748 **
s(Julian):SiteByLocationAngelo_Treetop    11.5617     23 97.311  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground   1.1772     22  2.359  0.11685
s(Julian):SiteByLocationArmstrong_Treetop  0.4713     22  0.571  0.29028
s(Julian):SiteByLocationCaspar_Ground      5.5926     23 17.472  0.00250 **
s(Julian):SiteByLocationCaspar_Treetop     5.1388     22 26.919 1.83e-05 ***
s(Julian):SiteByLocationLyme_Ground        2.1445     23  7.216  0.01645 *
s(Julian):SiteByLocationLyme_Treetop       6.8583     23 42.960  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground   2.8367     23 16.369  0.00024 ***
s(Julian):SiteByLocationMalloPass_Treetop  5.8432     23 32.513 3.52e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.418   Deviance explained = 51.9%
-REML = 1987.5  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.502)
Link function: log

Formula:
Lano ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)      0.68925    0.06215  11.091  < 2e-16 ***
Site1           1.13635    0.09729  11.680  < 2e-16 ***
Site2          -0.50217    0.14497  -3.464 0.000532 ***
Site3           0.14704    0.11150   1.319 0.187242
Site4          -0.77354    0.15430  -5.013 5.36e-07 ***
Location1       -1.03998    0.06215 -16.734  < 2e-16 ***
Site1:Location1  0.70537    0.09729   7.250 4.17e-13 ***
Site2:Location1 -0.33101    0.14497  -2.283 0.022416 *
Site3:Location1 -0.53029    0.11150  -4.756 1.97e-06 ***
Site4:Location1  0.07939    0.15430   0.514 0.606910
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                       edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground      6.198e+00     22  36.150 2.08e-06 ***
s(Julian):SiteByLocationAngelo_Treetop    1.095e+01     23 138.307  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  5.533e+00     22  37.997  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 2.213e+00     22   7.850    0.013 *
s(Julian):SiteByLocationCaspar_Ground     2.979e-03     23   0.001    0.825
s(Julian):SiteByLocationCaspar_Treetop    4.973e+00     22 135.605  < 2e-16 ***
s(Julian):SiteByLocationLyme_Ground       6.986e+00     23  57.069  < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      8.065e+00     23 127.937  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  5.355e-04     23   0.000    0.675
s(Julian):SiteByLocationMalloPass_Treetop 4.782e+00     23  76.352  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.363   Deviance explained = 56.6%
-REML = 3076.4  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.835)
Link function: log

Formula:
Myca ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      1.65812    0.06593  25.149  < 2e-16 ***
Site1           -1.17052    0.11317 -10.343  < 2e-16 ***
Site2           -1.20869    0.18747  -6.447 1.14e-10 ***
Site3            0.35357    0.15042   2.351  0.01875 *
Site4            0.20756    0.09050   2.294  0.02181 *
Location1        0.99185    0.06593  15.044  < 2e-16 ***
Site1:Location1  0.28555    0.11317   2.523  0.01163 *
Site2:Location1  0.19204    0.18747   1.024  0.30565
Site3:Location1 -0.37049    0.15042  -2.463  0.01378 *
Site4:Location1 -0.28579    0.09050  -3.158  0.00159 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                         edf Ref.df Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground      6.452     22  41.50  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop     6.895     23 112.79  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground   9.538     22  99.54  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop  6.454     22  42.18  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     12.698     23 289.56  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    12.644     22 119.93  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground        7.291     23 193.34  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      15.007     23 222.69  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground   5.609     23 136.23  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 11.824     23 142.75  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.689   Deviance explained = 71.8%
-REML = 4364.4  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(7.454)
Link function: log

Formula:
Myev ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)      -15.18      38.28  -0.397    0.692
Site1            13.40      38.28   0.350    0.726
Site2           -51.67     153.10  -0.337    0.736
Site3            11.67      38.28   0.305    0.760
Site4            13.21      38.28   0.345    0.730
Location1         13.39      38.28   0.350    0.727
Site1:Location1   -12.93      38.28  -0.338    0.736
Site2:Location1    52.18     153.10   0.341    0.733
Site3:Location1   -13.50      38.28  -0.353    0.724
Site4:Location1   -13.11      38.28  -0.342    0.732

Approximate significance of smooth terms:
                                     edf Ref.df  Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground     9.861683     22 112.227 < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    3.001695     23  13.525 0.00132 **
s(Julian):SiteByLocationArmstrong_Ground  9.983409     22  58.457 < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 1.516746     16   0.988 0.51066
s(Julian):SiteByLocationCaspar_Ground     0.002608     23   0.002 0.54385
s(Julian):SiteByLocationCaspar_Treetop    1.592154     22   2.997 0.12824
s(Julian):SiteByLocationLyme_Ground       9.200876     23 205.462 < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      4.890580     23  54.854 < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  1.850878     23   4.925 0.04705 *
s(Julian):SiteByLocationMalloPass_Treetop 2.359304     23   8.705 0.00884 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.763   Deviance explained = 75.7%
-REML = 923.29  Scale est. = 1        n = 1413
```

```
Family: Negative Binomial(0.954)
Link function: log

Formula:
Mylu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      -3.6164     0.8971  -4.031 5.55e-05 ***
Site1             2.4352     0.9408   2.588  0.00964 **
Site2             0.5738     0.9740   0.589  0.55575
Site3            -3.1891     3.2302  -0.987  0.32352
Site4             0.6883     0.9352   0.736  0.46172
Location1         0.1223     0.8971   0.136  0.89159
Site1:Location1   0.6800     0.9408   0.723  0.46981
Site2:Location1  -0.4231     0.9740  -0.434  0.66400
Site3:Location1   2.6850     3.2302   0.831  0.40586
Site4:Location1  -0.3850     0.9352  -0.412  0.68054
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                         edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground    8.641     22 279.960  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop   5.050     23  85.100  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  3.883     22  12.562 0.006633 **
s(Julian):SiteByLocationArmstrong_Treetop 2.488     22   7.972 0.016387 *
s(Julian):SiteByLocationCaspar_Ground    2.455     23   6.554 0.035204 *
s(Julian):SiteByLocationCaspar_Treetop   2.749     22  10.434 0.006346 **
s(Julian):SiteByLocationLyme_Ground      2.114     23   5.485 0.045929 *
s(Julian):SiteByLocationLyme_Treetop     7.284     23  46.598  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  5.256     22  12.862 0.018935 *
s(Julian):SiteByLocationMalloPass_Treetop 3.360     23  16.314 0.000459 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.484   Deviance explained = 89.5%
-REML = 903.77  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(1.909)
Link function: log

Formula:
Myth ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
    Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)     -1.3313     0.1341  -9.926  < 2e-16 ***
Site1          -0.7119     0.4508  -1.579 0.114264
Site2           1.0765     0.2221   4.848 1.25e-06 ***
Site3          -1.0389     0.2131  -4.875 1.09e-06 ***
Site4           0.5282     0.1762   2.997 0.002723 **
Location1       0.8857     0.1341   6.604 4.01e-11 ***
Site1:Location1   0.3067     0.4508   0.680 0.496205
Site2:Location1   1.2224     0.2221   5.505 3.69e-08 ***
Site3:Location1  -0.8434     0.2131  -3.958 7.56e-05 ***
Site4:Location1  -0.5934     0.1762  -3.367 0.000759 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                      edf Ref.df  Chi.sq p-value
s(Julian):SiteByLocationAngelo_Ground      8.9789     22  52.528 < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop     8.1791     23  42.729 < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  12.0239     22 346.168 < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop  3.7153     22   8.230 0.04737 *
s(Julian):SiteByLocationCaspar_Ground      2.8523     23   8.161 0.02206 *
s(Julian):SiteByLocationCaspar_Treetop     0.1581     22   0.165 0.34525
s(Julian):SiteByLocationLyme_Ground        4.3904     23  78.361 < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop       6.9207     23  51.650 < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground   3.8169     23  10.756 0.01421 *
s(Julian):SiteByLocationMalloPass_Treetop  2.5482     23  13.856 0.00058 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =   0.57   Deviance explained = 80.4%
-REML = 1393.3  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(1.304)
Link function: log

Formula:
Myvo ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)       -28.48  634119.16      0       1
Site1             25.50  634119.16      0       1
Site2            -29.86  634119.17      0       1
Site3            -43.42 2536476.64      0       1
Site4             23.90  634119.16      0       1
Location1          24.05  634119.16      0       1
Site1:Location1    -23.13  634119.16      0       1
Site2:Location1     30.67  634119.17      0       1
Site3:Location1     36.83 2536476.64      0       1
Site4:Location1    -22.37  634119.16      0       1

Approximate significance of smooth terms:
                                    edf Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     6.394e+00     22 62.582  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    1.676e+00     23  3.386 0.105520
s(Julian):SiteByLocationArmstrong_Ground  3.920e+00     22 20.729 0.000101 ***
s(Julian):SiteByLocationArmstrong_Treetop 1.534e+00     14  0.830 0.565926
s(Julian):SiteByLocationCaspar_Ground     3.822e+00     23  8.249 0.056400 .
s(Julian):SiteByLocationCaspar_Treetop    1.175e-11     22  0.000 1.000000
s(Julian):SiteByLocationLyme_Ground       8.092e+00     23 51.758  < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      3.656e+00     23 10.380 0.014990 *
s(Julian):SiteByLocationMalloPass_Ground  3.506e+00     23 18.748 0.000161 ***
s(Julian):SiteByLocationMalloPass_Treetop 2.882e+00     23  8.905 0.015305 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.407   Deviance explained = 70.6%
-REML =  472.9  Scale est. = 1        n = 1413
```

```
Family: Negative Binomial(0.951)
Link function: log

Formula:
Myyu ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)     -0.3236     0.1265  -2.558 0.010513 *
Site1          -1.2599     0.3371  -3.738 0.000186 ***
Site2          -0.3414     0.1830  -1.866 0.062104 .
Site3          -0.1011     0.3301  -0.306 0.759315
Site4          -0.8935     0.2075  -4.305 1.67e-05 ***
Location1        1.1653     0.1265   9.212  < 2e-16 ***
Site1:Location1   0.3260     0.3371   0.967 0.333429
Site2:Location1  -0.6990     0.1830  -3.819 0.000134 ***
Site3:Location1   0.7878     0.3301   2.386 0.017010 *
Site4:Location1  -0.5817     0.2075  -2.803 0.005065 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                       edf Ref.df Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground     12.697502     22 322.19  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop     4.170296     23  22.40 4.87e-05 ***
s(Julian):SiteByLocationArmstrong_Ground   8.324374     22 181.58  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop  0.001452     22   0.00    0.959
s(Julian):SiteByLocationCaspar_Ground      8.360795     23 180.21  < 2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop     7.959832     22  62.18  < 2e-16 ***
s(Julian):SiteByLocationLyme_Ground        7.207267     23  49.61  < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      12.526689     23  82.75  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground   6.684637     23 188.66  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 13.476777     23 189.40  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.655   Deviance explained = 82.2%
-REML =   2515  Scale est. = 1         n = 1413
```

```
Family: Negative Binomial(0.627)
Link function: log

Formula:
Tabr ~ s(Julian, by = SiteByLocation, k = 25, bs = "cc") +
   Site * Location

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)     0.6146     0.1020   6.027 1.67e-09 ***
Site1           1.5994     0.1253  12.763  < 2e-16 ***
Site2           0.6668     0.1604   4.158 3.21e-05 ***
Site3          -1.2236     0.1847  -6.626 3.45e-11 ***
Site4          -0.9670     0.1537  -6.293 3.12e-10 ***
Location1      -1.7578     0.1020 -17.235  < 2e-16 ***
Site1:Location1  1.4273     0.1253  11.389  < 2e-16 ***
Site2:Location1 -0.2402     0.1604  -1.498 0.134226
Site3:Location1 -0.5644     0.1847  -3.057 0.002239 **
Site4:Location1  0.5481     0.1537   3.567 0.000361 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                          edf Ref.df  Chi.sq  p-value
s(Julian):SiteByLocationAngelo_Ground      8.588468     22  64.341  < 2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop     8.046312     23 170.799  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground   4.642589     22  38.342  < 2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop  9.246812     22  60.093  < 2e-16 ***
s(Julian):SiteByLocationCaspar_Ground      0.003856     23   0.002    0.563
s(Julian):SiteByLocationCaspar_Treetop     4.172467     22  98.421  < 2e-16 ***
s(Julian):SiteByLocationLyme_Ground        3.398507     23  29.778  < 2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      10.081585     23 200.980  < 2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground   5.987727     23  31.810 4.26e-06 ***
s(Julian):SiteByLocationMalloPass_Treetop  4.714715     23  64.136  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.239   Deviance explained =   69%
-REML = 3466.4  Scale est. = 1         n = 1413
```

Appendix S6: Residual diagnostics for GAM species activity model results.

After running each species model, I used function gam.check( ) to produce residual plots, check model convergence and test adequacy of the basis model choices.

Warnings for models that failed to converge (Anpa, Coto, and Myvo) are indicated in red font. Note: residual plots are not included below for failed models.

Antrozous pallidus (Anpa)

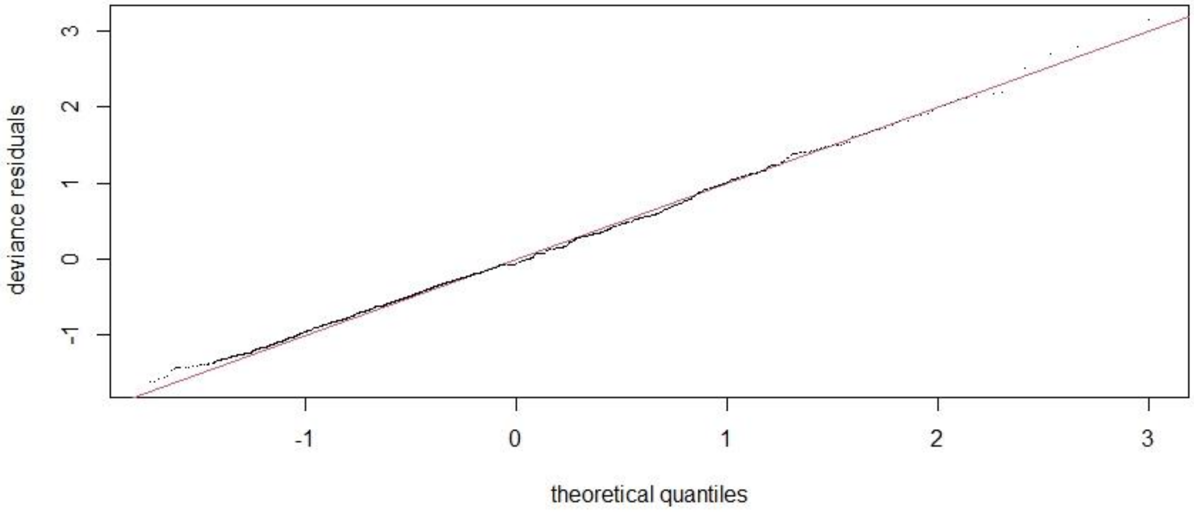
```
> gam.check(fit.25.cc.Anpa)


Method: REML   Optimizer: outer newton

step failed after 19 iterations.

Gradient range [-0.006789881,0.009205579]

(score 258.4728 & scale 1).

Hessian positive definite, eigenvalue range [5.87446e-12,7.582081].

Model rank =  240 / 240


Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                            k'      edf k-index p-value

s(Julian):SiteByLocationAngelo_Ground     2.30e+01 3.30e+00    0.88    0.16

s(Julian):SiteByLocationAngelo_Treetop    2.30e+01 2.10e+00    0.88    0.13

s(Julian):SiteByLocationArmstrong_Ground  2.30e+01 5.84e+00    0.88    0.16

s(Julian):SiteByLocationArmstrong_Treetop 2.30e+01 3.66e-05    0.88    0.15

s(Julian):SiteByLocationCaspar_Ground     2.30e+01 1.53e+00    0.88    0.16

s(Julian):SiteByLocationCaspar_Treetop    2.30e+01 1.18e-11    0.88    0.14

s(Julian):SiteByLocationLyme_Ground       2.30e+01 1.98e+00    0.88    0.14

s(Julian):SiteByLocationLyme_Treetop      2.30e+01 2.33e+00    0.88    0.17

s(Julian):SiteByLocationMalloPass_Ground  2.30e+01 1.87e+00    0.88    0.10

s(Julian):SiteByLocationMalloPass_Treetop 2.30e+01 1.89e+00    0.88    0.12

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

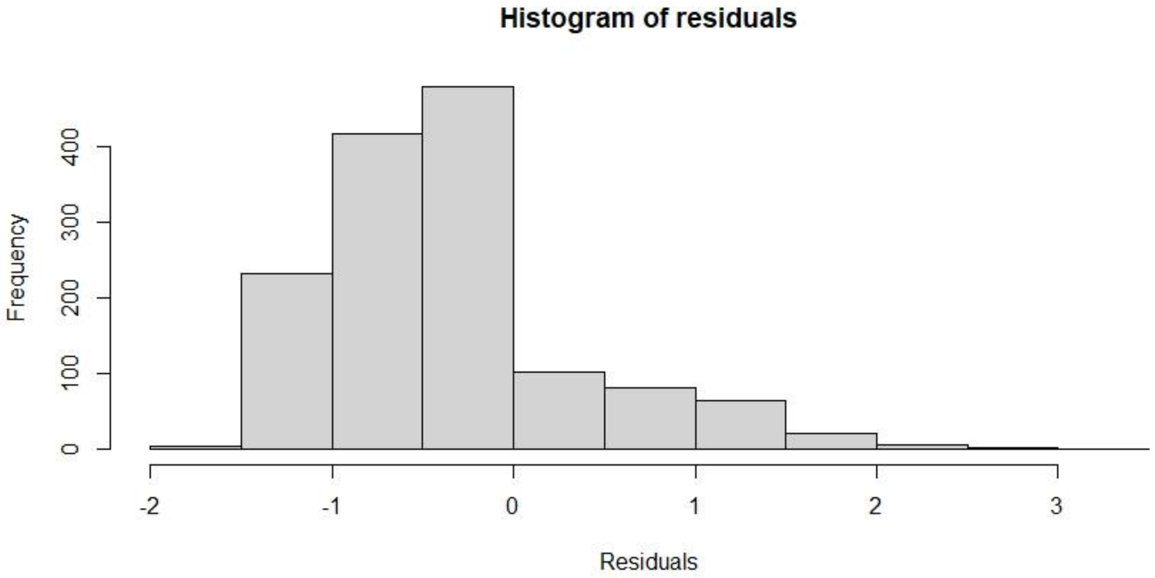
Corynorhinus townsendii (Coto)

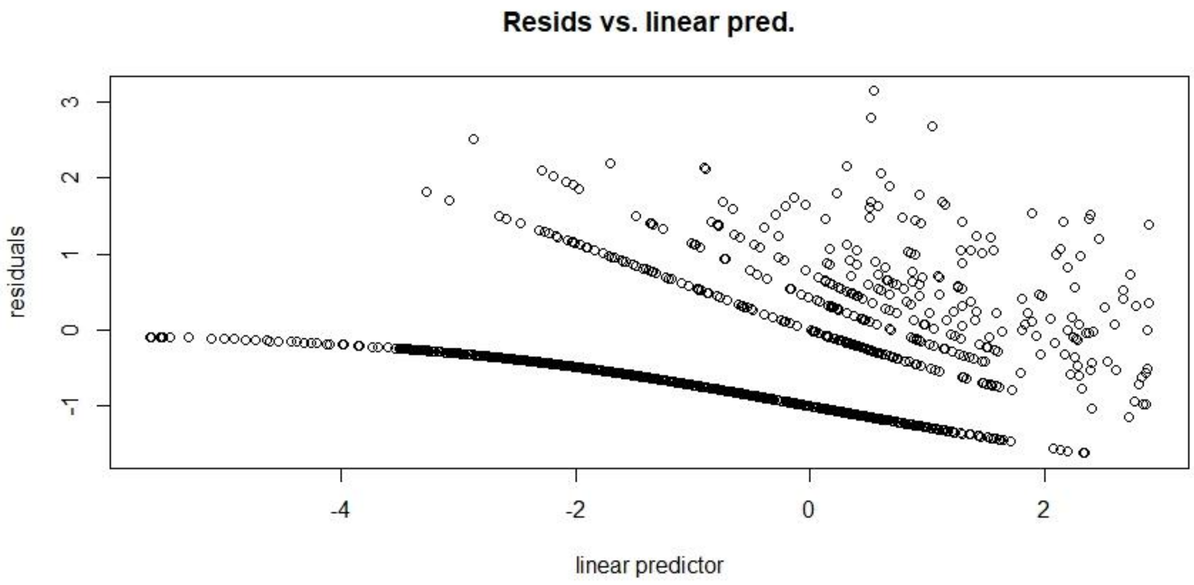
```
> gam.check(fit.25.cc.Coto)

Method: REML   Optimizer: outer newton
step failed after 29 iterations.
Gradient range [-0.0005148279,0.00189028]
(score 127.5232 & scale 1).
Hessian positive definite, eigenvalue range [5.151424e-12,1.927648].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                              k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     2.30e+01 3.34e-05    0.91   0.065 .
s(Julian):SiteByLocationAngelo_Treetop    2.30e+01 2.57e+00    0.91   0.075 .
s(Julian):SiteByLocationArmstrong_Ground  2.30e+01 2.56e+00    0.91   0.090 .
s(Julian):SiteByLocationArmstrong_Treetop 2.30e+01 1.71e+00    0.91   0.100 .
s(Julian):SiteByLocationCaspar_Ground     2.30e+01 1.03e-11    0.91   0.070 .
s(Julian):SiteByLocationCaspar_Treetop    2.30e+01 1.75e+00    0.91   0.065 .
s(Julian):SiteByLocationLyme_Ground       2.30e+01 4.09e+00    0.91   0.060 .
s(Julian):SiteByLocationLyme_Treetop      2.30e+01 1.59e+00    0.91   0.080 .
s(Julian):SiteByLocationMalloPass_Ground  2.30e+01 2.29e+00    0.91   0.105
s(Julian):SiteByLocationMalloPass_Treetop 2.30e+01 7.43e-01    0.91   0.045 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

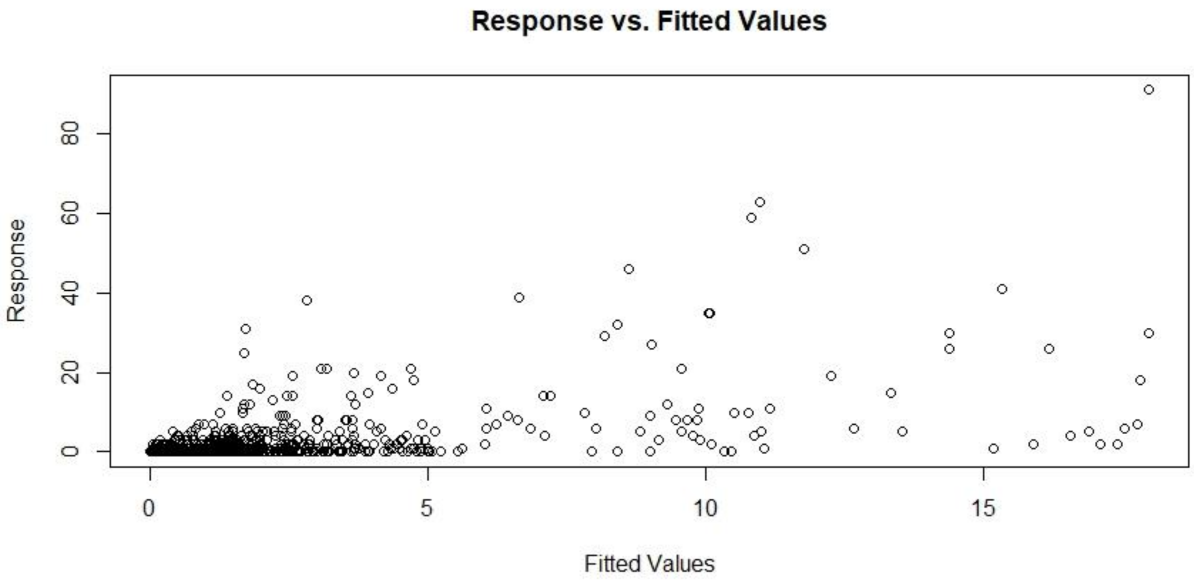
Eptesicus fuscus (Epfu)

```
> gam.check(fit.25.cc.Epfu)


Method: REML   Optimizer: outer newton
full convergence after 5 iterations.
Gradient range [-1.281372e-08,1.360445e-11]
(score 1659.358 & scale 1).
Hessian positive definite, eigenvalue range [0.698204,143.3231].
Model rank =  240 / 240


Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.


                                          k'   edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00  4.37    0.68  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    23.00  2.06    0.68  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  23.00  5.51    0.68  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 23.00  2.79    0.68  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     23.00  5.49    0.68  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    23.00  3.88    0.68  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       23.00  4.72    0.68  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      23.00  5.69    0.68  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  23.00  3.83    0.68  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 23.00  5.13    0.68  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
3
2
1
0
-1
-1
0
1
2
3
theoretical quantiles

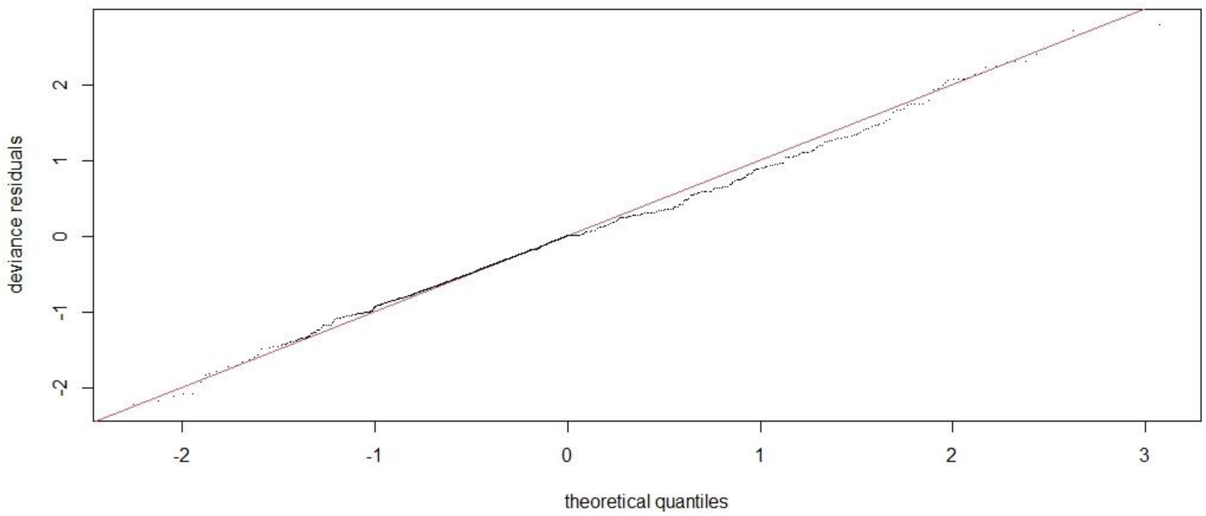

Histogram of residuals
Frequency
400
300
200
100
0
-2
-1
0
1
2
3
Residuals

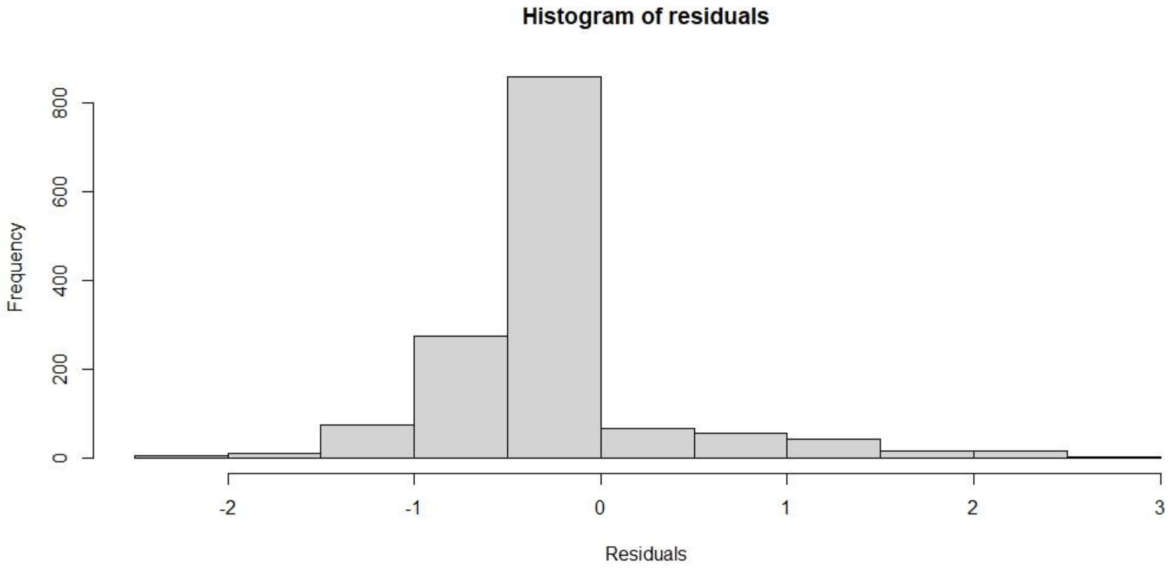

Resids vs. linear pred.
residuals
3
2
1
0
-1
-4
-2
0
2
linear predictor


Response vs. Fitted Values
Response
80
60
40
20
0
0
5
10
15
Fitted Values

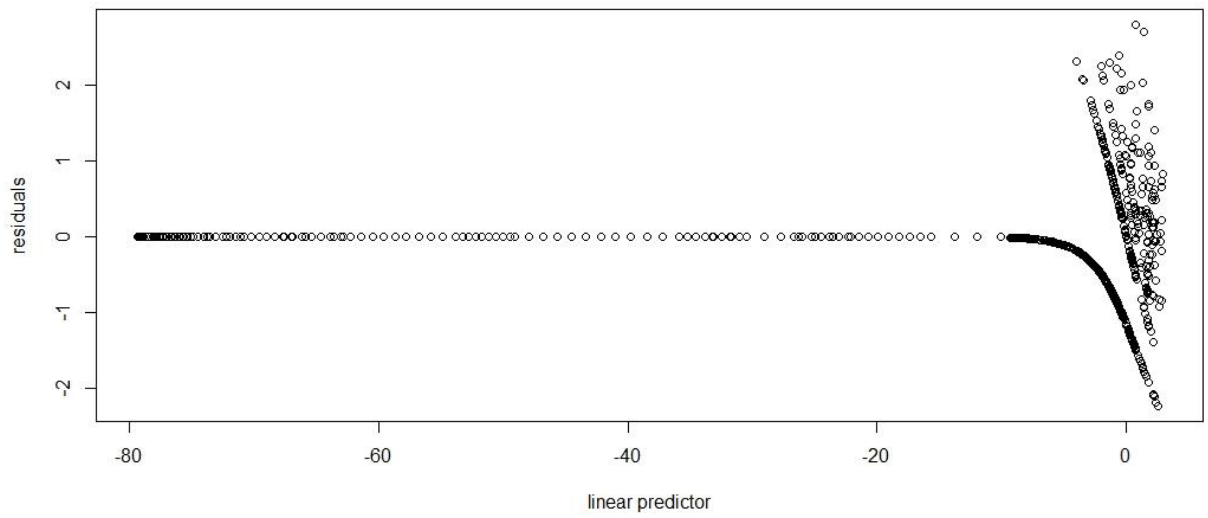
Lasiurus blossevillii (Labl)

```
> gam.check(fit.25.cc.Labl)

Method: REML   Optimizer: outer newton
full convergence after 10 iterations.
Gradient range [-0.00022622,1.397688e-09]
(score 968.5594 & scale 1).
Hessian positive definite, eigenvalue range [0.0002156066,54.89457].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                          k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     2.30e+01 8.87e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    2.30e+01 1.06e+01    0.82  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  2.30e+01 4.87e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 2.30e+01 4.19e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     2.30e+01 1.83e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    2.30e+01 9.54e-04    0.82   0.010 **
s(Julian):SiteByLocationLyme_Ground       2.30e+01 1.07e-03    0.82  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      2.30e+01 5.26e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  2.30e+01 4.42e+00    0.82  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 2.30e+01 6.02e+00    0.82   0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

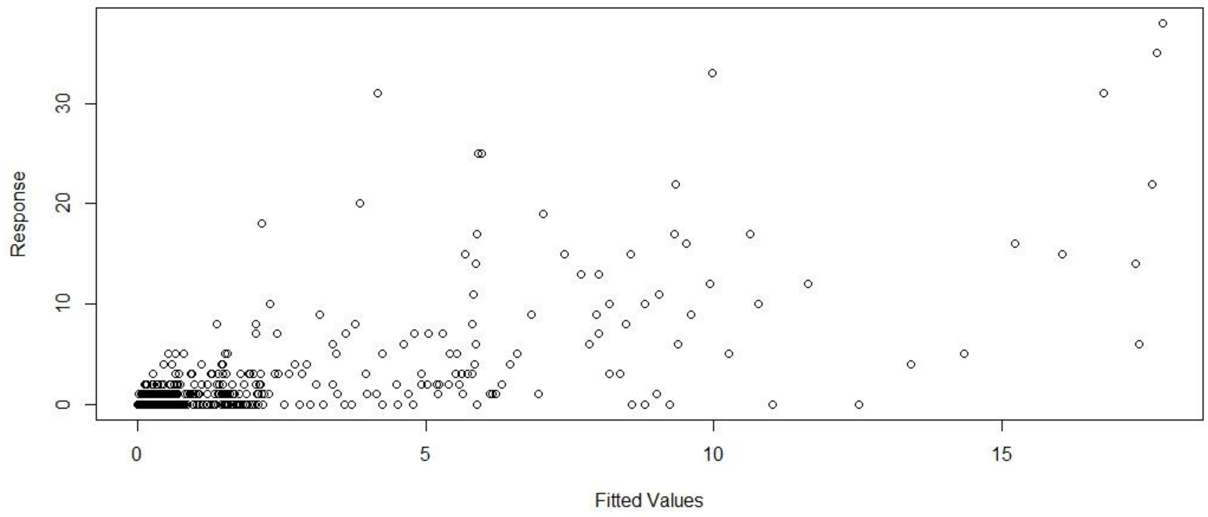

deviance residuals
2
1
0
-1
-2
-2
-1
0
1
2
3
theoretical quantiles


Histogram of residuals
Frequency
800
600
400
200
0
-2
-1
0
1
2
3
Residuals

Resids vs. linear pred.

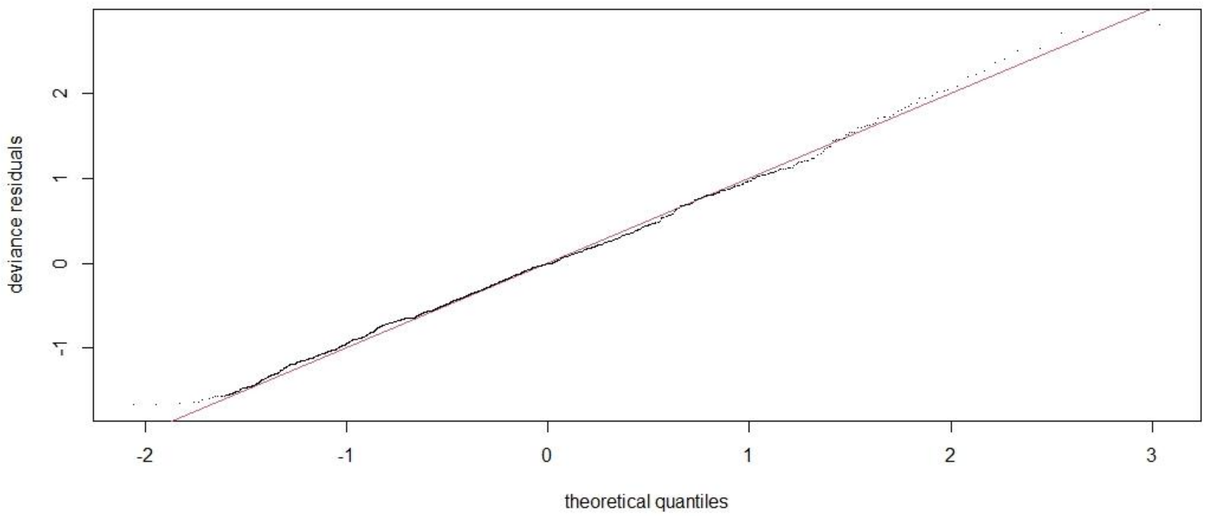


Response vs. Fitted Values

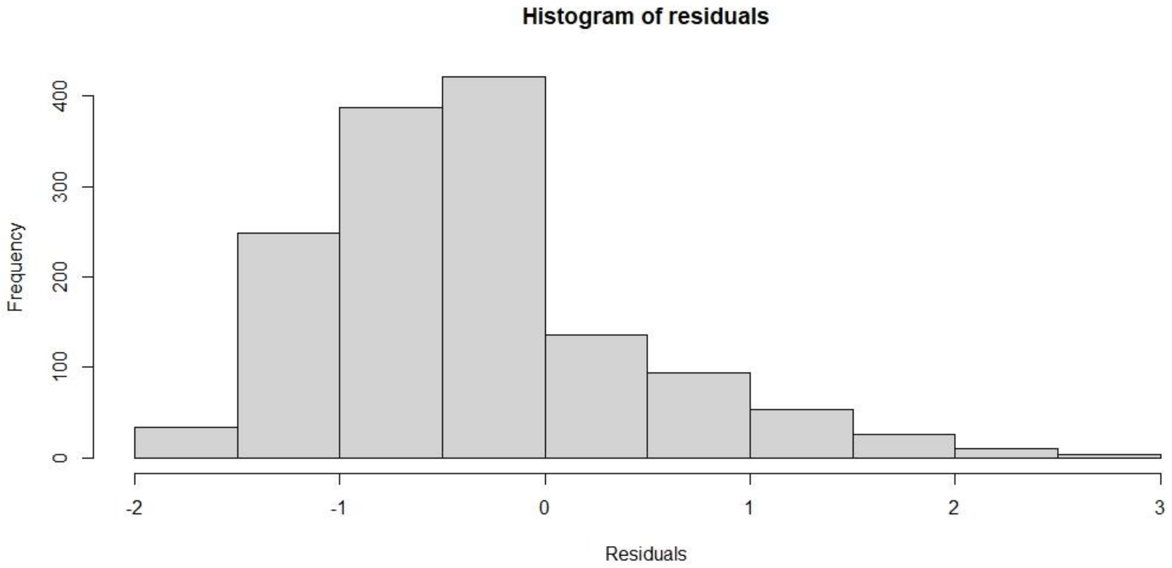


Lasiurus cinereus (Laci)

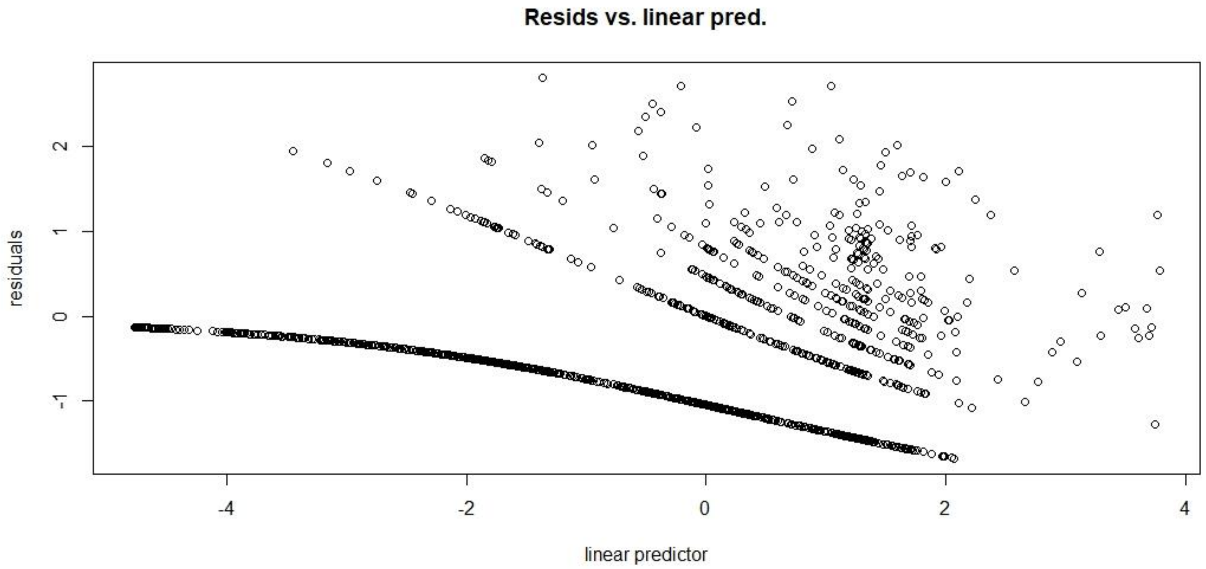
```
> gam.check(fit.25.cc.Laci)


Method: REML   Optimizer: outer newton
full convergence after 6 iterations.
Gradient range [-0.0003993598,8.1899e-10]
(score 1987.527 & scale 1).
Hessian positive definite, eigenvalue range [0.03095558,186.8653].
Model rank =  240 / 240


Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.


                                     k'    edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.000  2.214    0.64  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    23.000 11.562    0.64  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  23.000  1.177    0.64  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 23.000  0.471    0.64  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     23.000  5.593    0.64  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    23.000  5.139    0.64  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       23.000  2.145    0.64  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      23.000  6.858    0.64  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  23.000  2.837    0.64  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 23.000  5.843    0.64  <2e-16
***Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

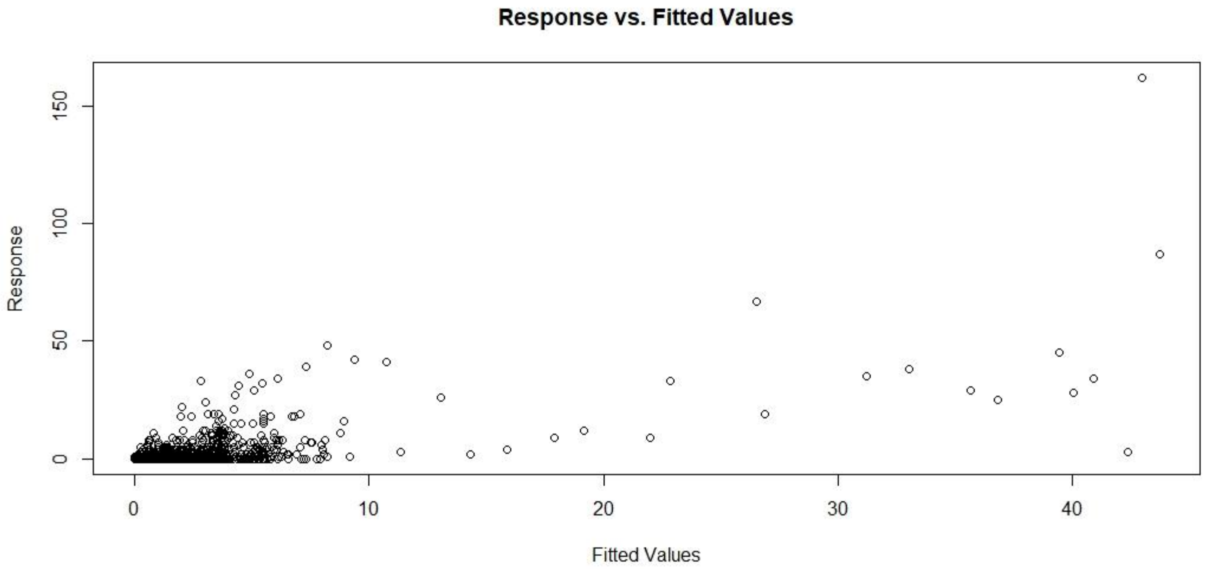


deviance residuals
2
1
0
-1
-2
-1
0
1
2
3
theoretical quantiles



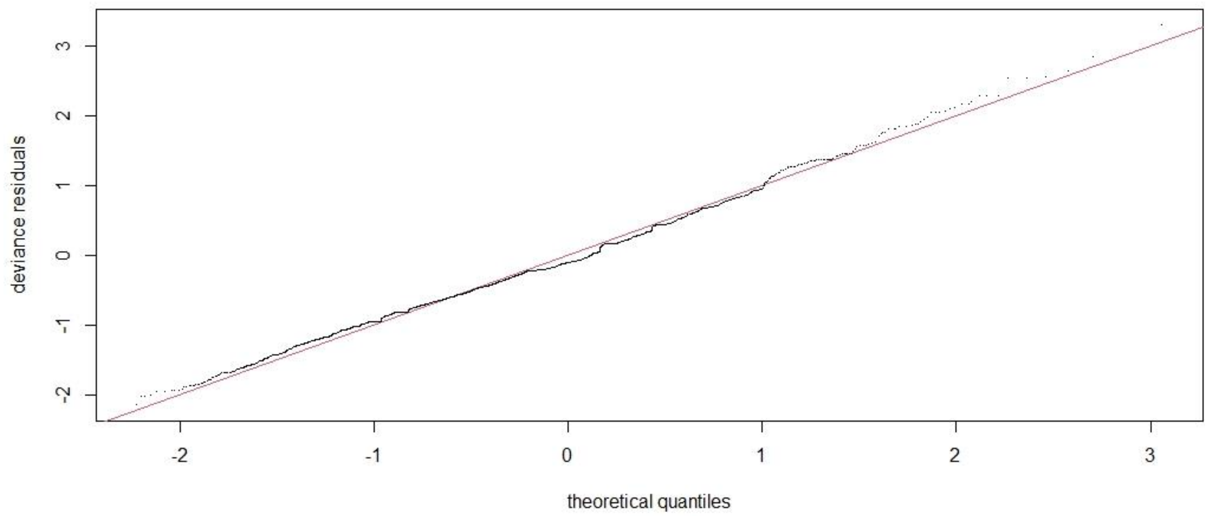
Histogram of residuals
Frequency
400
300
200
100
0
-2
-1
0
1
2
3
Residuals

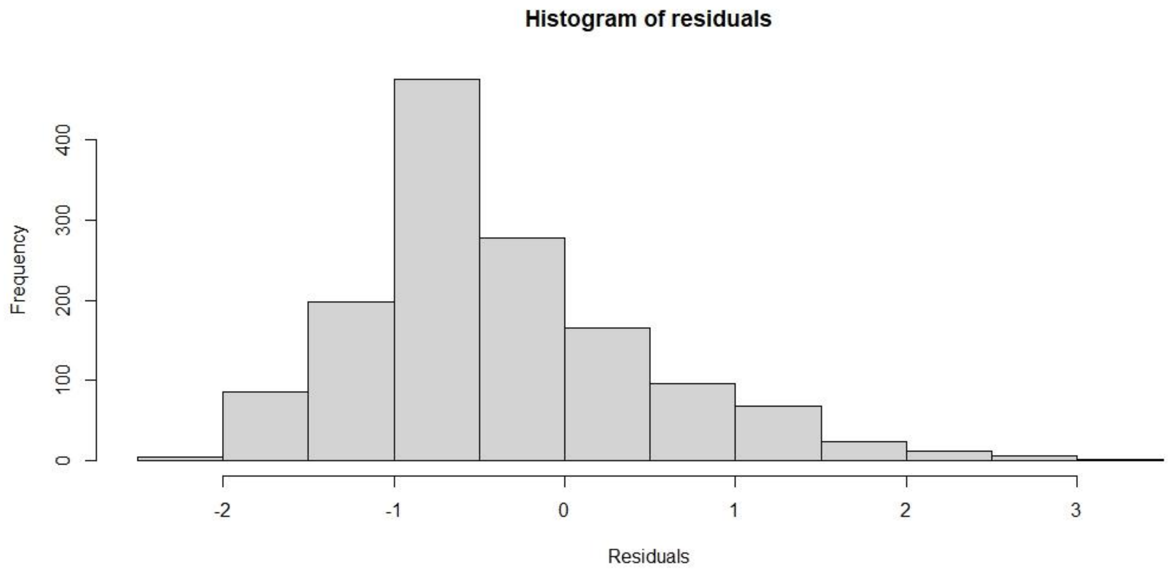

Resids vs. linear pred.

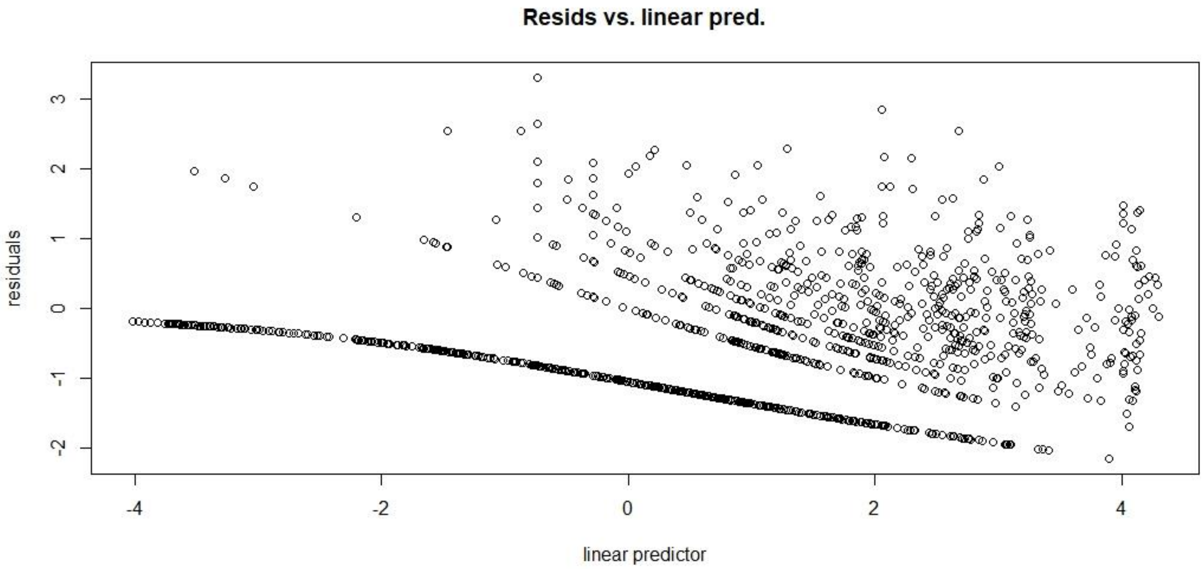

Response vs. Fitted Values

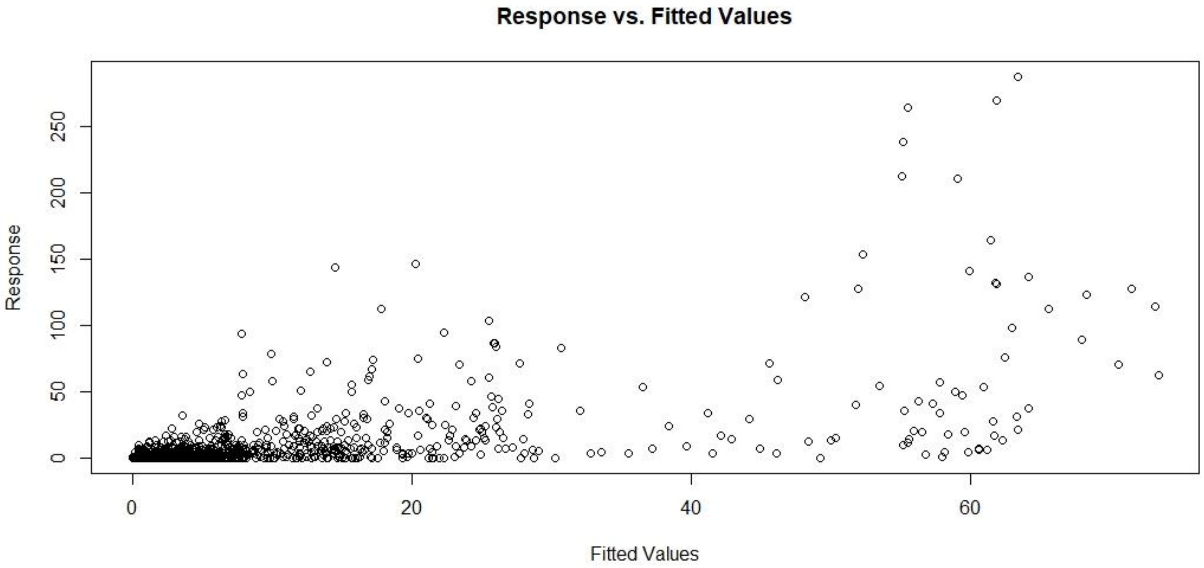
Lasionycteris noctivagans (Lano)

```
> gam.check(fit.25.cc.Lano)

Method: REML   Optimizer: outer newton
full convergence after 9 iterations.
Gradient range [-0.001103668,0.000385779]
(score 3076.425 & scale 1).
Hessian positive definite, eigenvalue range [0.0001486743,299.3374].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                       k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     2.30e+01 6.20e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    2.30e+01 1.09e+01    0.57  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  2.30e+01 5.53e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 2.30e+01 2.21e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     2.30e+01 2.98e-03    0.57  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    2.30e+01 4.97e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       2.30e+01 6.99e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      2.30e+01 8.06e+00    0.57  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  2.30e+01 5.36e-04    0.57  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 2.30e+01 4.78e+00    0.57  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
3
2
1
0
-1
-2
-2
-1
0
1
2
3
theoretical quantiles

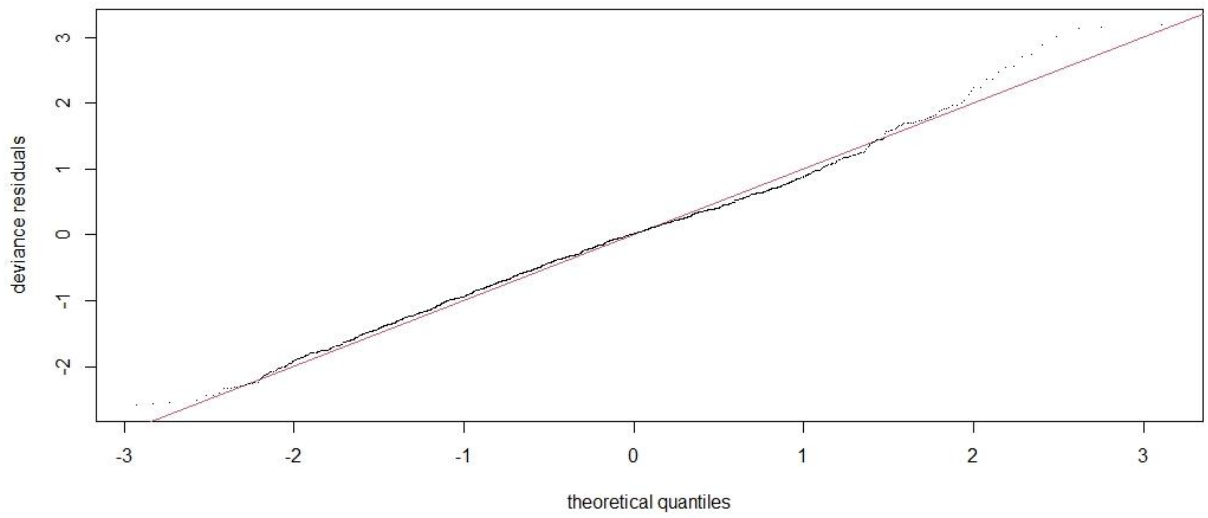

Histogram of residuals
Frequency
400
300
200
100
0
-2
-1
0
1
2
3
Residuals

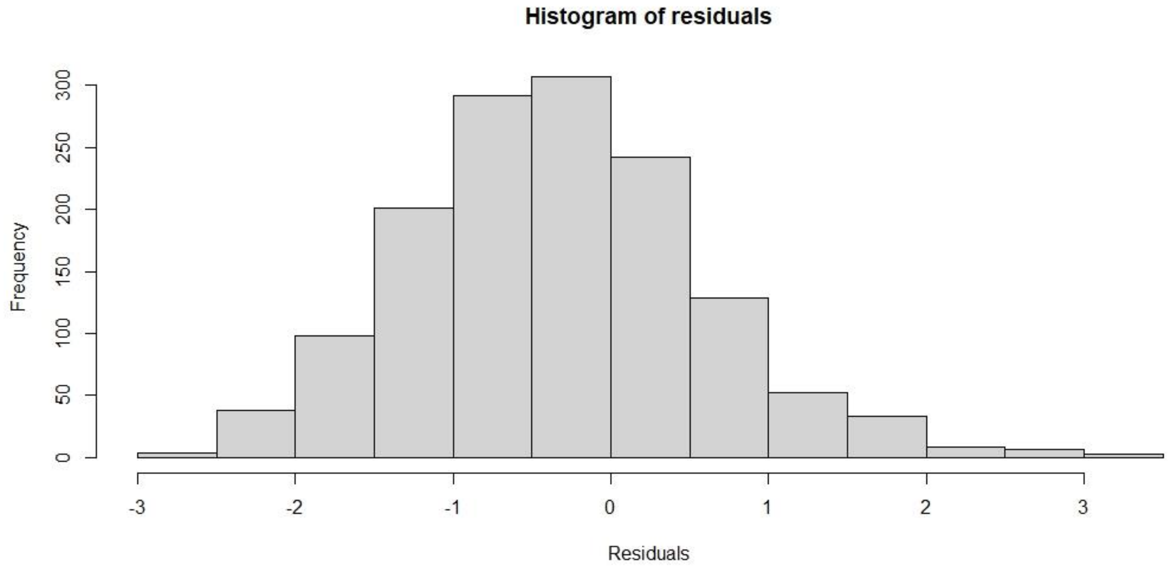

Resids vs. linear pred.
residuals
3
2
1
0
-1
-2
-4
-2
0
2
4
linear predictor

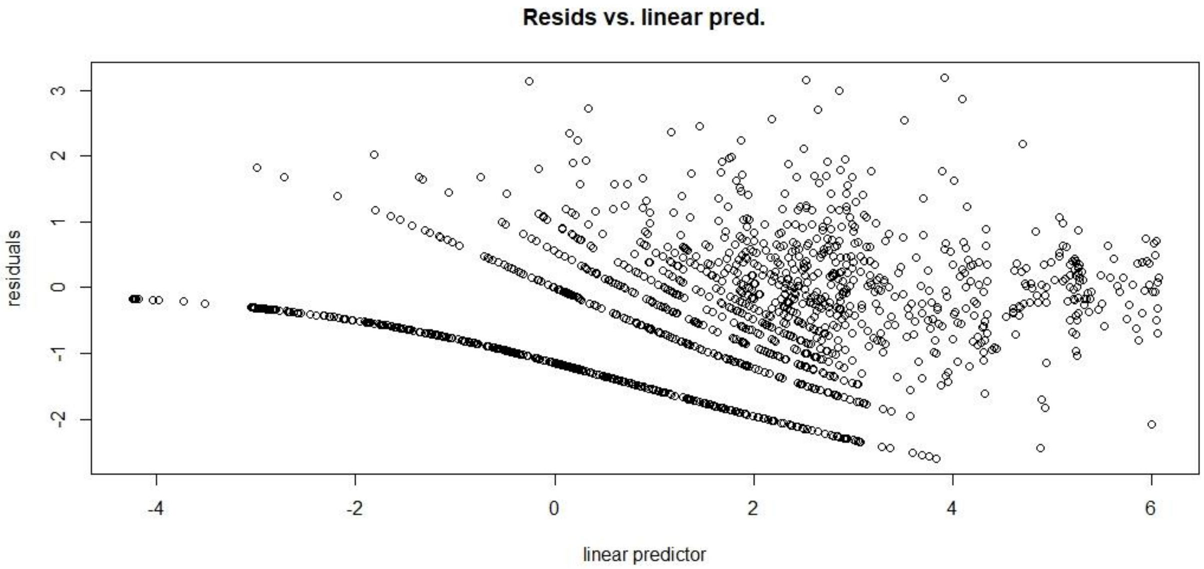

Response vs. Fitted Values
Response
250
200
150
100
50
0
0
20
40
60
Fitted Values

Myotis californicus (Myca)

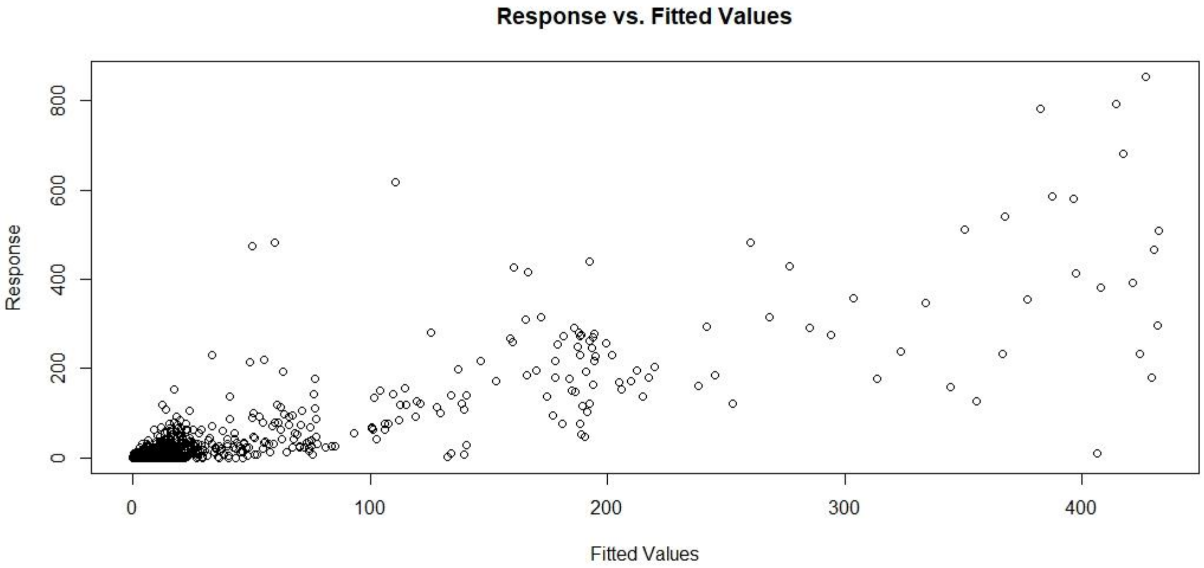
```
> gam.check(fit.25.cc.Myca)

Method: REML   Optimizer: outer newton
full convergence after 4 iterations.
Gradient range [-2.891326e-07,8.657498e-07]
(score 4364.364 & scale 1).
Hessian positive definite, eigenvalue range [1.210011,393.8608].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                       k'   edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00  6.45    0.74  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    23.00  6.89    0.74  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  23.00  9.54    0.74  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 23.00  6.45    0.74  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     23.00 12.70    0.74  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    23.00 12.64    0.74  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       23.00  7.29    0.74  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      23.00 15.01    0.74  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  23.00  5.61    0.74  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 23.00 11.82    0.74  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
-2
-1
0
1
2
3
theoretical quantiles
-3
-2
-1
0
1
2
3


Histogram of residuals
Frequency
0
50
100
150
200
250
300
Residuals
-3
-2
-1
0
1
2
3



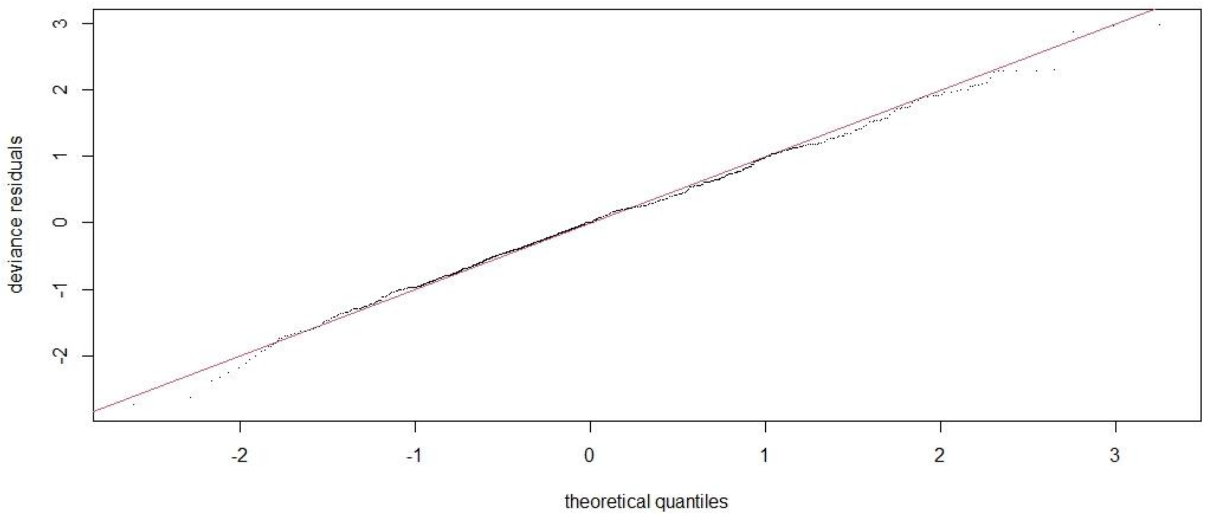
Resids vs. linear pred.

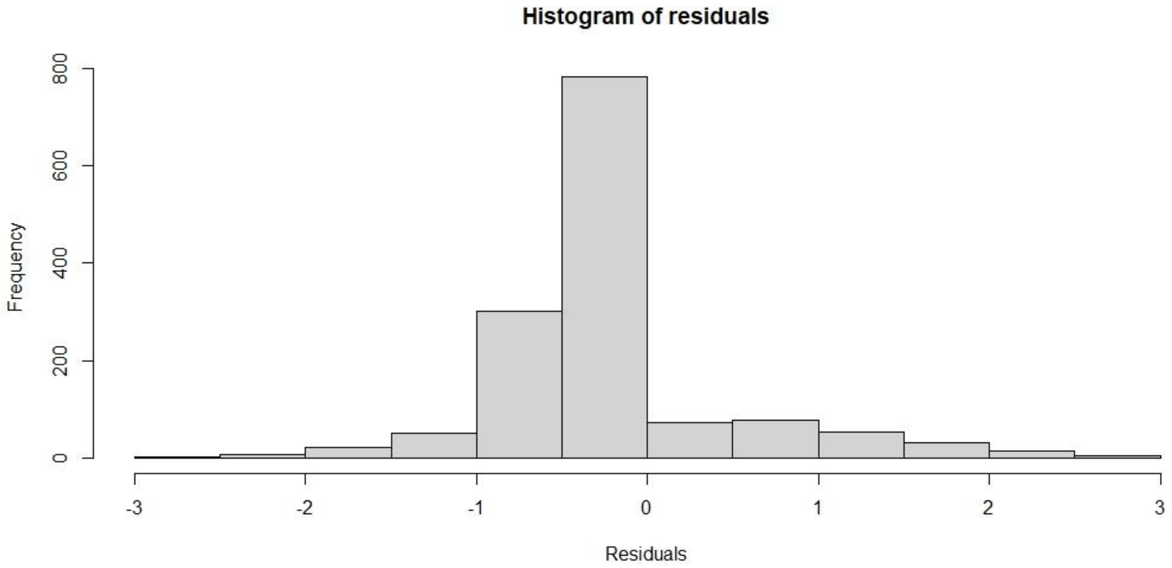


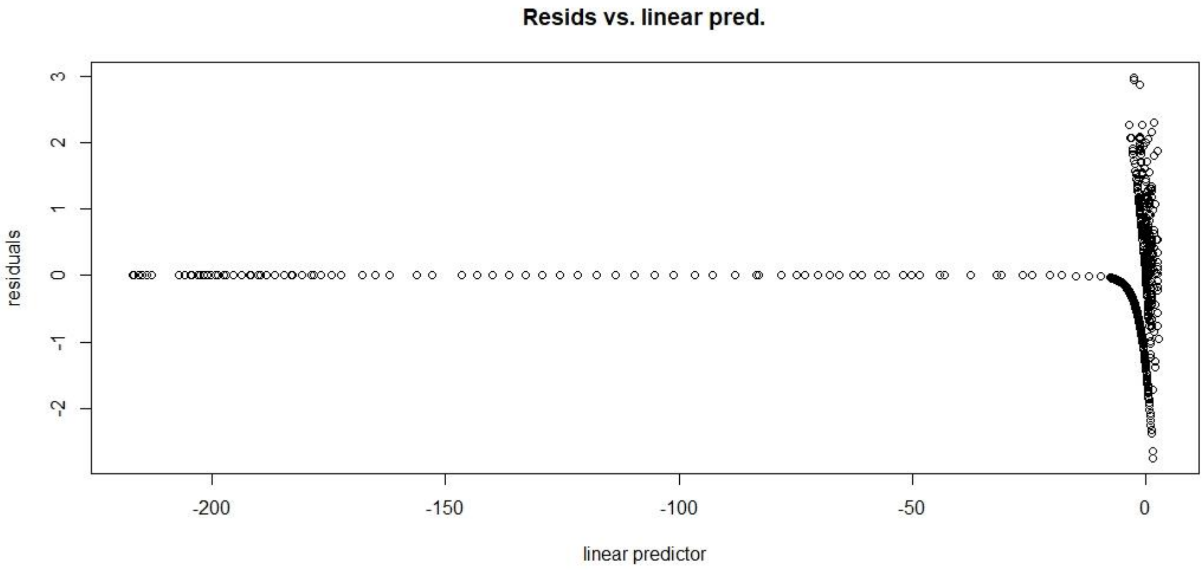
Response vs. Fitted Values

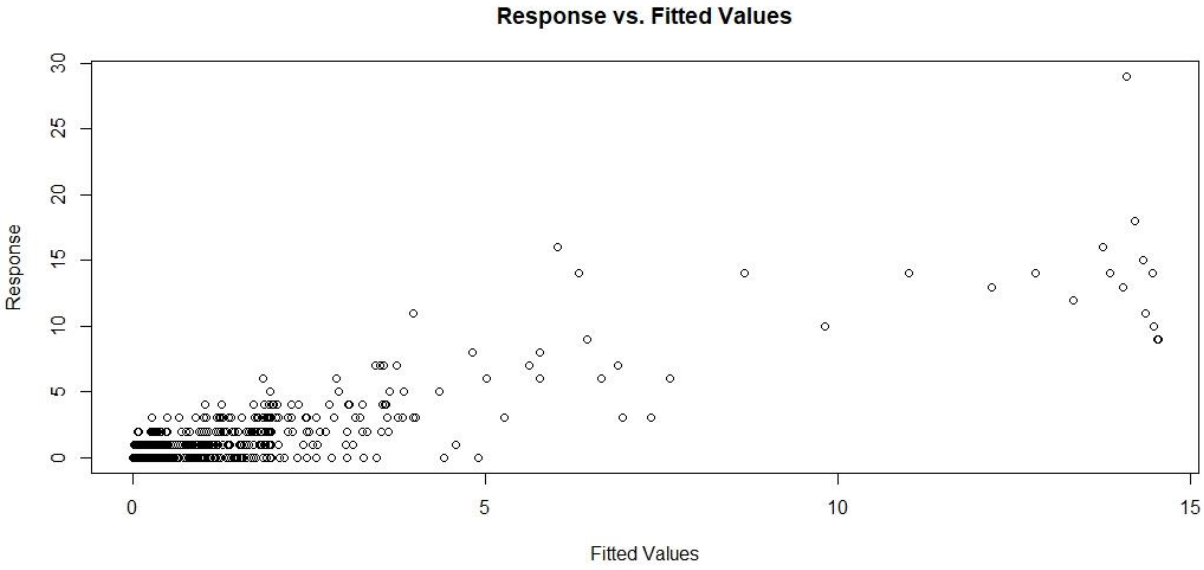
Myotis evotis (Myev)

```
> gam.check(fit.25.cc.Myev)

Method: REML   Optimizer: outer newton
full convergence after 8 iterations.
Gradient range [-0.0004735501,5.12133e-10]
(score 923.2934 & scale 1).
Hessian positive definite, eigenvalue range [0.0004739931,7.014055].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                       k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00000  9.86168    0.92    0.49
s(Julian):SiteByLocationAngelo_Treetop    23.00000  3.00170    0.92    0.48
s(Julian):SiteByLocationArmstrong_Ground  23.00000  9.98341    0.92    0.47
s(Julian):SiteByLocationArmstrong_Treetop 23.00000  1.51675    0.92    0.47
s(Julian):SiteByLocationCaspar_Ground     23.00000  0.00261    0.92    0.43
s(Julian):SiteByLocationCaspar_Treetop    23.00000  1.59215    0.92    0.42
s(Julian):SiteByLocationLyme_Ground       23.00000  9.20088    0.92    0.49
s(Julian):SiteByLocationLyme_Treetop      23.00000  4.89058    0.92    0.42
s(Julian):SiteByLocationMalloPass_Ground  23.00000  1.85088    0.92    0.48
s(Julian):SiteByLocationMalloPass_Treetop 23.00000  2.35930    0.92    0.47

---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
3
2
1
0
-1
-2
-2
-1
0
1
2
3
theoretical quantiles

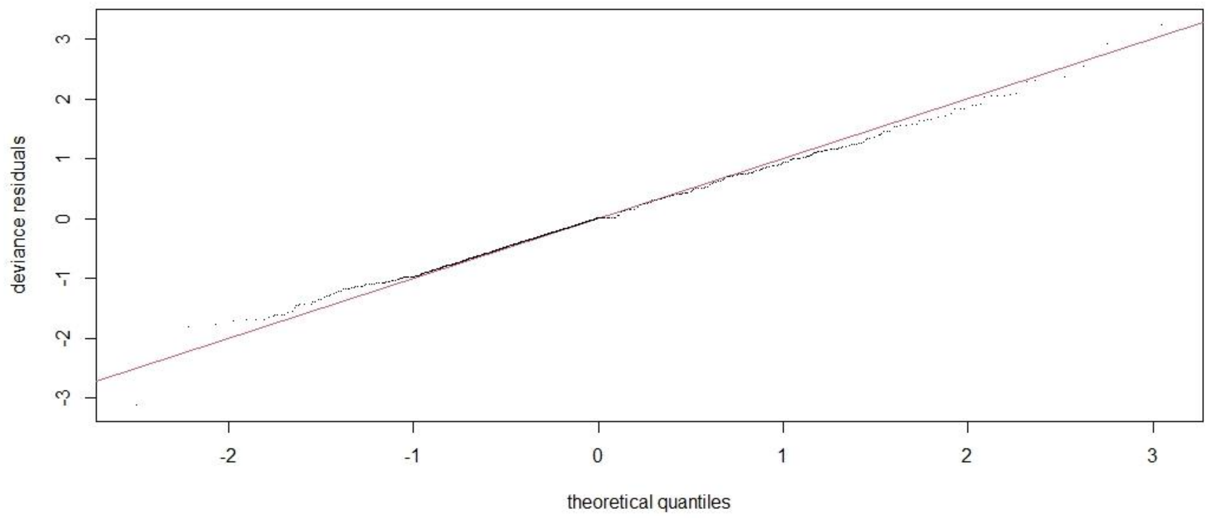

Histogram of residuals
Frequency
800
600
400
200
0
-3
-2
-1
0
1
2
3
Residuals

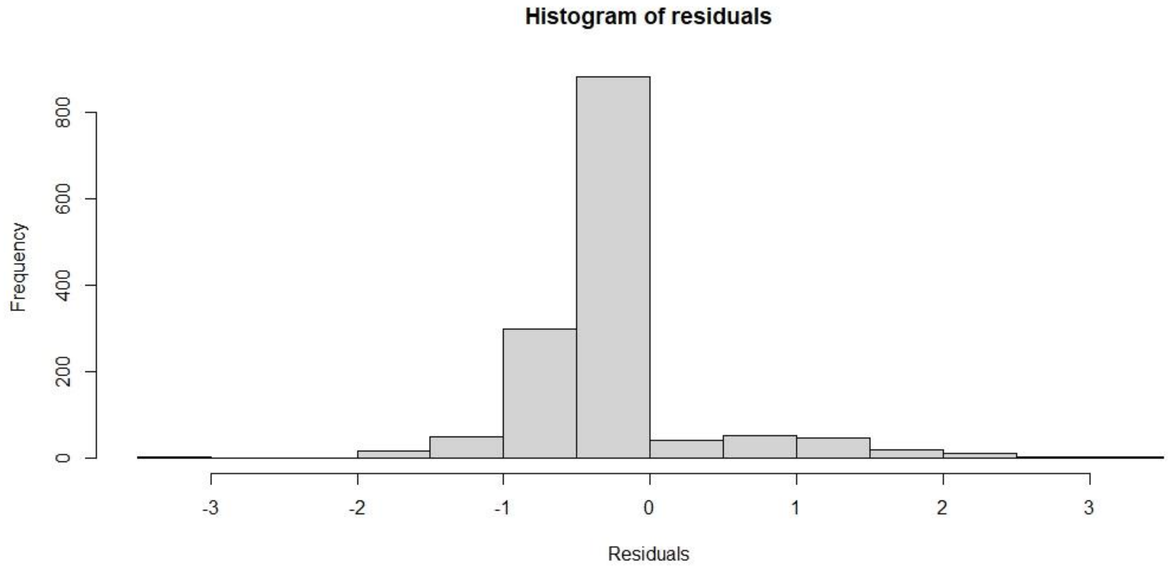

Resids vs. linear pred.
residuals
3
2
1
0
-1
-2
-200
-150
-100
-50
0
linear predictor

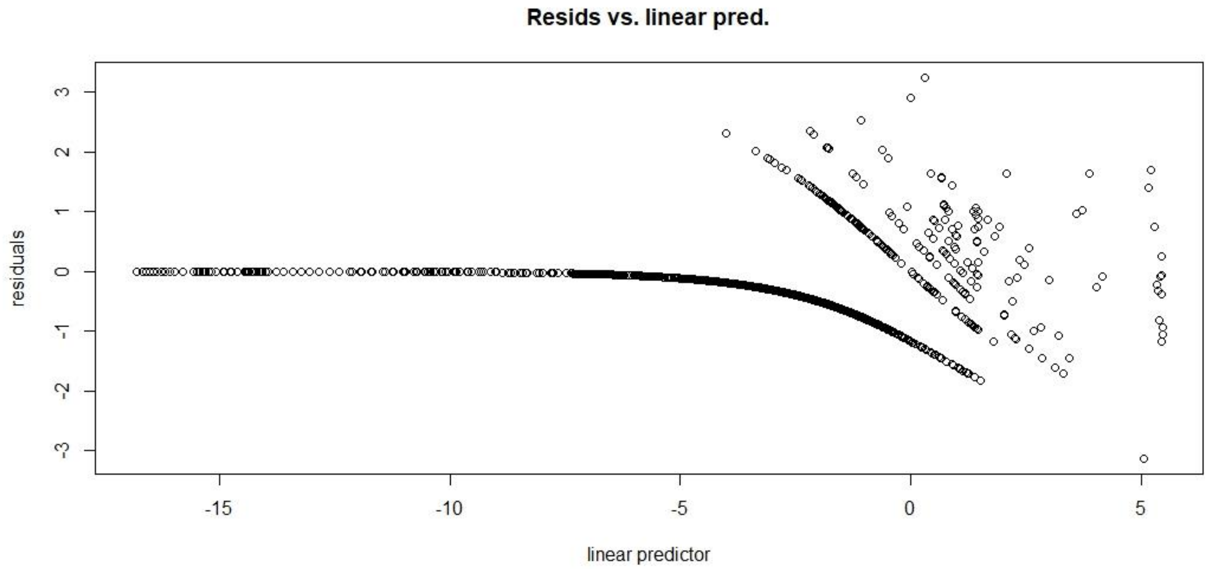

Response vs. Fitted Values
Response
30
25
20
15
10
5
0
0
5
10
15
Fitted Values

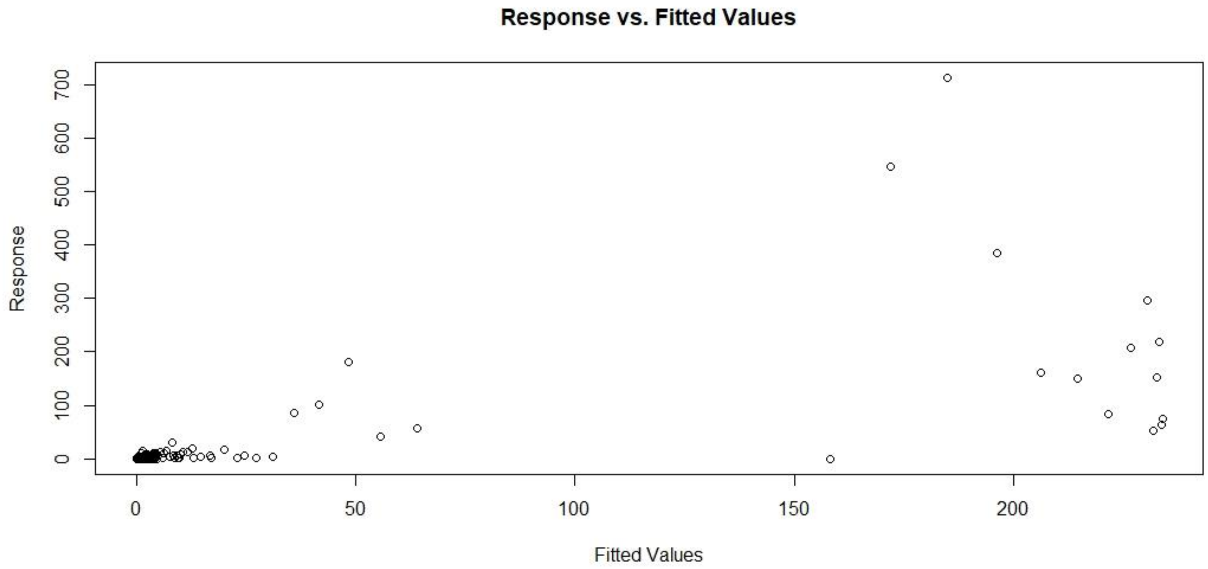
Myotis lucifugus (Mylu)

```
> gam.check(fit.25.cc.Mylu)

Method: REML   Optimizer: outer newton
full convergence after 4 iterations.
Gradient range [-6.192254e-09,0.0001566008]
(score 903.7667 & scale 1).
Hessian positive definite, eigenvalue range [0.33782,50.28221].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                        k'   edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00  8.64    0.86    0.14
s(Julian):SiteByLocationAngelo_Treetop    23.00  5.05    0.86    0.14
s(Julian):SiteByLocationArmstrong_Ground  23.00  3.88    0.86    0.15
s(Julian):SiteByLocationArmstrong_Treetop 23.00  2.49    0.86    0.16
s(Julian):SiteByLocationCaspar_Ground     23.00  2.45    0.86    0.16
s(Julian):SiteByLocationCaspar_Treetop    23.00  2.75    0.86    0.12
s(Julian):SiteByLocationLyme_Ground       23.00  2.11    0.86    0.12
s(Julian):SiteByLocationLyme_Treetop      23.00  7.28    0.86    0.13
s(Julian):SiteByLocationMalloPass_Ground  23.00  5.26    0.86    0.12
s(Julian):SiteByLocationMalloPass_Treetop 23.00  3.36    0.86    0.16
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
-3
-2
-1
0
1
2
3
-2
-1
0
1
2
3
theoretical quantiles

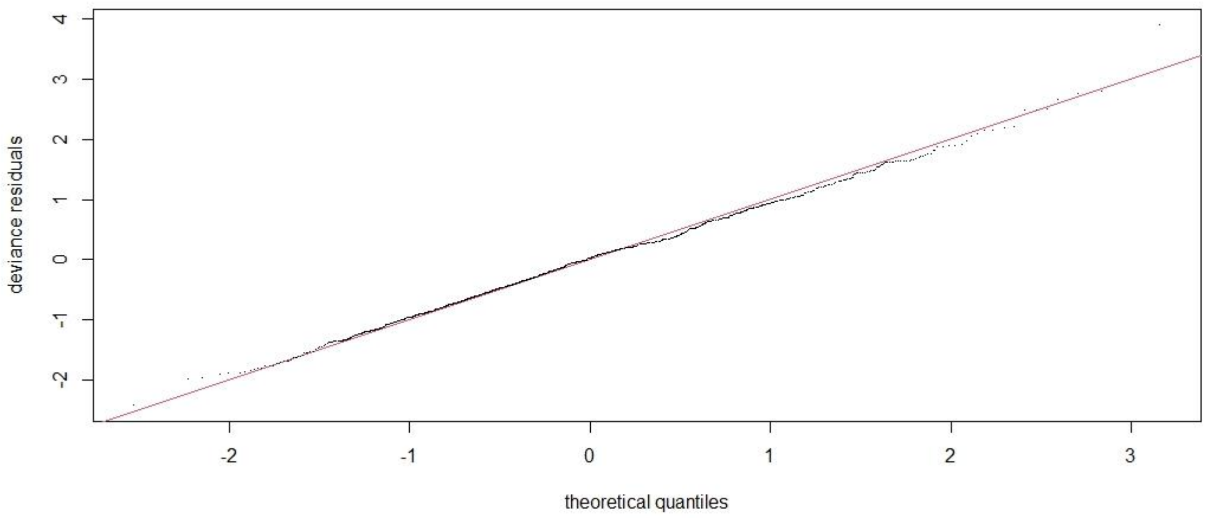

Histogram of residuals
Frequency
0
200
400
600
800
-3
-2
-1
0
1
2
3
Residuals


Resids vs. linear pred.
residuals
3
2
1
0
-1
-2
-3
-15
-10
-5
0
5
linear predictor

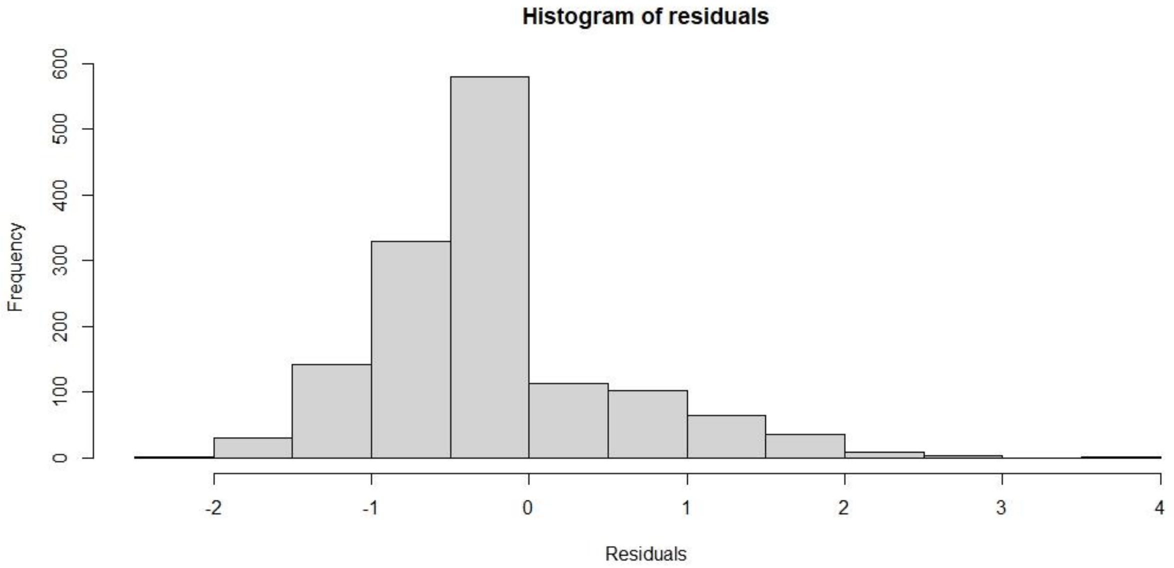

Response vs. Fitted Values
Response
700
600
500
400
300
200
100
0
0
50
100
150
200
Fitted Values

Myotis thysanodes (Myth)

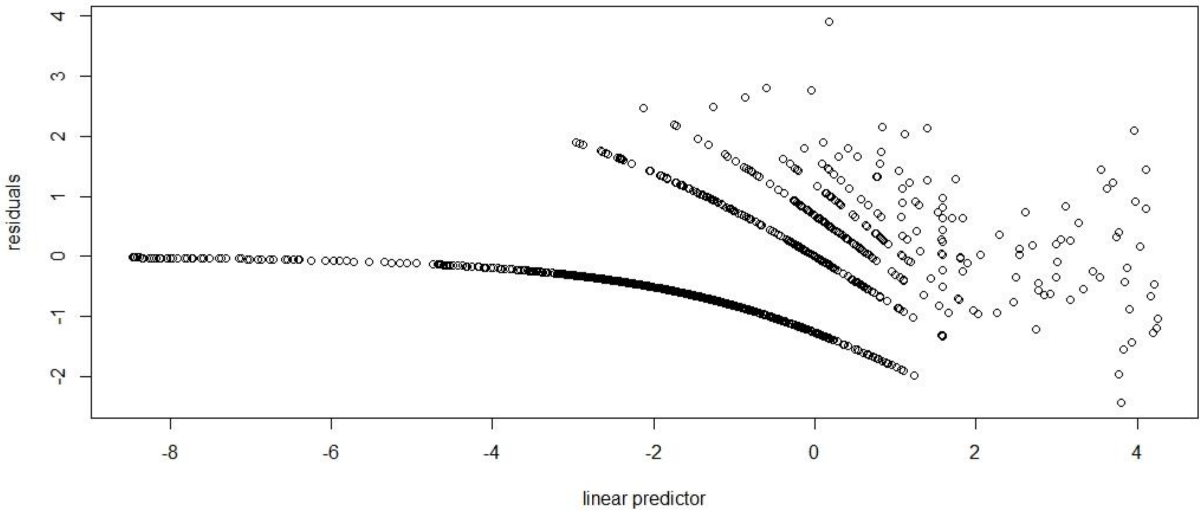
```
> gam.check(fit.25.cc.Myth)

Method: REML   Optimizer: outer newton
full convergence after 6 iterations.
Gradient range [-0.001449224,1.185958e-10]
(score 1393.265 & scale 1).
Hessian positive definite, eigenvalue range [0.004406225,52.78181].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                           k'    edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.000  8.979    0.92    0.82
s(Julian):SiteByLocationAngelo_Treetop    23.000  8.179    0.92    0.84
s(Julian):SiteByLocationArmstrong_Ground  23.000 12.024    0.92    0.86
s(Julian):SiteByLocationArmstrong_Treetop 23.000  3.715    0.92    0.85
s(Julian):SiteByLocationCaspar_Ground     23.000  2.852    0.92    0.86
s(Julian):SiteByLocationCaspar_Treetop    23.000  0.158    0.92    0.86
s(Julian):SiteByLocationLyme_Ground       23.000  4.390    0.92    0.82
s(Julian):SiteByLocationLyme_Treetop      23.000  6.921    0.92    0.84
s(Julian):SiteByLocationMalloPass_Ground  23.000  3.817    0.92    0.80
s(Julian):SiteByLocationMalloPass_Treetop 23.000  2.548    0.92    0.88
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```



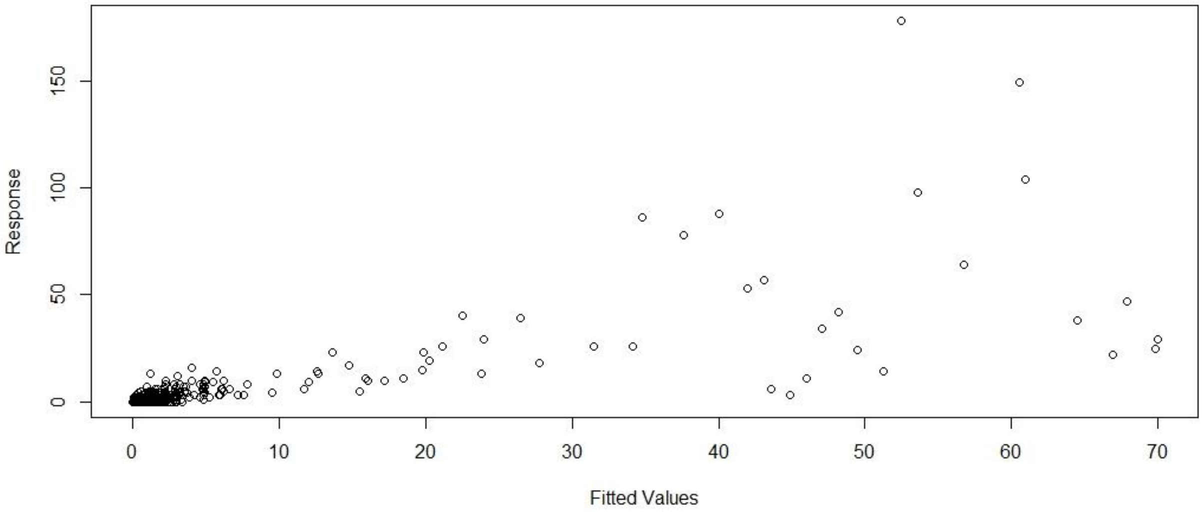
deviance residuals
4
3
2
1
0
-1
-2
-2
-1
0
1
2
3
theoretical quantiles



Histogram of residuals
Frequency
600
500
400
300
200
100
0
-2
-1
0
1
2
3
4
Residuals



Resids vs. linear pred.



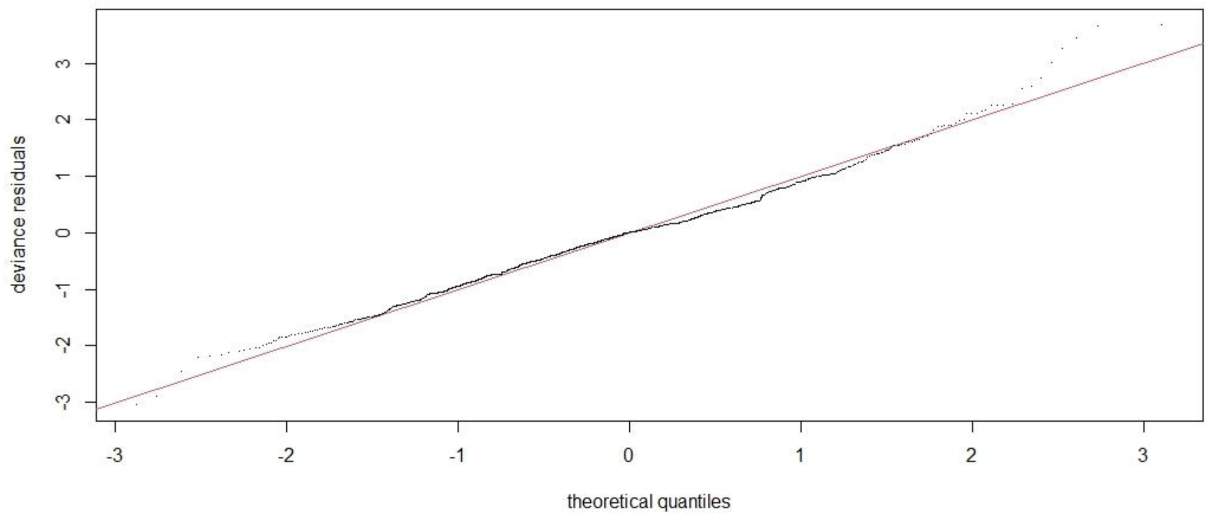
Response vs. Fitted Values

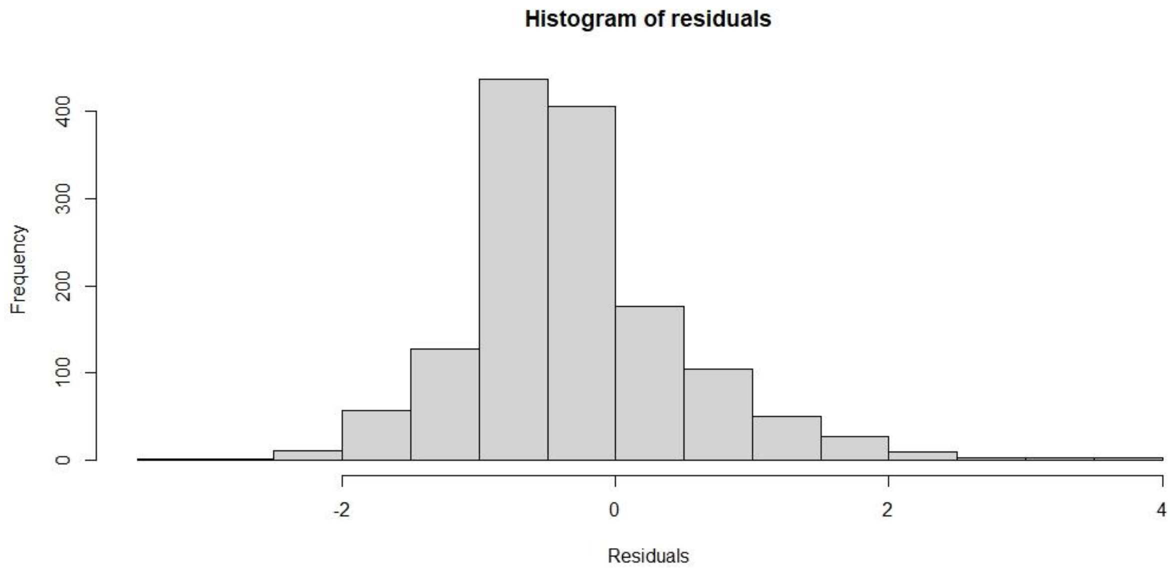
Myotis volans (Myvo)

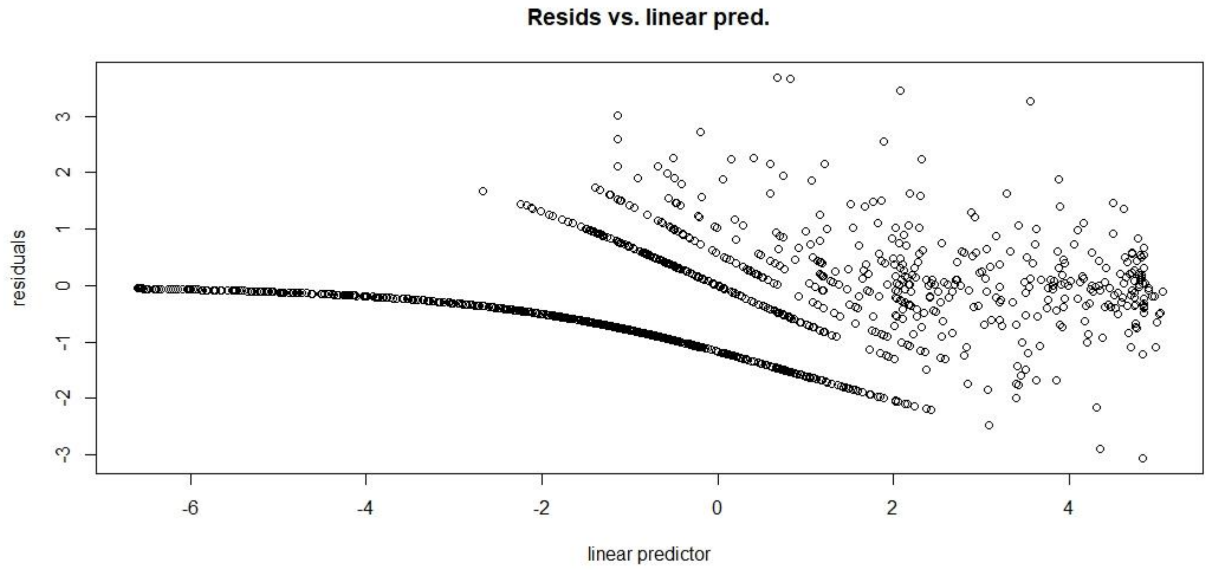
```
> gam.check(fit.25.cc.Myvo)

Method: REML   Optimizer: outer newton
step failed after 54 iterations.
Gradient range [-0.01019194,0.004415907]
(score 472.9029 & scale 1).
Hessian positive definite, eigenvalue range [5.870886e-12,15.54822].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                        k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     2.30e+01 6.39e+00    0.95    0.86
s(Julian):SiteByLocationAngelo_Treetop    2.30e+01 1.68e+00    0.95    0.85
s(Julian):SiteByLocationArmstrong_Ground  2.30e+01 3.92e+00    0.95    0.87
s(Julian):SiteByLocationArmstrong_Treetop 2.30e+01 1.53e+00    0.95    0.81
s(Julian):SiteByLocationCaspar_Ground     2.30e+01 3.82e+00    0.95    0.88
s(Julian):SiteByLocationCaspar_Treetop    2.30e+01 1.18e-11    0.95    0.88
s(Julian):SiteByLocationLyme_Ground       2.30e+01 8.09e+00    0.95    0.86
s(Julian):SiteByLocationLyme_Treetop      2.30e+01 3.66e+00    0.95    0.88
s(Julian):SiteByLocationMalloPass_Ground  2.30e+01 3.51e+00    0.95    0.86
s(Julian):SiteByLocationMalloPass_Treetop 2.30e+01 2.88e+00    0.95    0.84
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Myotis yumanensis (Myyu)

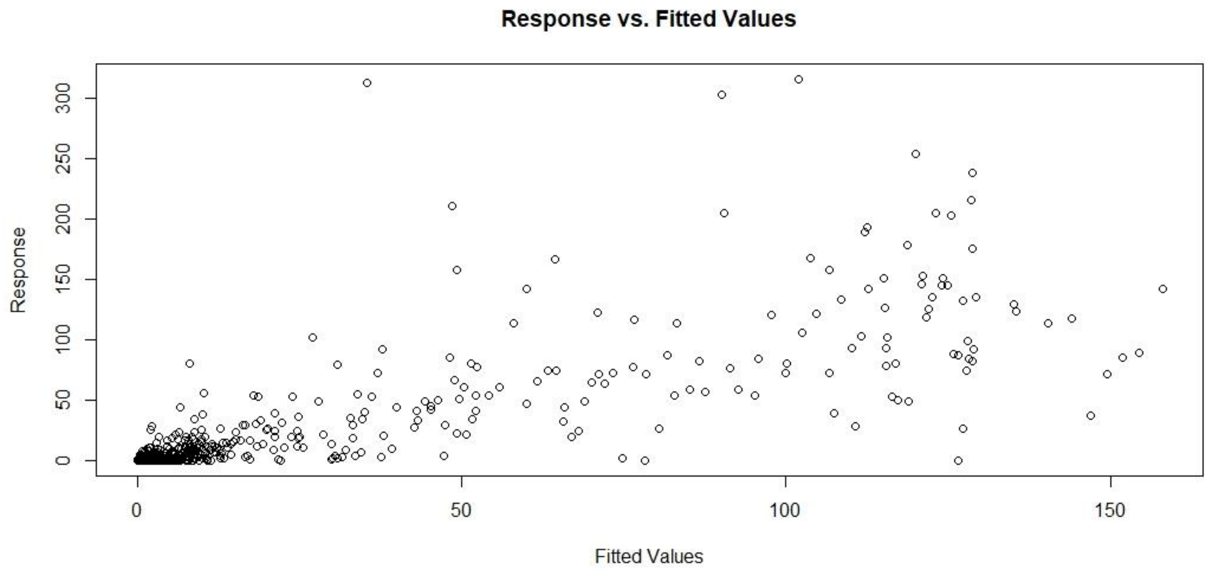
```
> gam.check(fit.25.cc.Myyu)

Method: REML   Optimizer: outer newton
full convergence after 8 iterations.
Gradient range [-0.0006639888,0.0001503166]
(score 2514.951 & scale 1).
Hessian positive definite, eigenvalue range [0.0006635186,162.6086].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                           k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00000 12.69750    0.81  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    23.00000  4.17030    0.81  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  23.00000  8.32437    0.81  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 23.00000  0.00145    0.81   0.015 *
s(Julian):SiteByLocationCaspar_Ground     23.00000  8.36079    0.81   0.015 *
s(Julian):SiteByLocationCaspar_Treetop    23.00000  7.95983    0.81  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       23.00000  7.20727    0.81   0.015 *
s(Julian):SiteByLocationLyme_Treetop      23.00000 12.52669    0.81   0.005 **
s(Julian):SiteByLocationMalloPass_Ground  23.00000  6.68464    0.81   0.005 **
s(Julian):SiteByLocationMalloPass_Treetop 23.00000 13.47678    0.81  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
-3
-2
-1
0
1
2
3
-3
-2
-1
0
1
2
3
theoretical quantiles


Histogram of residuals
Frequency
0
100
200
300
400
-2
0
2
4
Residuals



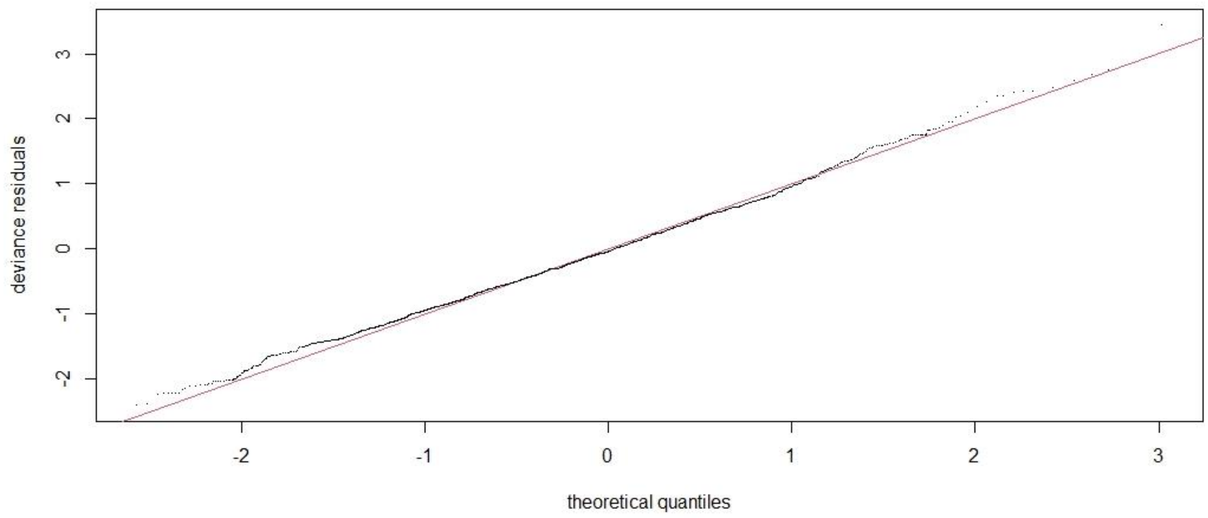
Resids vs. linear pred.

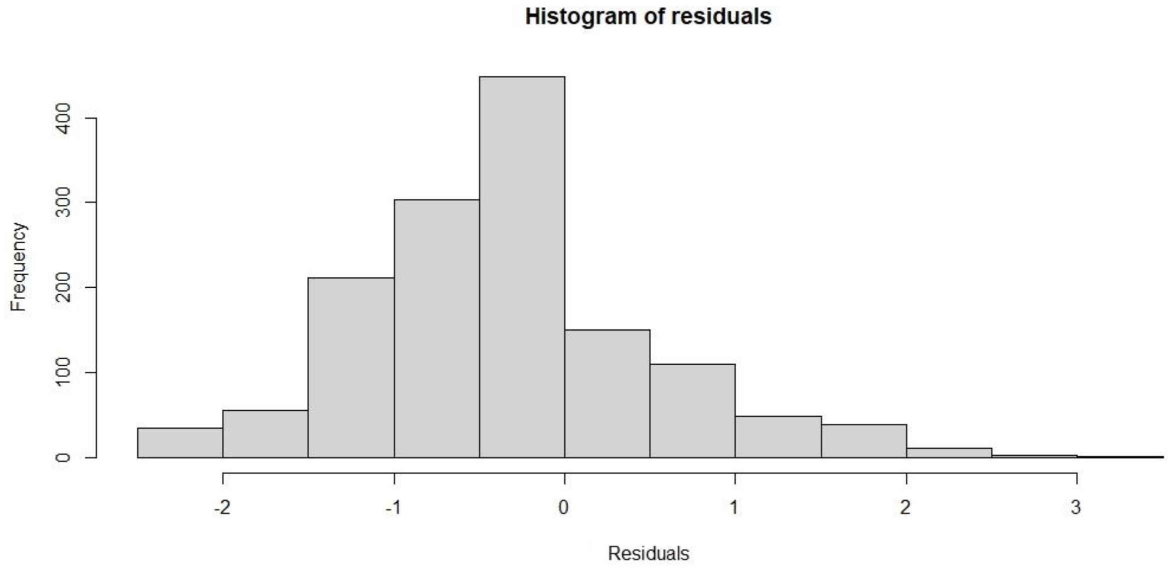


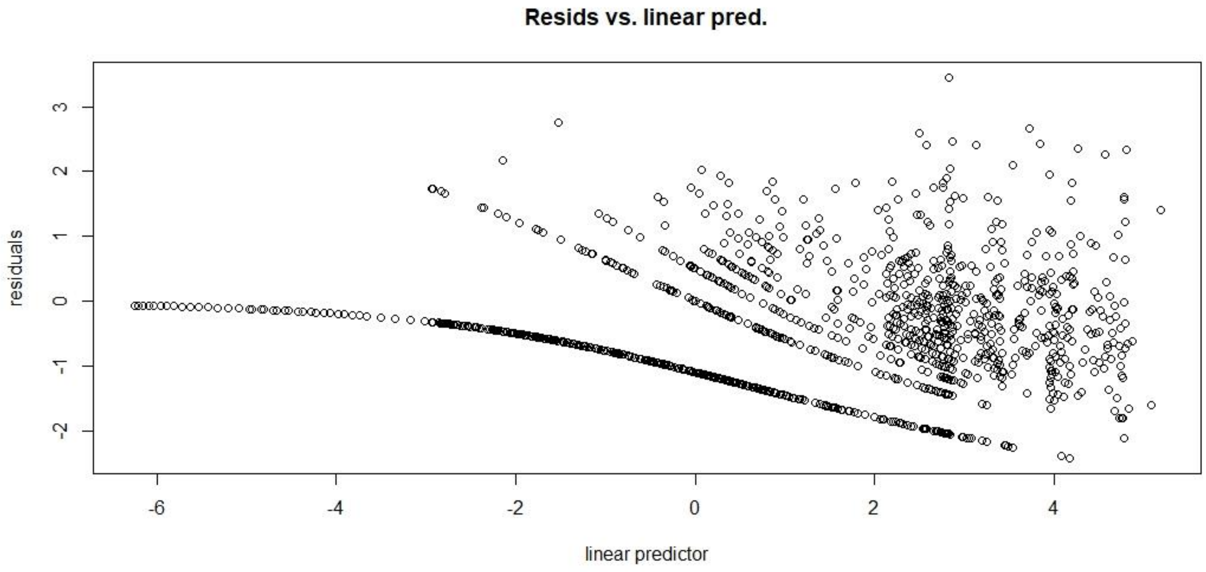
Response vs. Fitted Values

Tadarida brasiliensis (Tabr)

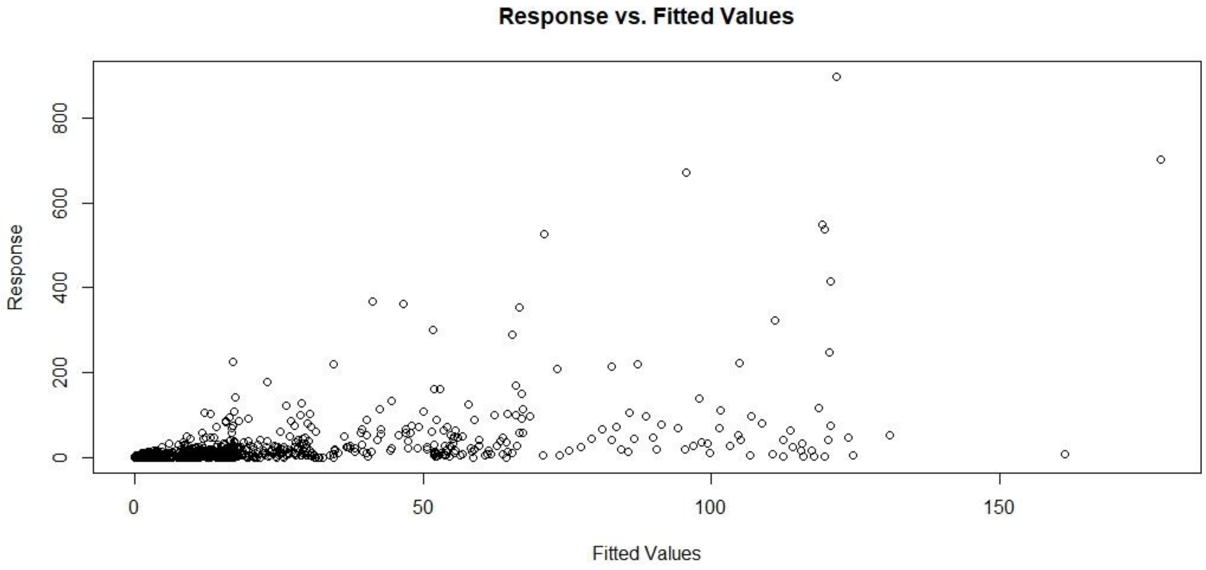
```
> gam.check(fit.25.cc.Tabr)

Method: REML   Optimizer: outer newton
full convergence after 8 iterations.
Gradient range [-0.0007536965,5.918643e-11]
(score 3466.436 & scale 1).
Hessian positive definite, eigenvalue range [0.0007544173,357.6889].
Model rank =  240 / 240

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                           k'      edf k-index p-value
s(Julian):SiteByLocationAngelo_Ground     23.00000  8.58847    0.65  <2e-16 ***
s(Julian):SiteByLocationAngelo_Treetop    23.00000  8.04631    0.65  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Ground  23.00000  4.64259    0.65  <2e-16 ***
s(Julian):SiteByLocationArmstrong_Treetop 23.00000  9.24681    0.65  <2e-16 ***
s(Julian):SiteByLocationCaspar_Ground     23.00000  0.00386    0.65  <2e-16 ***
s(Julian):SiteByLocationCaspar_Treetop    23.00000  4.17247    0.65  <2e-16 ***
s(Julian):SiteByLocationLyme_Ground       23.00000  3.39851    0.65  <2e-16 ***
s(Julian):SiteByLocationLyme_Treetop      23.00000 10.08158    0.65  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Ground  23.00000  5.98773    0.65  <2e-16 ***
s(Julian):SiteByLocationMalloPass_Treetop 23.00000  4.71471    0.65  <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```


deviance residuals
3
2
1
0
-1
-2
-2
-1
0
1
2
3
theoretical quantiles


Histogram of residuals
Frequency
400
300
200
100
0
-2
-1
0
1
2
3
Residuals



Resids vs. linear pred.



Response vs. Fitted Values

Appendix S7: Photos of acoustic deployment set up.

Figure 1: Conventional ground level acoustic monitoring.

Figure 2: Annotated photos of paired treetop and ground-level detector set up. Arrows indicate the position of microphones.

Figure 3: Microphone was attached to a telescopic pole and extended out from branch at treetop.

Figure 4: Measuring microphone height.

Figure 5: Monthly maintenance of monitoring equipment included retrieving SD cards and changing batteries.

Figure 6: SM2 detectors in weatherproof cases for ground and treetop.

Figure 7: SM2 detector internal view.

Figure 8: SM4 detector set up for treetop detectors.

Chapter 3 Supporting Information

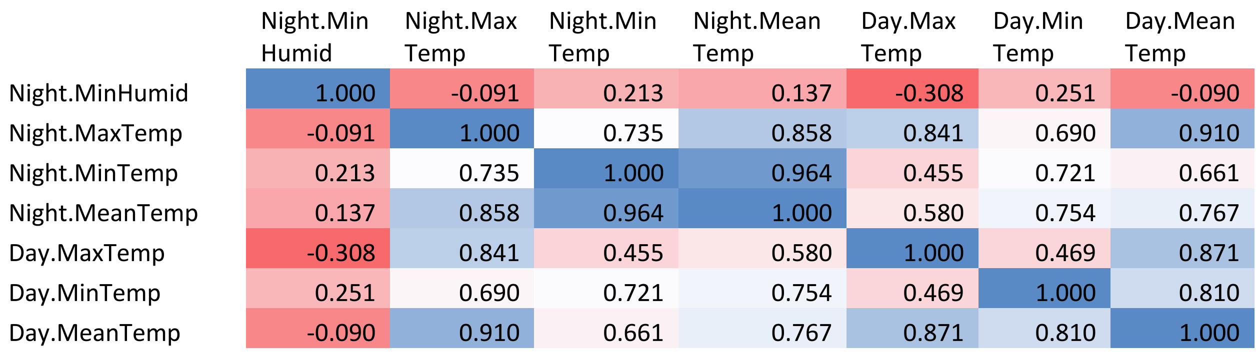
for

Microclimatic drivers of winter bat activity in coastal forests

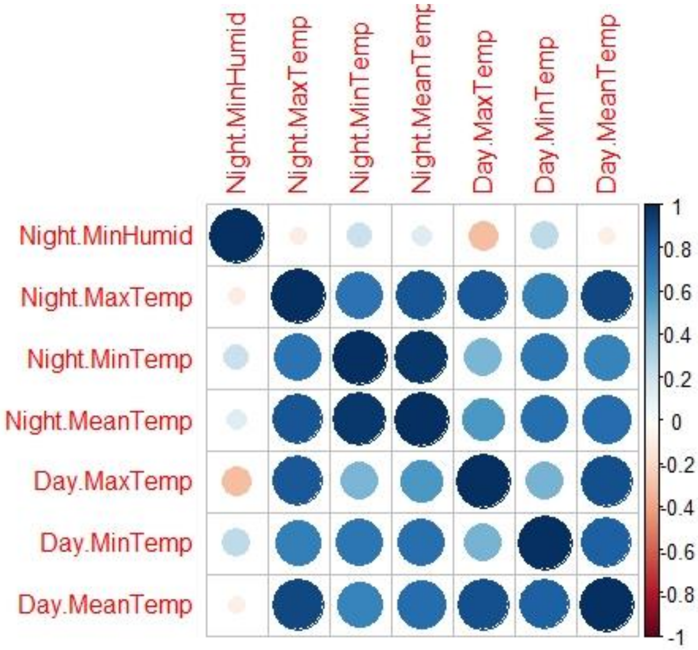
Contents

Appendices S1-S3

Appendix S1: Spearman’s rank correlation results between microclimate variables.



	Night.Min Humid	Night.Max Temp	Night.Min Temp	Night.Mean Temp	Day.Max Temp	Day.Min Temp	Day.Mean Temp
Night.MinHumid	1.000	-0.091	0.213	0.137	-0.308	0.251	-0.090
Night.MaxTemp	-0.091	1.000	0.735	0.858	0.841	0.690	0.910
Night.MinTemp	0.213	0.735	1.000	0.964	0.455	0.721	0.661
Night.MeanTemp	0.137	0.858	0.964	1.000	0.580	0.754	0.767
Day.MaxTemp	-0.308	0.841	0.455	0.580	1.000	0.469	0.871
Day.MinTemp	0.251	0.690	0.721	0.754	0.469	1.000	0.810
Day.MeanTemp	-0.090	0.910	0.661	0.767	0.871	0.810	1.000



Appendix S2: GLMM species presence model summary results for daytime temperature model.

To predict the probability of species presence in relation to only daytime maximum temperature, I used the model: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site). Following are the model summary results for each of the 8 species modeled.

Eptesicus fuscus (Epfu)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Epfu.Full

     AIC      BIC   logLik deviance df.resid
   171.6    186.6    -81.8    163.6      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.7935 -0.3250 -0.1898 -0.1167  7.0782

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 1.037    1.018
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)        -2.98726    0.56133  -5.322 1.03e-07 ***
scale(Day.MaxTemp)  0.83045    0.24821   3.346 0.000821 ***
Location1           0.05298    0.21880   0.242 0.808686

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.307
Location1   -0.032  0.046
```

Lasiurus blossevillii (Labl)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Labl.Full
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))

     AIC      BIC   logLik deviance df.resid
   156.9    171.9    -74.4    148.9      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.5343 -0.3116 -0.1826 -0.0864  6.2292

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 1.879    1.371
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -3.3716     0.7788  -4.329  1.5e-05 ***
scale(Day.MaxTemp)   0.5750     0.2054   2.799  0.00512 **
Location1           -0.4825     0.2609  -1.850  0.06434 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.115
Location1    0.104 -0.232
```

Lasiurus cinereus (Laci)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Laci.Full

     AIC      BIC   logLik deviance df.resid
   243.6    258.6   -117.8    235.6      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-5.0483 -0.4046 -0.2258 -0.0930  5.9625

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 0.07132  0.2671
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -1.9153     0.2476  -7.735 1.03e-14 ***
scale(Day.MaxTemp)   1.2576     0.2104   5.977 2.28e-09 ***
Location1           -1.2419     0.2100  -5.913 3.36e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.395
Location1    0.495 -0.269
```

Lasionycteris noctivagans (Lano)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Lano.Full

     AIC      BIC   logLik deviance df.resid
   227.6    242.7   -109.8    219.6      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.4653 -0.4113 -0.2583 -0.1379  6.5964

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 4e-14    2e-07
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -2.1646     0.2190  -9.885  < 2e-16 ***
scale(Day.MaxTemp)   1.0837     0.1974   5.490 4.02e-08 ***
Location1           -0.8005     0.1954  -4.097 4.18e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.489
Location1    0.469 -0.209
optimizer (Nelder_Mead) convergence code: 0 (OK)
boundary (singular) fit: see ?isSingular
```

Myotis californicus (Myca)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Myca.Full

     AIC      BIC   logLik deviance df.resid
     374      389     -183      366      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.3186 -0.7151 -0.3837  0.8588  5.9065

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 0.8066   0.8981
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -0.7186     0.4265  -1.685    0.092 .
scale(Day.MaxTemp)   0.6934     0.1578   4.393 1.12e-05 ***
Location1            0.1873     0.1354   1.383    0.167
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.103
Location1   -0.025  0.040
```

Myotis thysanodes (Myth)

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Myth.Full

     AIC      BIC   logLik deviance df.resid
   148.1    163.1    -70.1    140.1      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.1464 -0.2538 -0.1202 -0.0419  7.0680

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 4.449    2.109
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -3.9618     1.2304  -3.220  0.00128 **
scale(Day.MaxTemp)   0.7870     0.3153   2.496  0.01255 *
Location1            0.5972     0.2914   2.050  0.04040 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.264
Location1   -0.154  0.237
```

Myotis yumanensis (Myyu)

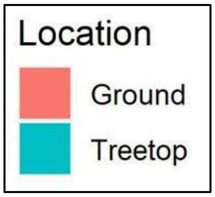
```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Myyu.Full

     AIC      BIC   logLik deviance df.resid
   220.8    235.8   -106.4    212.8      311

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.4332 -0.3468 -0.2550 -0.1098  5.1093

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 2.325    1.525
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)
(Intercept)         -2.5349     0.7499  -3.380 0.000724 ***
scale(Day.MaxTemp)   0.5878     0.2364   2.487 0.012886 *
Location1            0.1527     0.1858   0.822 0.410954
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.167
Location1   -0.043  0.057
```

Tadarida brasiliensis (Tabr)

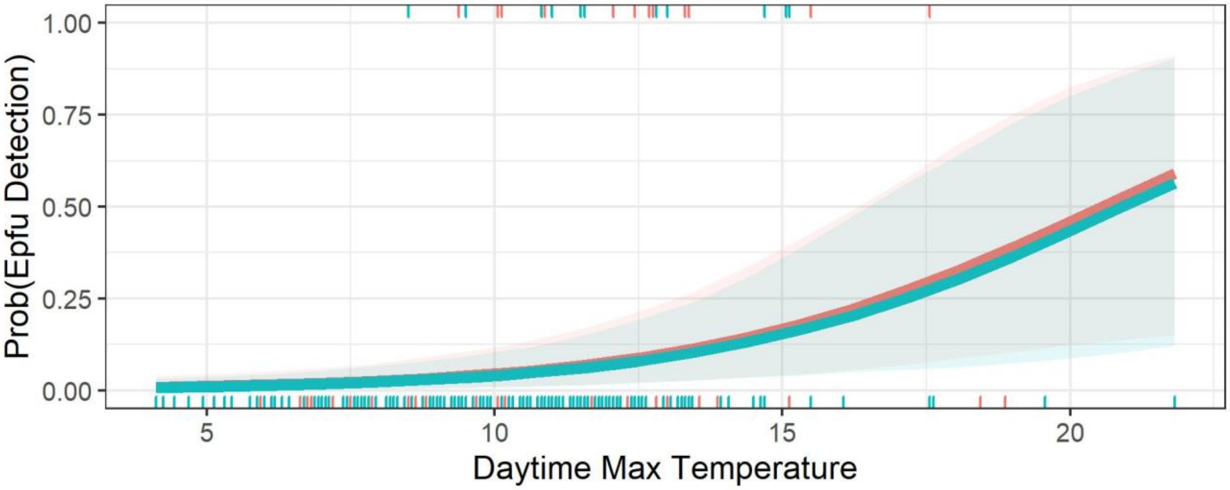
```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Presence ~ scale(Day.MaxTemp) + Location + (1 | Site)
   Data: Tabr.Full

     AIC      BIC   logLik deviance df.resid 
   276.9    291.9   -134.4    268.9      311 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-3.4378 -0.4668 -0.2472  0.5249  5.1027 

Random effects:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 0.1166   0.3415  
Number of obs: 315, groups:  Site, 5

Fixed effects:
                   Estimate Std. Error z value Pr(>|z|)    
(Intercept)         -1.2798     0.2352  -5.442 5.27e-08 ***
scale(Day.MaxTemp)   1.2917     0.2009   6.430 1.28e-10 ***
Location1           -1.2778     0.1829  -6.985 2.85e-12 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) s(D.MT
scl(Dy.MxT) -0.262       
Location1    0.342 -0.349
```

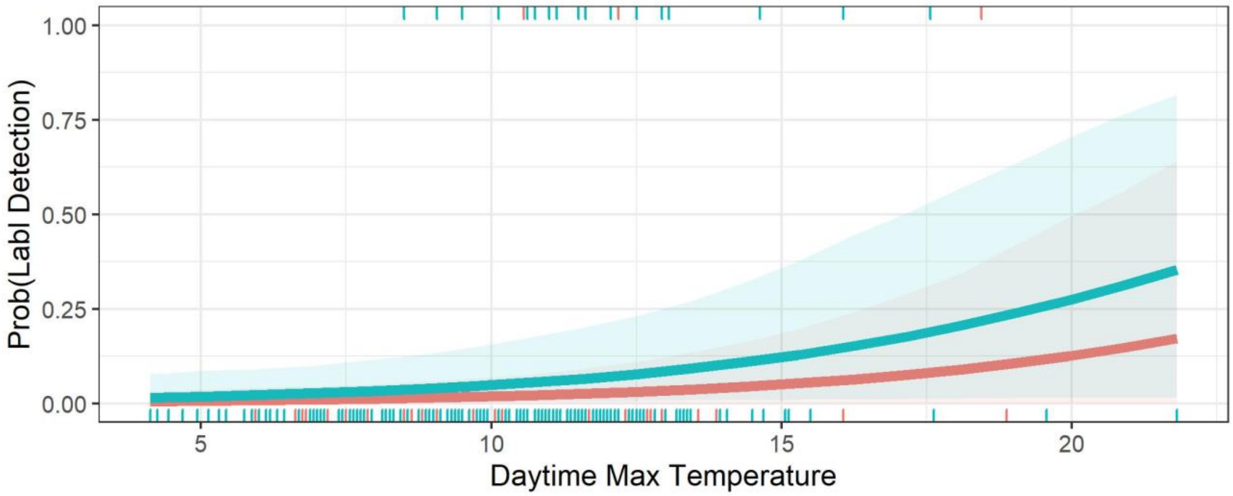
Appendix S3: Predicted probability of detection for daytime temperature model results.

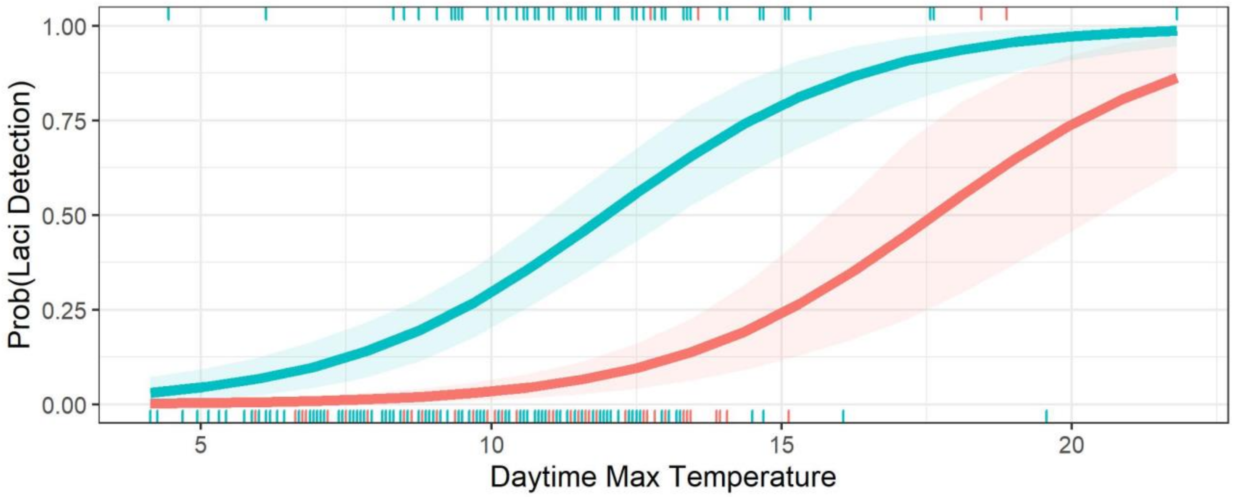
The following plots show the predicted probability of detecting each species in relation to maximum daytime temperature based on the GLMM models used in Appendix S2.



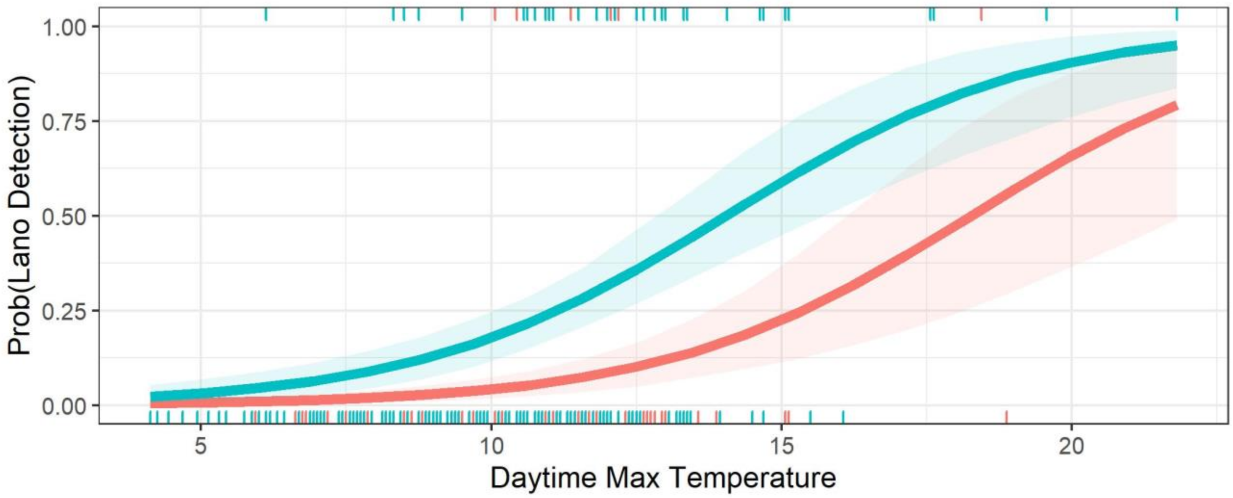
In all of the following plots, red lines and 95% confidence intervals represent 'ground' detector locations and blue represent 'treetop' detector locations.



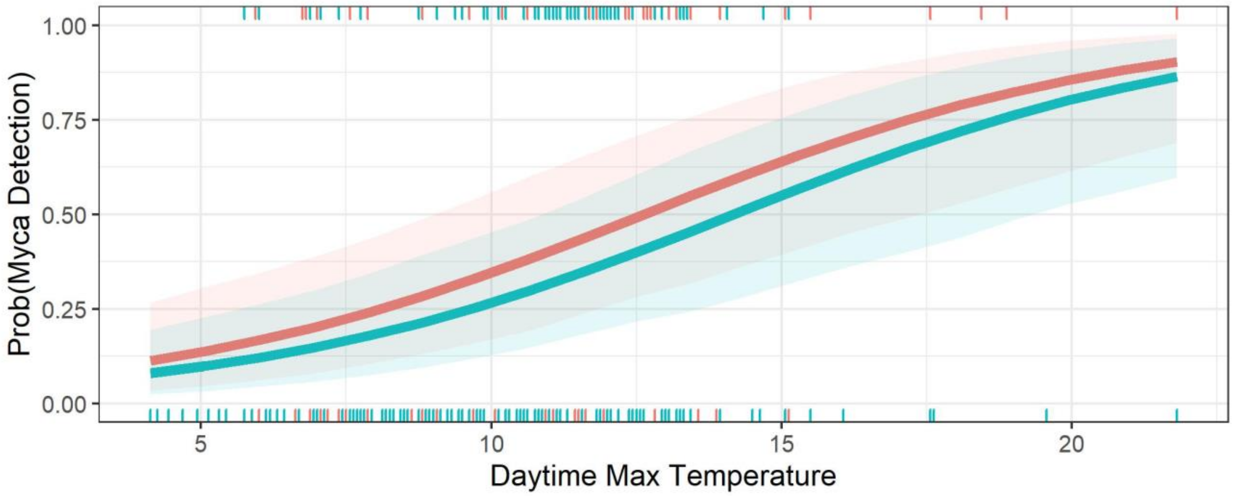




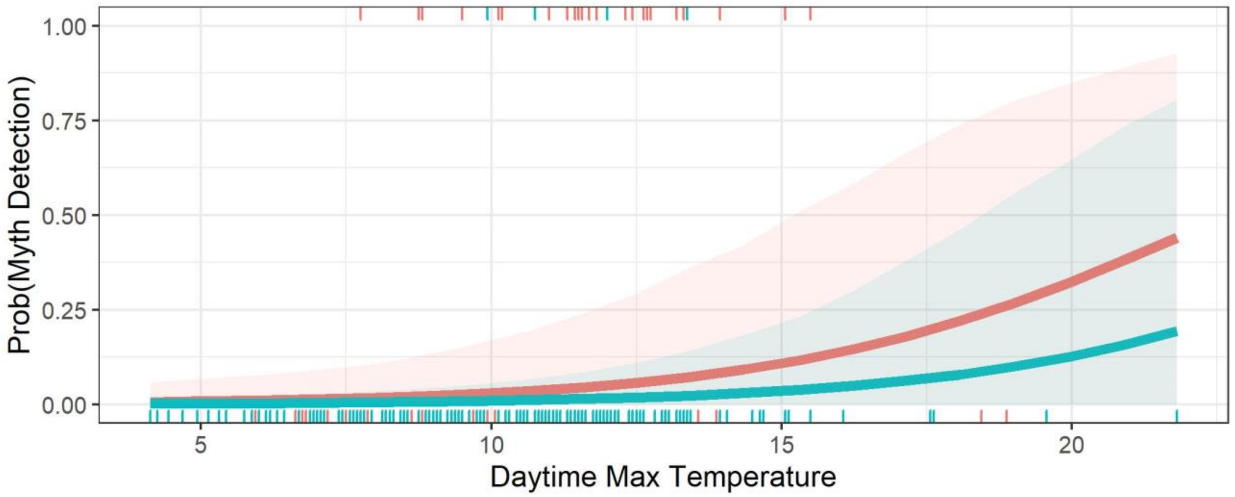
Prob(Laci Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature

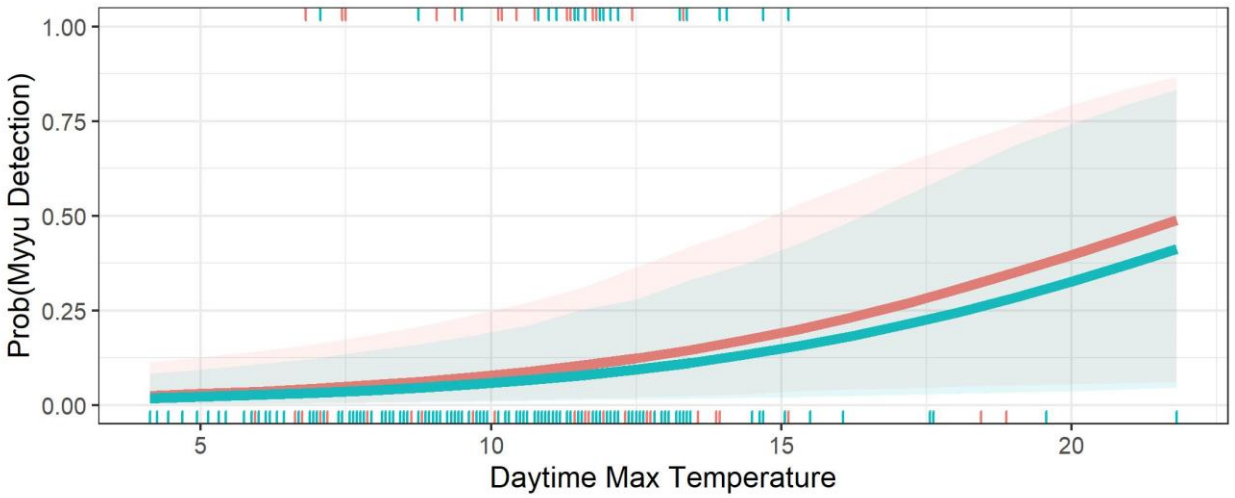


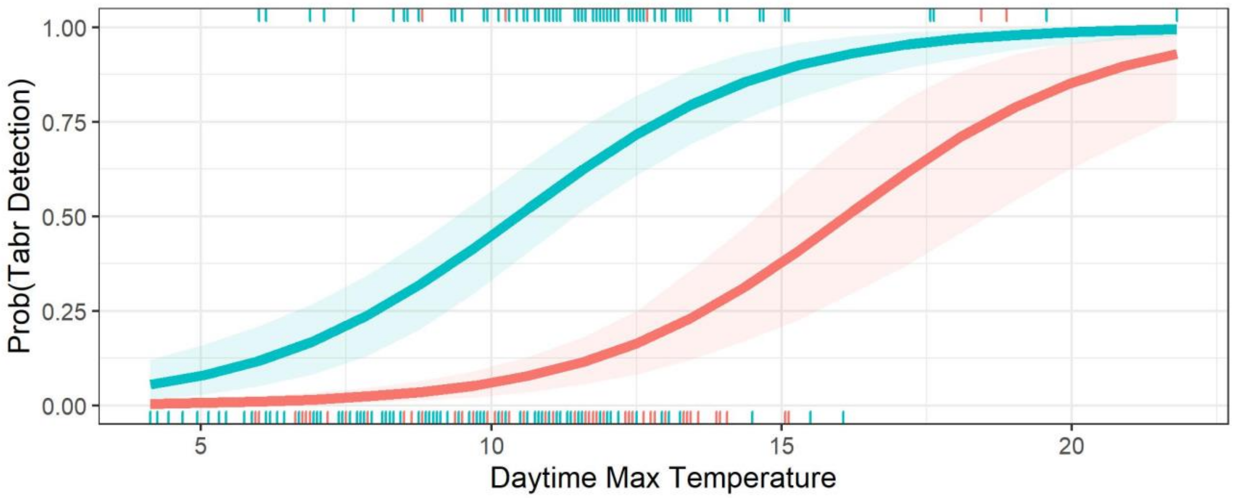
Prob(Lano Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature



Prob(Myca Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature


Prob(Myth Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature


Prob(Myyu Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature


Prob(Tabr Detection)
1.00
0.75
0.50
0.25
0.00
5
10
15
20
Daytime Max Temperature