Advancing community viability analysis: assessing community resistance and persistence of Mojave Desert birds to climate change

A dissertation

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Abstract

Understanding interspecific interactions is central to community ecology, and incorporating interspecific interactions into conservation work allows scientists to improve management efforts. Indeed, there has been an increasing call for applied management to place greater focus on the effects of species interactions. There have been some efforts to pull together a suite of different types of population and community modeling into a concept of "community viability analysis" (CVA), particularly to help address the lack of community-based conservation. However, such efforts have been ad hoc or overly narrow. This dissertation introduces a comprehensive CVA framework, enhancing our understanding of how one might investigate or evaluate community dynamics from a conservation perspective by addressing the intricate interplay of interspecific interactions and external pressures. I then implement CVAs in two different ways, analyzing the same study system of conservation concern, the terrestrial Mojave Desert community, with particular emphasis on 151 bird species. Each approach was designed to answer a different question. First, whether there was an unappreciated relationship between birds and secondary use of underground thermal refugia that might alter expected effects of climate change. Through a combination of thermal models, field surveys, and analysis of citizen science data, I found that even if underground thermal refugia use was not a historic behavior for birds, published and field results are consistent with birds currently adopting this behavior. As part of this research, I improved estimates of body density and measured feather reflectance, thus enhancing models of thermal vulnerability. My second CVA investigated the relative expected effects of ongoing bird declines in the Mojave compared mammal and reptile loss on the community via secondary cascading extinctions. I constructed a food web of the Mojave Desert terrestrial community (300 nodes, 4080 edges) to investigate this question, and found that the impact of bird species loss was relatively low compared to mammal or reptile losses. Notably, I also found that relatively high interconnectivity among avian species formed subwebs, enhancing network resistance to bird losses. This thesis work bridges conservation and community ecology, presenting a holistic approach for addressing complex community dynamics and guiding effective conservation actions.

For my wife, Lauren
My parents, Theresa and Kurt
My brothers, Ryan and Sam
And my nana, Elva

I couldn’t have made it to this point without you
I love you all

And for our coming little one

Whom I love already

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Chapter 1

Introduction

Understanding interspecific interactions (i.e., synecology, or community ecology) is crucial to conservation biology. Species do not exist in isolation; in fact, the loss of species or alteration of their interactions transforms ecosystems (Paine 1974, Terborgh et al. 2001, Estes et al. 2010), sometimes causing additional species extinctions through cascading effects (Säterberg et al. 2013), and can even harm human health (Markandya et al. 2008). Incorporating interspecific interactions into conservation work allows scientists to better predict the impacts of perturbations to communities (e.g., Jönsson and Thor 2012), track effects of invasive species (Galiana et al. 2014), bolster ecosystem services (Buechley and Şekercioğlu 2016), and rehabilitate degraded landscapes (Soulé et al. 2003). Without combining research on community interactions with targeted management on particular species, we run the risk of adopting management approaches that either do not work (such as with initial efforts to preserve the large blue butterfly (*Maculinea arion*) in the United Kingdom (Muggleton and Benham 1975, Johst et al. 2006) or result in some form of harm we did not predict (such as that exhibited in some predator culling programs (Letnic and Koch 2010, Bowen and Lidgard 2013).

Fortunately, the field of community ecology has been developing for almost a century, providing years of research from which conservation efforts can draw. There are published works developing best practices for examining interspecific interactions (Paine 1974, Schmitz 2008), tracking flow of energy and matter (Lindeman 1942, Allesina and Bodini 2004), and measurements of (and arguments about) system stability (Pimm 1984, Brose et al. 2006). There is even a field of mathematics (network theory) useful for visualizing and quantifying various aspects of community dynamics (Cartozo et al. 2006, Alcantara and Rey 2012). Historically, however, wildlife management, and more recently conservation, has focused primarily on single-species research and management (Sabo 2008) – particularly in the U.S., where the Endangered Species Act provides a legal lever to focus on single species (Scott 2006, Eichenwald et al. 2020). While this focus on individual species has been effective at preventing extinctions of some species (Walters et al. 2010, Luther et al. 2016), there are situations for which it is not suited. Species decline, for example, can be triggered indirectly by threats elsewhere in the community (Johst et al. 2006, Middleton et al. 2013). Indeed, an average of 49% of species that go extinct first in a real-world food web are impacted indirectly by the species forced into decline by a perturbation (Säterberg et al. 2013). Recent models suggest that focusing management funding on single species of interest can result in more community-wide extinctions than expected if management funding were randomly allocated among species in a trophic web (McDonald-Madden et al. 2016). This is because the single-species focus does not account for the possible impact of species loss throughout a system, which might explain the recent push to create species population viability models that are coupled to the dynamics of other species (e.g., Lacy et al. 2013, Prowse et al. 2013).

Indeed, there has been an increasing call for applied management to shy away from a concentration on single species and place greater focus on the impact of interactions (Soulé et al. 2003, Soulé et al. 2005, Memmott 2009, Säterberg et al. 2013). Soulé et al. (2003) specifically highlights how the decline of marine kelp forests might be mitigated through the management of community interactions. However, Tallis et al. (2010) asserts that the perceived complexity of communities has precluded most scientists from using it for conservation purposes. Therefore, determining how to best use the tools and conceptual framework of community ecology to achieve applied conservation goals is an important current obstacle for researchers and environmental managers to overcome. Some community-focused conservation approaches have been successful, such as Middleton et al. (2013) using interaction-based viability models to reveal that invasive fish caused increased grizzly bear *Ursos arctos horribilis* predation of elk *Cervus canadensis*, resulting in elk population declines. Their approach, like an increasing number of other research projects, builds the traditional single-species viability modeling method Population Viability Analysis (PVA) out to include multispecies interactions. There have been some efforts to pull together a suite of different types of population and community modeling into a concept of "community viability analysis," particularly to help address the lack of community-based conservation. However, such efforts have not been systematic or integrated across the possibilities of what might constitute community viability analysis (Witting et al. 1994, Ebenman et al. 2004, Ebenman and Jonsson 2005, Prowse et al. 2013). Organizing the various efforts and integrating them under single framework will make the approach more coherent and provide an important conceptual framework and metrics for resource managers.

Community Ecology

Communities have been of formal interest to ecologists for at least 100 years and have been treated as everything from an entity akin to a cybernetic system (whereby the community is more than the sum of its parts because of synergies) to being no more than an assemblage of species with no emergent properties (i.e., no more than a sum of its parts) (Hagen 1992). In theory, a community is comprised of the complete set of organisms belonging to all species living in a particular place and time (Vellend 2016). In practice, however, depicting and studying communities like this are rarely (if ever) done due to information deficiencies and impracticality. (Vellend 2016). Consequently, researchers create models of communities that focus on subsets of the real community, delineating the boundaries via taxonomic or functional groups, trophic positions, or species interactions, and often focusing on keystone species (Vellend 2016). These simplifications allow flexibility for communities to include as many or as few species, trophic levels, interactions, etc. as needed (Vellend 2016), ranging from large food webs (Dunne 2006) to more focused predator/prey interactions (Barbosa and Castellanos 2005).

Varied approaches to working with community models can lead to insights, or inadvertently to problems. For example, one long-term argument in community ecology is whether species diversity increases or decreases community stability. The inexact nature of what is meant by "community stability" has been partly responsible for decades of debate (Ives 2005). In the 1950s and 1960s, influence from Odum (1953) resulted in Macarthur (1955) taking the stance that community stability could be defined by the capacity of energy to flow through a community; i.e., measuring the "choices" energy has in following paths up food webs. With more species comes greater numbers of energy pathways; therefore, increasing species diversity of a community will result in greater stability by this definition (Ives 2005). This was consistent with some applications outside of ecology as well, such as communication and traffic networks (Shannon and Weaver 1949), from which ecology took many of its concepts and tools. In the 1970s and 1980s, however, the definition of community stability shifted focus to the properties of species persistence within the community. Because diverse communities tend to have greater species turnover (species loss and gain) over time, they were thought to be less stable from that perspective (Ives 2005). In the 1990s, a third perspective suggested that while communities with more species diversity may have a larger probability of individual turnover, the persistence of the community web may be greater due to compensatory fluctuations in the density of other species (Ives 2005). That is, although diversity might increase the fluctuations of individual species, the aggregate density of all species in the community may fluctuate less. Consequently, resolution to the question about the relationship between species diversity and community stability is that it depends on the definition of "stability."

Despite its potential for conflict, however, I think that a diversity of approaches to community research is a net benefit because of the greater variety of tools and research questions asked. On the one hand, ecologists may investigate the stability of community structure and energy flowing terms of resistance (the capacity of a species/community/system to remain unchanged despite external forces or perturbations, such as climate change or invasive species), and resilience (the capability of the species/community/system to return to a prior baseline following a perturbation). In contrast, ecologists may investigate finer scale mechanisms, abstracting community complexity into simpler modules (Schmitz 2010). Many approaches to investigating communities can focus on questions of community viability, so any community viability analysis framework should include a broad spectrum of community research approaches and goals.

Viability Analysis

One of the most important tools in species conservation planning is population viability analysis (PVA), where estimates of vital rates, environmental stochasticity, dispersal, land use, and management are used to project the likelihood of population persistence (Traill et al. 2007, Mortensen and Reed 2016, McGowan et al. 2017). Like all models, PVAs have limitations (e.g. Coulson *et al.* 2001), but they have been a valuable tool to resource managers. PVAs are particularly helpful for comparing relative efficacy of management alternatives and to show the range of possible population size trajectories over time (Beissinger and Westphal 1998, Reed et al. 2002). The focus of PVA has been almost exclusively single-species assessments. However, increasing recognition of the importance of interspecific interactions to population dynamics and conservation (e.g., Soulé et al. 2003, Estes et al. 2011, Säterberg et al. 2013) has led to growing numbers of joint species population projection models, where two single-species models are linked via the effects on one on the other (Lacy et al. 2013, Prowse et al. 2015, Lany et al. 2018).

Logically, there might be no reason to extend this approach across a community with an ever-increasing suite of interacting species' dynamics to ultimately generate a type of community viability analysis (CVA), so long as one is mindful of complications caused by ever-increasing model complexity (Ginzburg and Jensen 2004). There is already a long history of community-based assessments related to food web structure and energy flow through ecosystems (reviewed by Dunne 2006) that provide perspectives and possible metrics that could contribute to developing a broad concept of community viability. Indeed, conservation biologists have already shown interest in community metrics such as the effects of keystone species (Mills et al. 1993), the problem of cascading (secondary) extinctions (Sahasrabudhe and Motter 2011), as well as an interest in interaction-based management (Slocombe 1993). However, discussion of CVAs per se in the literature is limited, and the term "community viability analysis" has appeared in several apparently unrelated forms in recent decades.

Community ecology bridges ecosystem and population ecologies in a continuum, occupying the middle ground and overlapping the two extremes (Figure 1) (Berlow et al. 2004, Schmitz 2010). Community ecologists use different methods, metrics, and organizational concepts depending on where they fall on this spectrum. Some community ecologists, for example, examine larger system-based questions such as the existence of alternate stable states and hysteresis (Beisner et al. 2003, Petraitis 2013). Investigations of community stable states can be divided into two different approaches: community-based, where state variables such as species and interactions within the system are the subject of investigation, and ecosystem-based, where environmental drivers that change the system itself are the subject of investigation (Beisner et al. 2003). There are also community ecologists that approach their work from a reductionist perspective, where they examine interspecific interactions at a finer scale (Sabo 2008, Schmitz 2010). This approach can be used to examine specific interactions and dynamics in a community, such as herbivore resource limitation and indirect top-down control of food webs by carnivores (Schmitz 2010). Finally, there are community ecologists that focus on the dynamics of a single species. However, such researchers are particularly interested in how inter-specific interactions influence single-species dynamics and explicitly model these effects (Berlow et al. 2004). Consequently, I see benefits to using CVA as an umbrella concept that encompasses all these possibilities, treating CVA as a suite of analytical approaches and metrics, each of which evaluates a potential component of community dynamics or processes. I envision that CVA should parallel the field of community ecology and include metrics across the spectrum depicted in Figure 1.

Metrics that could be construed as types of CVA existed prior to the 21st century, such as Conner's (1988) proposal to focus on ecologically functional populations and Slocombe's (1993) push to adopt ecosystem-based management. The earliest published reference to the term 'community viability' I have found is by Witting et al. (1994). They defined CVA as having two possible approaches: an examination of how a suite of species interactions impact the extinction risk of a single focal species, and an investigation of how the extinction of one species impacts the extinction probability of another. This was not, however, the focus of their paper, and they were not specific about how such a CVA might be produced. Their suggestions differ from the first formal approach to CVA, which was proposed by Ebenman and colleagues (Ebenman et al. 2004, Ebenman and Jonsson 2005). In their vision, CVA was defined specifically as a way of predicting the likelihood of secondary extinctions following a species' loss from the community. They introduced a CVA metric called *quasi-collapse risk*, where they calculated the probability that the number of species in the community would fall below a particular value within a fixed time following loss of a given species.

Since 2005, several other interaction-based viability-like analyses have appeared in the literature that do not necessarily fit in either Ebenman and Jonsson's (2005) or Witting et al.'s (1994) CVA definition, although they could reasonably be considered a type of CVA (e.g., Lacy et al. 2013, Yun et al. 2017, Brodie et al. 2018). The time is right to draw together the possibilities of CVA and integrate them under a single framework. This is the central theme of my dissertation, creating a framework for CVA, and applying some of the concepts to a particular study system.

Study System

As this dissertation is focused on applications of community ecology to conservation, I needed a study system in which to operate. I examined potential ecosystems using the following criteria:

1. There needed to be a history of data collection on communities in the region. Access to such knowledge reduces the amount of time required for my own research by allowing me to develop informed hypotheses and rapidly validate models.
2. The hypotheses I generated by after examining the preexisting data needed to include an interaction-based component.

Based on these criteria, I settled on the Mojave Desert in the American southwest. Although it was a wetter and more hospitable environment before the end of the last glacial maximum, approximately 20,000 years ago, it has since transitioned to the arid, desert region of today (Guerrero et al. 2012). It constitutes about one-tenth of the total desert area in North America and is roughly equivalent in size to the state of New York (Rundel and Gibson 1996b). The presence of nearby mountain ranges affects the desert's climate by limiting the passage of moist air from the Pacific Ocean, resulting in a precipitation regime dominated by winter rainfall (Charlton and Rundel 2017). Total mean precipitation levels in the Mojave Desert is correlated with elevation, although there is high annual variability (Rundel and Gibson 1996b).

Temperatures are generally warm, and the desert holds the record for the highest measured air temperature on the planet (El Fadli et al. 2013). However, the Mojave may experience cool Arctic air masses during the winter rainy season and hence receives some snow (Rundel and Gibson 1996b). The desert has experienced a rise in mean annual air temperature by approximately 2°C since the early 20th century (Bai et al. 2011); in fact, harsh conditions in the area make the desert an analogue for astrobiological research of Mars (Belov et al. 2019).

Vegetation in the Mojave Desert is diverse and exhibits variations in response to climate and landform development. It is often subject to stress due to water deficits (Lane 1984), therefore, vegetation in the Mojave Desert is characterized by its adaptability to the harsh desert environment (Figure 3). Vegetation is generally dominated by creosote (*Larrea spp.*), which covers nearly two-thirds of the total desert area (Rundel and Gibson 1996b). In some cases, the iconic and Mojave-restricted Joshua tree (*Yucca brevifolia*) creates woodlands with a variety of codominant shrubs with increased cover (Rundel and Gibson 1996b). Pinyon pines (*Pinus monophylla*) and junipers (*Juniperus spp.*) replace Joshua trees as the dominant species at higher elevations (Johnson 1976). Mojave animal diversity is relatively low with little endemism, and the desert shares many of its species with the neighboring Sonoran Desert (Rundel and Gibson 1996b) (Figure 3).

There is a long history of research on animal communities in the ecosystem (Rundel and Gibson 1996a), fulfilling requirement (1), above. Joseph Grinnell, one of the first ecologists and pioneer of the ecological niche concept (Grinnell 1917), spent years collecting survey data on Mojave mammals and birds with his students. These surveys were repeated in the 21st century by another lab, providing long-term information on the Mojave Desert bird and mammal community (Iknayan and Beissinger 2018, Riddell et al. 2019, Riddell et al. 2021). These surveys revealed that Mojave birds have catastrophically declined, which was primarily attributed to the impact of climate change (Iknayan and Beissinger 2018, Riddell et al. 2019, Riddell et al. 2021). In contrast, the Mojave mammal community has shown relatively stable population levels, which Riddell et al. (2021) suggested was likely due to their ability to dig underground burrows to escape from outside temperatures. As birds generally cannot burrow underground, it follows that they should be more exposed to climate change (Riddell et al. 2021).

This conclusion actively provided me with a hypothesis to evaluate, fulfilling requirement (2). While birds lack the capacity to construct their own burrows, they have been observed utilizing burrows created by other animals for temporary refuge from predators and extreme heat (Austin and Smith 1974, Bowers and Dunning 1985, Pike and Mitchell 2013, Agha et al. 2017, Puffer et al. 2022). Such behaviors are inconsistent with the idea that bird declines occurred because they cannot use underground refugia. Community ecology literature suggests that interaction-based effects on population dynamics can sometimes be hidden by or supplement the impacts of other variables (e.g., Peckarsky et al. 2008), and I hypothesized that the predicted impact of climate change on bird populations was complicated by the presence of species interactions based on the availability of underground burrows.

Goals

The goals of this dissertation are to outline and demonstrate one potential approach on bridging the divide between conservation and community ecology, focusing on the idea of community viability. Each chapter builds upon the previous one, establishing a solid foundation for my proposed approach and demonstrating its practical application. In Chapter 2, I review previous research on the effects of interspecific interactions on species and ecosystems and establish a foundation for a community ecology-based approach to conservation. As stated in previous sections, I call this framework “community viability analysis.” In Chapter 3, I begin laying the groundwork for an analysis of the Mojave Desert ecosystem by turning a critical eye to the data needed for such an analysis. Here, I evaluate the validity of approximate estimations of species biophysical characteristics – specifically, estimating density from morphological measurements of birds. Such parameters are crucial to the accuracy of any modeling effort; therefore, I need to ensure that any estimation I use is valid. In Chapter 4, I collect biophysical parameters for a complex mechanistic thermal model of each of the birds living in the Mojave Desert and run a preliminary model to calculate avian relative thermal vulnerabilities to approximate a likely “order of extinction” from the effects of climate change. This allows us to estimate which bird species are at greater risk in the desert and finishes the groundwork for the CVA itself.

In Chapter 5, I generate hypotheses for potential drivers of population collapse in a specific area of conservation concern by reviewing the ecological context surrounding the declines. In this case, I perform what I term a “persistence-based CVA” to determine whether a proposed behavioral adaptation – that birds in the Mojave Desert may attempt to take refuge in pre-dug burrows to prevent death from heat exposure – provide more accurate estimates of pre-measured boundaries of species richness over the course of the 20th and early 21st centuries. I use the mechanistic thermal models tested from Chapters 3 and 4 to see whether burrow use or non-burrow use is a more likely mechanism of avian survival. However, prevailing wisdom suggests that birds do not typically utilize underground burrows as thermal refugia (Austin and Smith 1974), although this may be because it is difficult to document avian burrow use (Dean and Vickery 2003) as there is anecdotal evidence of them doing so (Pittman Jr. 1960, Austin and Smith 1974, Bowers and Dunning 1985, Coate 1994, Dean and Vickery 2003, Pike and Mitchell 2013, Puffer et al. 2022). I therefore also combine my own field surveys with citizen science data to test whether burrow-use is in fact a possible mechanism, establishing a set of correlation-based evidence that can support the creation of manipulative experiments (according to the principles of adaptive management, which we incorporate into our CVA from Chapter 1).

Finally, in Chapter 6 I perform one additional CVA, which is resistance-based (see Chapter 1). This is a different method than in Chapter 5, as here I test the overall Mojave Desert animal community's capacity to remain largely constant in the face of animal extinctions. I assess whether the collapse of birds is relatively more important to the structure of the overall community than if other vertebrates went extinct instead. While in Chapter 5 I focus on CVAs using a combination of mechanistic models and field surveys, in Chapter 6 I rely on network analysis to test for cascading secondary extinctions after losses of birds, reptiles, or mammals.

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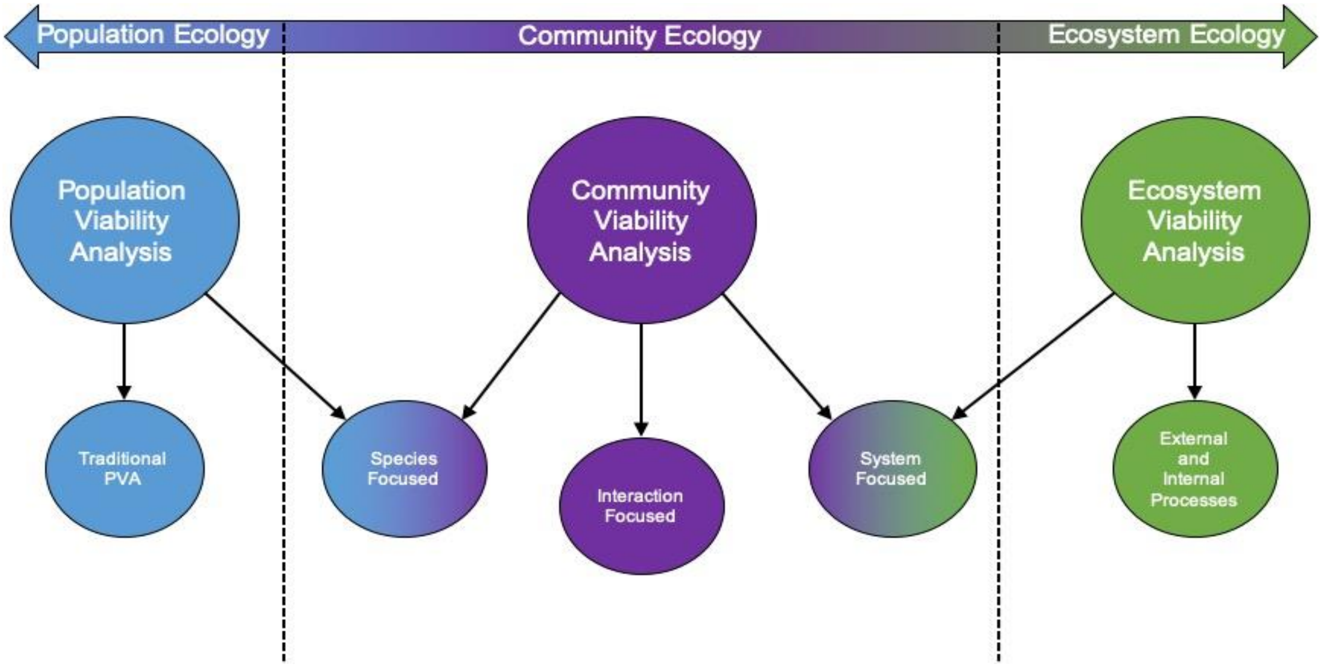

Figure 1-1 A visual representation of our interpretation of an ecology gradient, where community ecology is in the continuum between ecosystem and population ecology (between dashed lines). Like community ecology, we see community viability analysis as having some overlap with population viability analysis (species-focused CVA) at one end of the spectrum and ecosystem viability analysis (system-focused CVA) at the other. Our CVA framework does not include single-species viability analysis without explicit species effects (traditional PVA), nor does it include ecosystem analyses that discount species interactions.

Figure 1-2 Approximate area of the Mojave Desert ecoregion. Image by Simon Pierre Barrette, distributed under a CC BY-SA 3.0 license.

Figure 1-3 Photos from fieldwork in the Mojave Desert, taken from camera traps and one of my field assistants (Arianna Efstatos).

Chapter 2

An expanded framework for community viability analysis (Adam J. Eichenwald, J. Michael Reed). Published in BioScience (2021) 71:626-636.

Abstract

Community viability analysis (CVA) has been put forth as an analogue for population viability analysis (PVA), an accepted conservation tool for evaluating species-specific threat and management scenarios. The original proposal recommended that CVAs examine resistance-based questions. PVAs, however, are broadly applicable to multiple types of viability questions, suggesting that the original CVA definition may be too narrow. In the present article, we advance an expanded framework in which CVA includes any analysis assessing the status, threats, or management options of an ecological community. We discuss viability questions that can be investigated with CVA. We group those inquiries into categories of resistance, resilience, and persistence, and provide case studies for each. Finally, we broadly present the steps in a CVA.

Introduction

One of the most important tools in species conservation planning is population viability analysis (PVA), in which estimates of population size, vital rates, environmental stochasticity, dispersal, land use, and management can be used to project the likelihood of population persistence (e.g., Mortensen and Reed 2016). PVAs are particularly useful for comparing relative efficacy of management alternatives and for showing the range of possible population trajectories (Reed et al. 2002). Until recently, the focus of PVA has been almost exclusively single-species analyses. However, increasing recognition of the importance of interspecific interactions to population dynamics and conservation (e.g., Soulé et al. 2003, Estes et al. 2011, Säterberg et al. 2013) has led to growing numbers of linked species population projection models (Lacy et al. 2013, Prowse et al. 2015).

One could imagine extending this PVA approach across a community of species to ultimately generate a type of community viability analysis (CVA), ignoring complications caused by ever-increasing model complexity (Ginzburg and Jensen 2004). However, this may not be the most practical tactic, and other approaches have already been taken to create community-based assessments of performance. These can relate to food web structure and energy flow through ecosystems (Dunne 2006), community states (Dethlefsen and Relman 2011), or other forms of complex analyses (Geary et al. 2020) that contribute to developing a broad concept of community viability. Indeed, conservation biologists have already demonstrated interest in community metrics such as the effects of keystone species (Mills et al. 1993) and cascading (secondary) extinctions (Sahasrabudhe and Motter 2011), as well as in interaction-based management (Slocombe 1993).

Discussions of CVA per se in the literature, however, are limited, and the phrase *community viability analysis* has appeared in several different, apparently unrelated, forms in recent decades. Witting and colleagues (1994) speculated that a CVA could investigate how the loss of one species impacts the extinction probability of a different, target species. This was not the focus of their paper, and they were not specific about how such a CVA might be done. The first formal definition of a CVA that we know of provided just such an approach: Ebenman and colleagues (Ebenman et al. 2004, Ebenman and Jonsson 2005) introduced a CVA metric called quasi collapse risk, in which they calculated the probability that certain numbers of species would remain in the community following the loss of another focal species. Although we agree that Ebenman and Jonsson's (2005) suggested approach is a CVA, we propose expanding their interpretation to achieve their stated goal: to create a community analogue to PVA. This concept expansion is important, because PVAs and CVAs have been suggested as possible steps to a new active management approach encouraging more focus on conservation of ecosystems rather than just populations (Tallis et al. 2010). Ecosystem-based management has been recommended by the United Nations Environment Programme and the US National Oceanic and Atmospheric Administration (NOAA), further supporting the need to broaden the CVA framework.

In the present article, we expand the original definition of CVA to develop a framework defining its potential role as a community analogue to PVA. We specifically define a CVA, in parallel to a PVA (Lacy 2019), as any analysis assessing the status, threats, and management options of an ecological community. We then examine how to conduct a CVA and provide examples of the types of questions one might ask. Our goals are to create a framework that encompasses the breadth of potential CVAs, to reduce confusion over what might be meant by the concept, and to increase its utility for species, community, and ecosystem conservation.

Advantages to expansion

There are multiple advantages to researchers and resource managers in expanding and formalizing the concept of CVA. To make our argument, first consider the PVA label. The initial models to assess population viability were produced in the late 1970s (Shaffer 1979). However, there were many other models published earlier that projected population trajectories and responses to management. Introducing the PVA concept provided a focus to the emerging field of conservation biology and the development and refinement of analytical methods, allowing PVA to become a standard tool in conservation (Beissinger 2002). Similar advantages exist in developing a framework for CVA. We are currently in a comparable situation with communities as we were with populations in the 1980s, in that environmental managers are increasingly relying on multispecies models to predict effects of management actions on communities. Fisheries scientists in particular have been focused on accounting for ecosystem considerations

(Plagányi et al. 2014), likely because of the proven economic benefits of such an approach (Yun et al. 2017). As with the introduction of the PVA, CVA can benefit these managers by encouraging analytical approaches and tool development for conservation values, as well as acting as a reference point for deciding which community dynamics are most important for management goals. However, CVA is currently too narrow to be a true analogue to PVA, which reduces its utility for conservation and management.

What is a CVA?

CVA currently examines the risk and extent of secondary extinctions in a community following species loss (Ebenman and Jonsson 2005), which is one measure of resistance (or robustness in network analysis; Kitano 2004). Resistance in this context is the capacity of a community to remain unchanged despite external perturbations (Grimm and Wissel 1997). PVAs, in contrast, encompass a greater array of potential questions and describe the process of modeling rather than a specific product (Gilpin and Soulé 1986). PVA metrics include, but are not limited to, the minimum population size needed for an x% probability of persisting y years (Shaffer 1981), whether or not a significant population decline will occur (Reed and Murphy 1998), and resilience of a population to perturbations (Field et al. 2019). We propose that CVA be expanded to encompass the same variety of questions as PVAs (as was described in our introduction) and to have the same capacity for flexibility with new approaches and target goals.

What is Viability?

The result of a PVA is not a conclusion relying on a single metric to dictate whether a population is viable. Such a treatment might be incomplete, because the assessment of viability is a question of what is acceptable by society for our goals and is not a biological truth (Lacy 2019). Rather, the outcome of a PVA is a suite of informa- tion that can include the probability that a population will persist to a target time, how changing that target time alters the results, the median and distribution of projected population size at that time, population trajectories at the target time, the sensitivity of the results to alterations of model parameter values and their distributions, singly and in combination, and an evaluation of how much vital rate values have to change to qualitatively alter the outcome of the model. Current interpretations of the term *viability* adopted by the US Fish and Wildlife Service for assessments of endangered species includes evaluations of resiliency, representation, and redundancy (Shaffer and Stein 2000). However, because viability is derived from human social values, one assessment could diverge with another even if both examined the same output. For a CVA, this might mean that a suite of analyses would provide a fuller picture of the viability of a community than would any single metric.

The meaning of *viability* in a CVA can be informed by historical debates about the term *community stability*. Such arguments were driven largely by differences in definitions (Ives 2005). Grimm and Wissel (1997) concluded that most interpretations of the term *stability* could be distilled into three categories: constancy, or the capacity of a system to stay unchanged; resilience, or the capacity of a system to return to a prior state following a perturbation; and persistence, or the capacity of a system to continue existing over ecological time. They further clarify that resistance is a more time-focused form of constancy, defined as the capacity of a system to stay unchanged despite the presence of a disturbance. Grimm and Wissel (1997) also noted that although persistence and resistance appear similar, they refer to different aspects of stability: staying essentially unchanged refers to a certain reference state or dynamics, including equilibrium, oscillations, or irregular but limited fluctuations. This means resistance examines the capacity of a focal system to maintain itself in the face of disturbances. Persistence through time, on the other hand, does not refer to any particular dynamic but only to the question whether a system persists as an identifiable entity in the absence of disturbances.

We suggest that the concept of community stability is a core aspect of viability, because viability analyses are generally concerned with evaluating resistance, resilience, and persistence (Lacy 2019). Therefore, we propose to follow Grimm and Wissel's (1997) observations and classify three general categories of viability for CVA: resistance analysis, which quantifies the ability of a community to not change significantly from the typical range of its reference state when faced with external pressure or disturbance; resilience analysis, which evaluates the capacity of a community to return to a prior reference state following perturbation; and persistence analysis, which assesses the capacity of a community to continue existing within prespecified conditions that demarcate it as a given entity (e.g., a kelp forest, specific food chain, alpine tundra, cloud forest). Analyses conducted within any of these categories must include specific reference to species composition, relationships among species, or ecological processes in their calculations. Furthermore, the assessment of whether a change is significant needs to be flexible to the question at hand and the knowledge of the evaluator or stakeholders.

Resistance-based Viability

Resistance is the ability of a community to remain largely constant (baseline composition, structure, processes) in the face of external forces. By modeling the effects of perturbations (such as species loss or habitat destruction) on the rest of the community, conservation biologists and resource managers might quantify the extent of an expected impact, identify unanticipated consequences, or evaluate alternative intervention strategies. Management intervention might include removing or suppressing other species in the community so that the loss of their interactions limits an extinction cascade (Sahasrabudhe and Motter 2011). One possible example of a resistance-based approach is to predict the effect of an introduced species on a given ecosystem, as was done by Jönsson and Thor (2012). They used quasi collapse risk assessment to predict the impact of the fungal pathogen *Hymenoscyphus pseudoalbidus* on the European lichen community via the fungus's negative effect on common ash (*Fraxinus excelsior*; figure 1). They estimated that on average a 12% proportion of lichen species were expected to go extinct under optimistic infection scenarios, but this proportion increased to 34% under the most likely infection scenario. Furthermore, the probability that there would be no secondary lichen extinctions following infection and die-off was virtually zero. As might be predicted, lichen species with low tree-host specificity had lower average coextinction probabilities and were more resistant to die-offs. Doizy and colleagues (2018) addressed a similar resistance-based question in which they simulated the introduction of an invasive insectivore, herbivore, carnivore, and omnivore to a community on a small island ecosystem off of the coast of Britain. They predicted that introduced generalist species, particularly omnivores, threatened native birds, which would then result in an indirect negative impact on the island's plant community.

Resistance analyses can be particularly useful in examining the comparative risks of various disturbances on a focal community. For example, Greenville and colleagues (2017) tested whether the impact of climate change on vegetation or the introduction of novel predators would be the greater threat to desert mammals in Australia. They found that although climate change is likely to negatively impact desert mammals via its effect on vegetation, top-down suppression of the community through the introduction of new predators would be the larger threat.

Resilience-based Viability

Resilience metrics are used to evaluate the capacity of a community to recover to its baseline state following alteration, such as how the Gulf of Mexico community might recover following the *Deepwater Horizon* oil spill (Morzaria-Luna et al. 2018). Resilience might by estimated by how many interactions in a system recover following an extirpated species' reintroduction (referred to as the *credit of ecological interactions*; Genes et al. 2017), or the expected length of time following species reintroductions until all the links between species are functional (referred to as *rewiring time*; Genes et al. 2017). This type of analysis can also be used to identify focal points for management actions, facilitating community resilience; this view of resilience measures the amount of external input required for community recovery. Marjakangas and colleagues (2018) demonstrated the utility of the credit of ecological interactions by calculating where in the Atlantic Forest frugivore reintroductions would reestablish the greatest number of species interactions over the largest area; this information could contribute to decisions about management resource allocation (figure 1).

Resilience metrics are particularly applicable to viability questions involving alternate stable states (i.e., equilibria under multiple sets of unique biotic and abiotic conditions; Beisner et al. 2003, Petraitis 2013). For communities that can exist in alternate states, we presume that the viable state is the desired one. European settlers, for example, transformed southern Australian forests into pasture, and the persistence of the resulting state makes it difficult to reverse the region to its more biodiverse forest ecosystem (Petraitis 2013). Note that in this example the reference state is the grassland, whereas the desired state is the forest. Consequently, resilience metrics could indicate the degree of change required to return a system to a desired state (i.e., to make the jump between states that exhibit hysteresis), or to indicate how much pressure can be exerted on a community before it shifts into an undesirable state. Dethlefsen and

Relman (2011) examined this question in a healthy human gut microbiome. Although antibiotic treatment is crucial to recovery from bacterial infections, it can also perturb the native microflora. Dethlefsen and Relman (2011) tested whether the human gut bacterial community returned to its normal state following the disturbance caused by antibiotic treatment and found that although the community exhibited some resilience it did not return to its original state.

Persistence-based Viability

The concept of persistence was the original impetus behind the first PVAs (Beissinger 2002). In the context of a CVA, persistence would focus on the likelihood that a community will stay within predetermined boundaries (species composition, links, processes) for a given period of time. Unlike examinations of resistance and resilience, tests of persistence occur in the absence of specific disturbances, although it can still allow for stochasticity. This means we test to see whether a given community is sustained at a reference level over time under anticipated conditions, but we may include in our analysis for the possibility of unforeseen random perturbations. This might be as simple as taking a known PVA metric and scaling it for communities, such as how the minimum viable population size concept has been modified into ecologically effective population size (EEPS; Ebenman et al. 2017). EEPS refers to the population size of a species below which one or more other species in the community becomes extinct. Estes and colleagues (2010) applied this concept in their reexamination of the classic Aleutian Island sea otter–urchin–kelp (*Enhydra lutris–Echinoidea–Laminariales*) trophic cascade (figure 1). Kelp forests thrive when otters are prevalent and consume sea urchins, which are voracious herbivores. In areas in which otters have been extirpated, urchins devour kelp and the community collapses. Estes and colleagues (2010) estimated a threshold for sea otter density of 6.3 otters per kilometer of coastline that marked the transition between a kelp-dominated ecosystem and an urchin-dominated one. On the basis of the strong relationship between sea otter density and kelp forest cover, Estes and colleagues (2010) suggested that tracking the extent of kelp forest would be a more cost-effective method for measuring sea otter recovery than is monitoring the otters.

Calculating community persistence likelihood over time can also help determine how to most effectively allocate funding and conservation efforts by comparing the impact of various management strategies. For example, McDonald-Madden and colleagues (2016) estimated the persistence of species within a suite of real and artificial communities in which persistence was calculated as the total number of species surviving 20 years where conservation funding is allocated according to different management scenarios. They found that allocating funds on the basis of return on investment (ROI), where the benefit of managing a species is the change in initial probability of persistence relative to the cost of managing that species, could result in 61% fewer species persisting over time compared with a control scenario that maximized species survival. The significant losses from ROI management were likely because the approach focused on saving individual species regardless of the impact on the broader community. Therefore, a species that costs more to rescue (therefore lowering its importance in ROI management) could have a net positive impact on the community. However, the ROI approach did not consider this possibility, potentially favoring a species with a lower cost of investment even if it provided limited functional benefits (Säterberg et al. 2013, McDonald-Madden et al. 2016). McDonald-Madden and colleagues (2016) identified multiple strategies for allocating conservation funding that minimized the number of species lost, such as the Google PageRank algorithm or the Keystone Index (which is used to assess the importance of trophic interactions between species in a food web).

Blurred Distinctions

Although each community viability question can be separated into one of the three aforementioned categories, the ecological processes that drive a community's resistance, resilience, or persistence are intertwined. For example, the processes that lead a community to be persistent may also contribute to its resilience. This means that our viability categories can overlap depending on how we phrase our questions, even if we are examining the same community with similar methods. For example, we classify Estes and colleagues' (2010) EEPS of otters in kelp forests as a persistence metric, because Estes and colleagues (2010) intended to determine the minimum population of otters that allows for the persistence of the kelp forest. However, if we were instead to ask how many otters can be harvested before the kelp forest shifts into an urchin barren, we would consider this to be a resilience-based question even though we could still use a version of EEPS to answer it. This may seem overly semantic. However, in their examination of stability Grimm and Wissel (1997) highlight that the validity of a prediction is delimited by the ecological situation under observation. A given prediction can only relate to a particular ecological situation, and the analysis changes when the situation changes. This means that if we were to use EEPS to uncover the resilience of the kelp forest community to a given disturbance impacting sea otters (e.g., harvesting), we could not then use our results to draw conclusions about the persistence over time of the community because of the otters' presence.

Boundaries of CVA

Community ecology bridges ecosystem and population ecologies in a continuum, occupying the middle ground and overlapping the two extremes (Berlow et al. 2004, Schmitz 2010). Ecologists use different methods and organizational concepts depending on where they fall on this spectrum. Some, for example, examine questions of alternate stable states and hysteresis of a community (Beisner et al. 2003, Petraitis 2013), whereas others approach their work from a reductionist perspective, where interactions and mechanisms are examined at finer scales (Sabo 2008, Schmitz 2010). This second approach can be used to examine specific mechanisms and dynamics of a community, such as herbivore resource limitation and indirect top-down control by carnivores (Schmitz 2010). At the finest scale, community ecologists can focus on a single interspecific interaction, such as predator– prey dynamics (Sabo 2008). Each of these scales lends itself to CVA.

By having an expanded definition of CVA, we can apply viability analyses to this broad variety of questions (table 1 and supplemental table S1). However, the diversity of approaches to community ecology research might make it difficult to draw a definitive distinction between populationand community-level assessments, creating a fuzzy transition between PVA and CVA (figure 2). Essentially, at what point does a PVA transition to being a CVA as we increase the number of interacting species (e.g., Prowse et al. 2015)? Such vagueness has already been problematic within the context of CVA. Witting and colleagues (1994) called a CVA what is now referred to as a PVA metamodel (Lacy et al. 2013), whereas Tallis and colleagues (2010) cited the Ebenman and Jonsson (2005) CVA as an example of an ecosystem viability analysis. Our solution to the vagueness problem is to employ the approach used in fuzzy logic (figure 2). Where traditional logic employs distinct, nonoverlapping categorization (i.e., analysis can be either a CVA or a PVA but not both), fuzzy logic allows for a gradient of possibilities (Fisher 2000). Therefore, a viability analysis involving a predator–prey dynamic has been called a PVA (e.g., Sabo and Gerber 2007), but we recognize that it at least conceptually contains aspects of a CVA. As modeled systems become more complicated, such as with tritrophic cascades or apparent competition, they become more akin to CVAs (figure 2).

Conducting a CVA

The basic steps for conducting a CVA are to delineate the focal community, to determine the viability questions and what methods and metrics address the questions, to perform the calculations required for the chosen metrics, to address uncertainty, and to validate the model. We briefly describe each.

Step 1: Delineate the focal community.

The first step to a CVA is to clearly identify, delineate, and justify the community that is the focus of the work. Grimm and Wissel (1997) provided a checklist that assists in this matter, which we adapt for a CVA: First, identify the level of description (i.e., what is the community?), then identify the variables of interest, determine the reference state or dynamic, establish what constitutes a disturbance, and decide on the spatial and temporal scale of the study.

Setting the boundary to a community is situation specific, and can include as many or few species, trophic levels, interactions, and so on as needed (Vellend 2016). This can be anything from small groups of strongly interacting species (also called *modules*, generally consisting of 2–4 species) to large food webs or even community phase states (where the community can be characterized by a set of dynamic state variables with their relations to each other defined by a set of parameters, and the selected set of variables will persist over time in a specific one out of a number of different possible configurations; Beisner et al. 2003). Included in this step is the delineation of species or functional groups and their direct interactions. Anything not included within the operative community is externalized, either as outside variables that may influence the community of study or as effects inherent to the system's dynamics (Vellend 2016). Unlike with species, however, the interactions within the community can be hypothetical, meaning a CVA can be conducted using interactions that may not yet be fully supported with field data. Such a choice is useful in cases in which researchers attempt to replicate real-world community demographic patterns with hypothesized interactions, which, if it is successful, would imply that these hypothesized interactions are present (e.g., Middleton et al. 2013, Prowse et al. 2013). Even if a given interaction is hypothetical, however, we cannot perform CVAs without data. Indeed, viability analyses are famously data hungry (Lacy 2019). Therefore, determination of the focal community also requires a researcher to identify available and required data.

Determination of the variable of interest (step 2) requires us to select which species and interactions within our chosen community are the focus of our analysis of viability. This step can help inform how to narrow the level of description to only what is necessary in step 1. If our variables of interest are two or three direct interactions or species, for example, then we would externalize everything not included in the module surrounding the variables. Once they are finalized, we can then identify the reference state of the community (step 3). This step specifically addresses the question of what we want the community to look like, which we use as our reference (i.e., normal) state. McDonald-Madden and colleagues (2016), for example, evaluated how multiple algorithms can inform the allocation of conservation funds for prolonging community persistence of multiple real-world and generated webs compared with a control management strategy. Yun and colleagues (2017) also established a baseline of their Baltic Sea fisheries community with a mathematical model projecting the consequences of single-species management over time, allowing for a comparison with projections from their advocated multispecies management model (figure 1). A given reference state can still include dynamics; for example, the classic population cycles of snowshoe hares (Lepus americanus) and lynx (Lynx canadensis; Peckarsky et al. 2008) are part of the normal reference state of the northern boreal forest. With a reference state in hand, we can then list which disturbances or drivers we believe keep or will keep us from reaching the target state (step 4). Finally, we decide the time and spatial scales over which we aim to make predictions (step 5).

In their original CVA paper, Ebenman and Jonsson (2005) focused primarily on the use of networks to describe and evaluate a community. Although researchers do not need to create an ecological network to perform a CVA, doing so involves the same steps as outlined above with the added step of generating a list of species or functional groups of interest (the nodes) and their interactions (their links; see Ulanowicz 2004). Interaction links can be directional, weighted, or neither, and represent interactions such as consumption, competition, symbioses, predation, and so on (Dormann and Blüthgen 2017). These networks can be static (i.e., they do not portray changes over time; e.g., de Visser et al. 2011), or they can be dynamic, incorporating anticipated changes over time in nodes and links (Ebenman and Jonsson 2005). Researchers tend to create networks focused on single functions rather than mixing, for example, pollinator links with predation links, although there have been recent explorations combining links of different functions into a single network (Dormann and Blüthgen 2017). Creating such combined networks is currently exceedingly difficult.

Step 2: Decide on viability questions, metrics, and models

Presumably if one is doing a CVA, it is to predict the future state of a community under current, anticipated, or proposed alternate conditions, or to compare multiple extant communities. The key is to find models and metrics relevant to the specific question (table 1 and supplemental table S1). There are multitudes of modeling methods, each of which requires different levels of data (see figure 1 in Geary et al. 2020) for an extensive list of modeling approaches and their use). Models are generally categorized as ecosystem based, and they are used to incorporate broad system components (e.g., populations, species, functional groups) and processes (e.g., predator–prey interactions, perturbations, dispersal) into one modeling framework (Geary et al. 2020). Each model has different associated metrics, which must be chosen to ensure that a focal research question is addressed. For example, we might care about maintaining food web topology, which could be calculated by some form of network model measuring betweenness centrality or link density (e.g., González et al. 2010, Morris et al. 2014). Alternatively, our focus may be on calculating the conditions required for the persistence of a given community phase state, which could be calculated with a state and transition model in the face of a triggering event (pulse perturbation) or a driver (press perturbation; Bestelmeyer et al. 2017).

One approach that has been suggested for evaluating community-related objectives has been taken from economics, which involves defining a suite of desirable states on the basis of constraints defined by management goals and precautionary principles (Cury and colleagues (2005) referred to these as viable states, which might be confusing in our situation). Rather than optimizing, it identifies acceptable solutions (referred to as *viable evolutions*; Cury et al. 2005). This approach can deal with one type of uncertainty (setting goals and boundaries) by setting constraints through the definition of what is undesirable, particularly when there are many stakeholders defining potentially conflictive values. One can then decide among a suite of acceptable outcomes from which to select a management plan (Cury et al. 2005).

Step 3: Enact Calculations

CVAs can be run once we have a delineated community and selected viability metrics. One of the most used analyses for complex communitybased calculations is individual- or agent-based models (IBMs), which are applicable across multiple types of community approaches (Schmitz 2000, Ebenman et al. 2004, Scotti and Jordán 2017, Lacy 2019). In an IBM, there is a suite of rules applied to each entity (individuals in a population, species, or functional group) that dictate interactions at each time step (Scotti and Jordán 2017). An alternative approach was used by Doizy and colleagues (2018) to depict the community as a matrix and use generalized models based on balance equations to investigate the consequences of invasive species on native extinctions. Such models describe the structure of a system in terms of gains and losses of variables such as biomass but do not restrict these processes to specific functional forms (Gross and Feudel 2006). These are only a few possible options, as was noted in step 2 (Geary et al. 2020).

The wide use of PVA for conservation purposes has been facilitated by the availability of software (such as Vortex and RAMAS), with manuals, online chat boards, and help desks that create a user-accessible approach to viability modeling. As with the early years of PVA, the few papers published on CVAs so far have generally presented models that are developed from the ground up, as do most papers that investigate communities in general. However, some software packages or programs that can be used for CVA exist, such as packages in R and Python (table 2). There is also other more specialized software that has potential for CVA. For example, because of the economic importance of multispecies management for fisheries, researchers at NOAA and the University of British Columbia have developed user-friendly software called Ecopath with Ecosim (EwE). EwE is the most applied tool for modeling marine ecosystems worldwide (Heymans et al. 2016). Through dynamic mass-balance modeling of food webs, EwE can be used to identify and quantify major energy flows in a community, describe interactions among species, and evaluate the effects of environmental changes on the community (Heymans et al. 2016). The software has been used to show that pressure from resident bald eagles (Haliaeetus leucocephalus) increases fish, crab, and mussel biomass in the Puget Sound via trophic cascades (Harvey et al. 2012) and that complex predation and competition interactions may counteract the putatively positive effect of climate change on primary productivity in Australian waters (Brown et al. 2010).

Another program available for CVA models is MetaModelManager, a multispecies population dynamics package that connects to the widely used PVA software package Vortex (designed by Lacy et al. 2013). Although these were initially designed for PVAs and likely fall into the gradient between CVA and PVA, they may provide an alternative for certain questions to building models from scratch—particularly because many conservation biologists and managers are already well versed in Vortex's use.

Step 4: Address Uncertainty

Uncertainty in model construction is the degree to which we know a parameter value or distribution, or model structure (e.g., what species or inter- actions to include). Uncertainty in predictions can increase as models become more complex, whereas uncertainty in parameters and potential omission of key interactions increase when models are too simplified (Geary et al. 2020). As is true with all models, there will be a degree of compromise in model structure in CVAs, as well as with parameter estimates, because of limited data, observer error, bias, and sampling variance (McGowan et al. 2011). Analyses that lack an assessment of uncertainty in structure and in predictions can provide a false sense of accuracy in results (Geary et al. 2020). Therefore, CVAs should always have some method of quantifying or addressing uncertainty (see table 1 in Geary et al. 2020 for a list of ways to address uncertainty in complex models).

Step 5: Model Validation

A central demand for models is their validation. As with all models, PVAs and CVAs are simplifications of the real world, which is another reason it is suggested that results from

PVAs—and, by extension, CVAs—should be used comparatively (Beissinger and Westphal 1998, Reed et al. 2002). Consequently, predictive reliability should not be held up as a standard for validation; unlikely outcomes happen in the real world. One level of validation is to determine the degree to which a model structure reflects the real world and the accuracy and precision of its parameters. Another type of validation can be to determine whether the modeled system behaves in a biologically reasonable manner when manipulated. In some cases, such as with communities with fewer or smaller species (including bacterial communities), it might be possible to replicate microcosm experiments and compare the distribution of outcomes with that predicted by the model (e.g., Jonsson et al. 2018, Schmitz 2000). We note, however, that such experiments are also models with similar benefits and limitations to computational models. Consequently, what we recommend is derived from the concept of adaptive management (Lacy 2019): Create a biologically reasonable model, use it to make predictions about the general behavior of a system (rather than a specific quantitative result), and then refine the model on the basis of observed results.

Conclusions

Incorporating community dynamics into management expands the realm of conservation questions that can be asked and increases the types of tools available for evaluating species and ecosystem conservation. CVA was proposed to assist in this process (e.g., Ebenman et al. 2004, Ebenman and Jonsson 2005), but so far it is a concept that has been used sporadically and narrowly in the literature. In the present article, we introduce a framework for CVA that expands on its original definition to resemble more closely that of a PVA. We postulate that a CVA, in parallel to PVA, should include any synthesis of knowledge assessing the status, threats and management options of an ecological community. Such assessments can be used to calculate resistance, resilience, or persistence as viability measures of a focal community. This expanded framework allows us to include multiple types of analyses across the breadth of community ecology—each of which can be tailored to answer specific viability questions—helping to draw together a range of ideas that can be focused on conservation assessment.

Fisheries science, which is currently at one forefront of community or ecosystem-based management, categorizes these types of multispecies models as conceptual, strategic, or tactical. Conceptual models develop an understanding of ecosystem processes, strategic models focus on broad scale assessments of patterns of change (such as system-wide maintenance of biodiversity), and tactical models are used to investigate management alternatives that often change on an annual basis (Plagányi et al. 2014). We envision CVAs as strategic models that can evolve into tactical models, similar to the way some multispecies fisheries models that started as conceptual or strategic are now used for day-to-day tactical decisions (Plagányi et al. 2014).

Approaching species and ecosystem conservation using CVAs allows resource managers to evaluate alternative conservation regimes that include quantitative examinations of species interactions or ecological and ecosystem services, something highlighted in the literature as urgently needed (Soulé et al. 2003, Säterberg et al. 2013). The introduction of metamodels designed to include species interactions (Lacy et al. 2013) is facilitating adoption of more community- based ideas in conservation (e.g., Prowse et al. 2015), as are the advances in ecosystem-based models in marine systems (Geary et al. 2020). However, having a formal framework for CVA can help focus management and research questions. It also allows for the possibility that a community might be viable under some criteria but not others. Furthermore, it provides an improved understanding of the questions we ask when discussing whether a community is viable, suggesting a more nuanced approach. Indeed, the same is true for PVA;

simply stating that a PVA was performed does not inform one of a study’s specific goals, metrics, or methods. Ultimately, the specificity of the questions being asked should lead to a better comprehension of a community’s vulnerability to various perturbations and responses to management alternatives. Also, as with PVA, we believe that calculations of CVA metrics should be treated comparatively rather than as quantitatively accurate, which will be useful for comparing the relative efficacy of potential management actions on communities and for asking what-if questions (cf. Coulson et al. 2001, Reed et al. 2002, Lacy 2019).

CVAs and their applications will have the same limitations that community ecologists have identified within the field in general—primarily, that community dynamics can be complicated and community boundaries difficult or arbitrary to define. Furthermore, a scarcity of data can present challenges for resource managers in assessing interaction- based methods of management (Tallis et al. 2010). We implemented flexibility into our CVA framework in part to provide a solution to this problem. We believe that our expanded framework will allow resource managers to use CVAs as a tool to better incorporate community ecology into ongoing conservation projects and plans, particularly when conducting ecosystem-based management.

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Supplemental material

Supplemental data are available at BIOSCI online.

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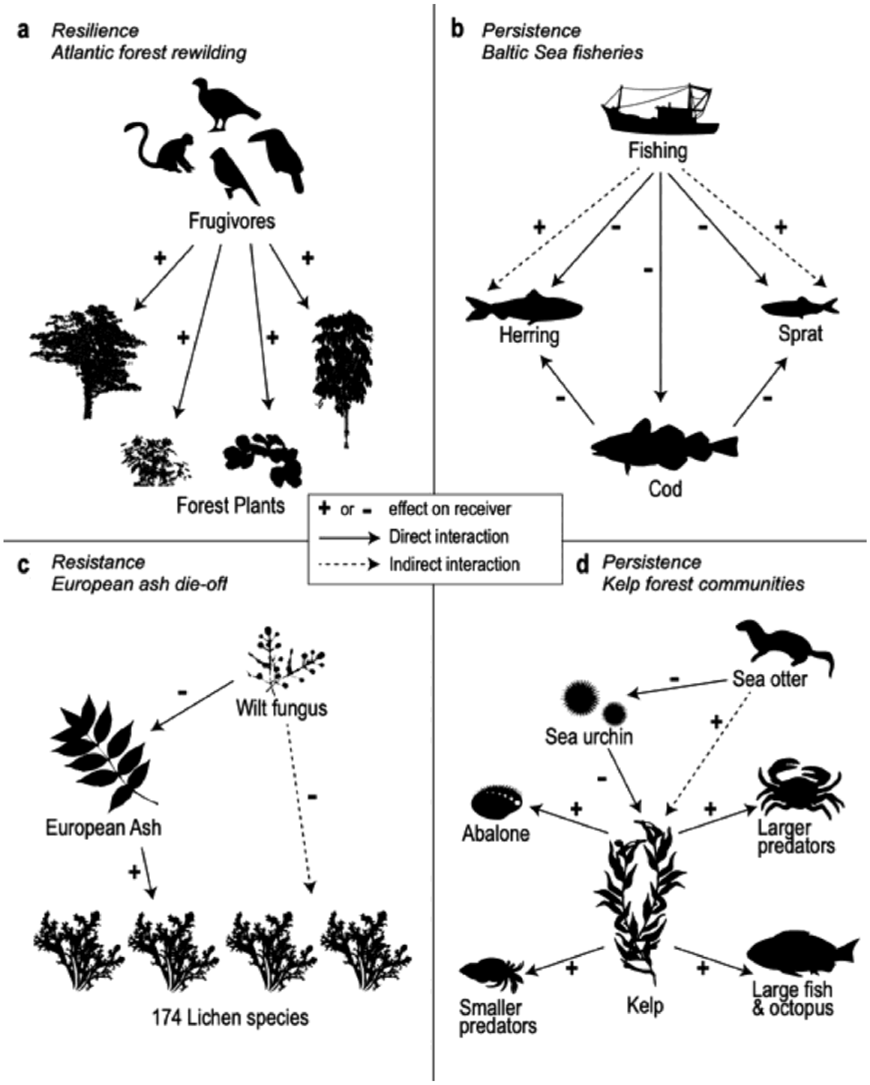

Figure 2-1 Visual representations of four communities examined through various community-based viability methods. Direct interactions are represented with solid arrows, whereas indirect interactions are represented with dashed arrows. The plus and minus represent whether the interaction has a positive or negative effect, respectively, in the direction of the arrow.

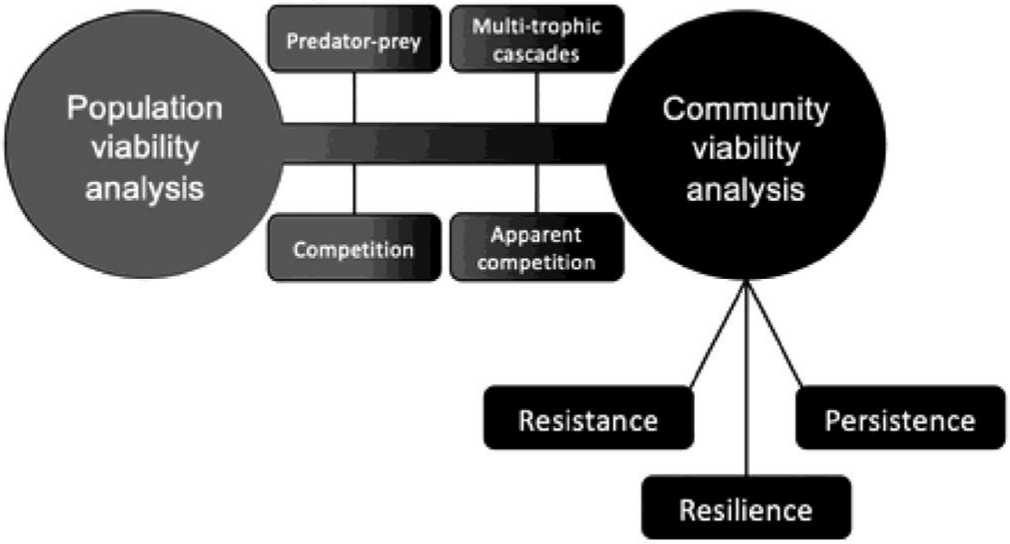

Figure 2-2 A visual representation of our interpretation of a gradient of viability assessment types, where community viability analysis (CVA) is on a continuum to the right of population viability analysis. CVA is split into three possible groups: resistance, resilience, and persistence. Certain approaches to viability, such as investigations of predator–prey and competition interactions, exist in a gradient that mixes components of two viability analyses.

Table 2-1 Types of community viability analysis (groups) with examples of metrics, including example research or management question from published case studies.

Viability type	**Example metric**	**Example research or management question**
Resistance	Probability species richness falls below some value within a fixed period, following loss of a target species	What is the probability that numbers of lichen species fall below a certain threshold following ash dieback in Europe? (Ebenman et al. 2004, Jönsson and Thor 2012)
	Comparative likelihood of two or more disturbances resulting in observed community dynamics	Is community change due to the invasion of European settlers more likely than was disease to have resulted in the extinction of the thylacine (Thylacinus cynocephalus)? (Prowse et al. 2013)
	Probability that a compensatory perturbation will increase the resistance of a community to a given disturbance	Can we minimize the number of secondary extinctions in the Coachella Valley food web after the loss of certain species by removing or suppressing other interacting species? (Sahasrabudhe et al. 2011)
Resilience	The number of interactions expected	How many interactions from the original Brazilian forest system will be reestablished with the

	to be rewired (reconfigured) in a focal area following species reintroduction	reintroduction of agoutis (Dasyprocta leporina)? (Genes et al. 2017)
	Recovery time from a perturbation in a system with a tipping point between stable states	How long does it take a forest to recover after harvest or burning in a tropical peat community in which there is a tipping point? (Dieleman et al. 2015)
	Probability that a community will recover to a reference state after a perturbation	Is the state of a human gut microbiome maintained in the face of treatment with antibiotics? (Dethlefsen and Relman 2011)
Persistence	Predicted success of alternative conservation strategies	What is the best method of allocating money for conservation to ensure the fewest possible extinctions in a managed food web? (McDonald-Madden et al. 2015)
	Population size below which one or more other species in the network become extinct	What is the population size of sea otters required to sustain the kelp forest community phase state due to a trophic cascade? (Estes et al. 2010)
	Neutral or increasing population trends of multiple interacting species	Can we cull increasing deer (Odocoileus spp.) populations in Alberta to stabilize or reverse population decline of caribou (Rangifer tarandus caribou) due to apparent competition via wolves (Canis lupus), but without extirpating wolves? (Serrouya et al. 2015)

Table 2-2. Example R and Python packages capable of performing analyses that might be used to assess community viability.

Code package	Capabilities
Cheddar (R)	Provides a representation of an ecological community and a range of functions for analysis and visualization. Allows interweb comparisons such as examining changes in community structure over environmental, temporal or spatial gradients (Hudson et al. 2013)
The Community Simulator (Python)	Simulates microbial population dynamics (Marsland et al. 2020)
NetworkExtinction (R)	Simulates the extinction of species in a food web and analyzes the resulting cascading effects (Corcoran et al. 2019)
foodweb (R)	Calculates twelve basic measures of food web network structure from binary, predator-prey matrices (Perdomo et al. 2012)
fluxweb (R)	Compute energy fluxes in trophic networks from resources to their consumers and can be applied to systems ranging from simple two-species interactions to highly complex food webs (Gauzens et al. 2019)
HMSC (R)	Model-based approach for analyzing community ecological data via Joint Species Distribution Modeling. This package uses a Bayesian framework with Gibbs Markov chain Monte Carlo (MCMC) sampling (Tikhonov et al. 2020)
statnet (R)	Collection of packages for statistical network analysis. Provides an integrated set of tools for the representation, visualization, analysis, and simulation of network data (Hunter et al. 2008)
timeordered (R)	Approaches for incorporating time into network analysis (Blonder 2018)
rmangal (R)	Archives published ecological networks and provides a mechanism for their retrieval (Poisot et al. 2016)
EcoTroph (R)	Software for modeling marine and freshwater ecosystems using trophic levels. Aggregates species into trophic levels to track biomass flows at larger scales. Links Ecopath with Ecosim to R (Colléter et al. 2013)
iGraph (Python and R)	Routines for simple graphs and network analysis (Csardi and Nepusz 2005)
Bipartite (R)	Focuses on webs consisting of only two levels (bipartite), e.g., pollination webs or predator-prey webs (Dormann et al. 2008)
NetworkX (Python)	Allows for the creation, manipulation, and study of the structure, dynamics, and functions of complex networks (Hagberg et al. 2008).

Chapter 3

Biased assessment of thermal properties of birds from estimated body density (Adam J. Eichenwald, J. Michael Reed). Published in Journal of Thermal Biology (2023) 112:103472.

Abstract

Parameter approximation is often necessary when calculating species thermal properties, and researchers historically have assumed animals are spherical when estimating volume and density. We hypothesized that a spherical model would result in significantly biased measures of density for birds, which are generally longer than they are tall or wide, and that these inaccuracies would significantly alter the outputs of thermal models. We calculated the densities of 154 bird species using sphere and ellipsoid volume equations and compared these estimates to one another and to published bird densities measured using more exact volume displacement methods. We also calculated evaporative water loss as a percentage of body mass per hour, a variable known to be critical for bird survival, twice for each species, once with the sphere-based density and once with the ellipsoid-based density. We found that volume and density estimates were statistically similar between published densities and those estimated using the ellipsoid volume equation, suggesting that this method is suitable for approximating bird volume and calculating density. In contrast, the spherical model overestimated body volume and therefore underestimated body densities. This resulted in the spherical approach consistently overestimating evaporative water loss as a percent of mass lost per hour than the ellipsoid approach. This outcome would result in mischaracterizing thermal conditions as lethal for a given species, including overestimating vulnerability to increased temperatures due to climate change.

Introduction

Body density (mass per unit volume) is a critical parameter for calculating the fundamental thermal constraints on an animal (Kearney et al., 2021). This parameter, however, is not often available for a given species. Both mass and volume are needed to calculate density, and although mass is relatively easy to measure and is available for many species (e.g., Chamberlain, 2021; Dunning, 2008; Silva and Downing, 1995), finding the volume of an animal is more difficult. Exact volumes of birds, for example, have sometimes been calculated using water displacement (Hazlehurst and Rayner, 1992) or by making casts (Dubach, 1981), but this can be tricky (or not allowed) if working with museum specimens that may not be damaged. There are published equations for estimating volume from body length for frogs (Tracy, 1972) and lizards (Norris, 1967). Generally, however, when we calculate a bird's volume we assume that the creature is a sphere (Buckley et al., 2021; Mitchell, 1976); this is likely a historical artifact because the equation for a sphere is relatively simple ($V = \frac{4}{3}\pi r^3$) and museums often record a specimen's body length (2r) before archiving it in a collection, or the length can be acquired readily. Every point on the outside of a sphere is at the same distance r from the center of the sphere; birds, however, are distinctly non-spherical, typically being significantly longer than they are tall or wide. These are characteristics of an ellipsoid rather than a sphere and is likely why well-used thermal programs such as NicheMapR assume an endotherm is represented by an ellipsoid by default (Kearney et al., 2021). Although the distinction may seem pedantic, the greater the difference between length and radius of a bird's body, the more volume will be overestimated by use the sphere equation. This would result in significantly smaller estimations of density and inaccurate conclusions regarding thermal constraints. Here we estimate the degree to which sphere-based volume calculations of birds underestimate body density, and whether ellipsoid measurements of volume result in sufficient approximations of body density for quantifying thermal properties of birds in a mechanistic model.

Methods

We obtained 5 specimens each (3 males and 2 females) for 154 species of birds at the Harvard Museum of Comparative Zoology (MCZ). Specimens were selected as part of a separate project on birds in the Mojave Desert. Species were included in the study if they appeared in the Mojave Desert surveys conducted by Iknayan and Beissinger (2018), or if their ranges as calculated by Fink et al. (2020) cross into the Mojave Desert. Waterbirds were excluded from these measurements unless the species was specifically surveyed for by Iknayan and Beissinger (2018).

For each specimen, we measured the length, width, and height to 0.1 mm using digital calipers. If the bird was too large for the calipers, as with some of the bigger raptors, we used a steel ruler to measure to the nearest millimeter. Length was measured from the base of the mandible to the base of the cloaca; as bird feathers are not part of the metabolic process, we did not include measurements of tail feathers as part of the body length. Width was measured at the widest part of the bird near the midpoint of the breast, not including the wings. Height was measured from back to the greatest distance of the breast.

These specimens usually did not have their masses recorded at the time of collection. We obtained mass data for each species from VertNet, a database that contains data for specimens from hundreds of museum collections around the world. For each species, we used the rvertnet package (Chamberlain, 2021) to search for specimens that had their masses and sexes recorded prior to their preparation for a museum collection, and we downloaded all data associated with these specimens. Through proofing, we discovered that apparent typographical errors existed in this dataset, usually in instances where the original data transcriber forgot to place a decimal point and inflated a single data value by a factor of 10 or 100. We removed outliers from each species using the outlier R package (Komsta, 2022) to ensure that mean mass was not influenced by what were likely typographical errors.

Sexual dimorphism in body size is common in birds (Owens and Hartley, 1998), which would result in different volumes and masses depending on sex, though there is no reason it should affect density. To ensure we were calculating density as accurately as possible, we assumed intraspecific males and females had different average masses. We calculated the volume for each specimen individually using the equations for both an ellipsoid and a sphere, assumed males of the same species had the same mass as the average of all the males of that species from VertNet, and assumed females of the same species had the same mass as the average of all the females of that species from VertNet. We then calculated the density of each specimen twice, once by dividing the mass by the ellipsoid-estimated volume and once by dividing the mass by the spherical-estimated volume. We then averaged these values to calculate a single average ellipsoid-based density and a single average sphere-based density per species.

After comparing volume and density estimates from ellipsoid and spherical estimates, we compared their densities estimates to known values from 15 of the species published by Seamans et al. (1995) and Dubach (1981). Due to unbalanced sample size and unequal variance (as revealed by a Levene's Test), we used a one-way ANOVA with a Welch's correction and a post hoc Bonferroni test to determine whether there is a significant difference between the pre-measured densities and the densities calculated using the sphere or ellipsoid volume equations.

Our next step was to see whether differences in densities as calculated by the ellipse and sphere equations resulted in significant differences in estimates of the birds' thermoregulatory processes and constraints. We used the endotherm function mechanistic thermal modeling R program NicheMapR (Kearney et al., 2021; Kearney and Porter, 2017) to generate thermal properties to test these predictions. For each species, we left all parameters in the function at their default settings except for mass and density, and we ran the mechanistic models twice for each species: once with the density calculated from the sphere equation, and once with the density calculated from the ellipse equation. The average species' mass was kept the same for each run so that density was the only variable to change. NicheMapR calculates many output variables, but we selected evaporative water loss as a percentage of body mass per hour as a characteristic variable. This variable is known to be critical for bird survival, particularly those living in desert regions (Albright et al., 2017). We used a paired t-test to compare estimated evaporative water loss as a percentage of body mass per hour as calculated with the ellipsoid and spherical methods to determine whether the two approaches for estimating bird densities result in consistent differences in thermal properties.

Results

Body volume estimated from spherical estimates of birds (770 specimens of 154 species) was consistently higher than when using the ellipsoid method, resulting in an average difference of 663.6 ± 173.2 kg/m3 in densities between the two methods (Fig. 1). This apparent bias increased with birds that were of higher body densities (Fig. 1). There were statistically significant differences found in the categories of known densities, ellipsoid-based estimates, and sphere-based estimates (ANOVA, $F = 1219.4$, corrected $df = 34.1$, $p < 0.001$), A post-hoc Bonferroni test revealed that there was no statistically significant difference between published empirical densities and those calculated using the ellipsoid volume equation (Bonferroni test, corrected $df = 26.6$, mean = 769.1, sd = 190.4, $p = 0.82$) (Fig. 2); densities calculated using the sphere volume equation were significantly lower (Bonferroni test, corrected df = 13.9, mean = 104.2, sd = 55.2, $p < 0.001$) (Fig. 2). Furthermore, the spherical approach gave consistently lower estimates of estimated evaporative water loss as a percent of mass lost per hour than the ellipsoid approach (paired t-test, $t = -22.5$, df = 153, p-value <0.001) (Fig. 3).

Discussion

We predicted that volume, and therefore density, of birds would be statistically systematically different based on whether we used the sphere or ellipsoid equation. We also expected that these differences would cause densities as predicted by the sphere equation to be less accurate, and that these differences would also influence conclusions about a species' thermal constraints. Indeed, we found that body volume from spherical estimates of birds was consistently higher than when using the ellipsoid method. This, in turn, resulted in a consistent bias in predicted body densities, with the spherical method underestimating densities compared to the ellipsoid method. When compared to empirical measures of body densities (Dubach, 1981; Seamans et al., 1995), the estimates based on the ellipsoid equation was not significantly different. Average body densities estimated by calculating volume with the sphere equation were on average 150.6% lower than those reported from empirical studies. Furthermore, we found that if data from the spherical equations were used to calculate thermal models, they would result in significantly higher estimations of evaporative water loss as a percentage of body mass per hour than from the ellipsoid equation.

This overestimation would lead to inaccurate depictions of an animal's response to its environment at current and predicted increases in temperature due to climate change (see Arnell et al., 2019). Desert birds, such as those measured in this study, are known to live at the edge of their thermal tolerance (Smith et al., 2015, 2017; Talbot et al., 2017), routinely withstanding evaporative water loss of at least 5% of body mass per hour despite a lethal level of 15% per hour (Albright et al., 2017). Overestimations of this variable would inevitably result in mischaracterizing certain thermal conditions as lethal for a given species when in fact the species is still able to survive. Accurate estimations of a bird's response to its thermal environment is critical for researchers aiming to predict how these species will fare under climate change conditions (e.g., Albright et al., 2017; Riddell et al., 2021; Riddell et al., 2019); therefore, scientists should avoid approximating an animal as a sphere when calculating volume or density for thermal equations.

We note that although our ellipsoid estimates of density were not different from empirical measures, some error in our approach could occur because of variation in the degree to which a bird is stuffed compared to its living volume. We anticipate, however, that this would have little effect on our conclusion about ellipsoid vs. spherical assessments. We also found that for some species, we estimated densities over 1000 kg/m^3. We find this unlikely, as water itself has a density of approximately 1000 kg/m^3. At face value, our calculations would suggest that those few species are denser than water. Instead, it is probable that these species do have higher densities than do others in the real world, but the specimens we measured in the MCZ had different masses when they were alive than the average calculated from VertNet. This could result in inflated body densities.

Conclusions

These results demonstrate that scientists aiming to create mechanistic thermal models of birds – and likely other endotherms – should not rely on sphere-based equations for calculating volume to estimate density. Instead, it is better to calculate density using volume obtained from the ellipsoid equation, which will require more data but will significantly improve accuracy of results and predictive capacity.

Funding

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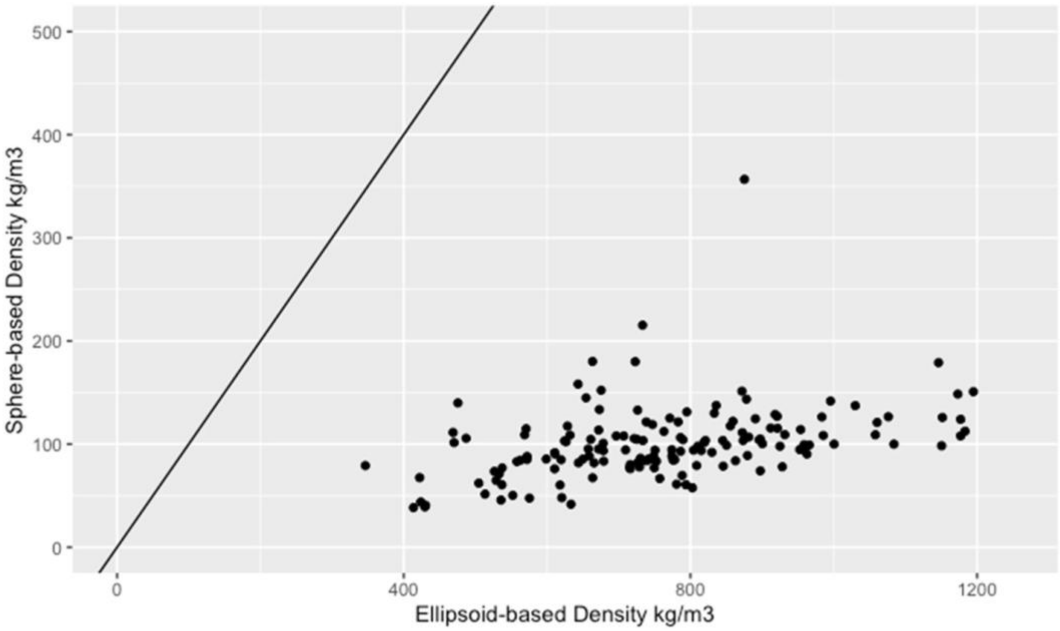

Figure 3-1 Densities of each measured species using the ellipsoid volume equation (x axis) and the sphere volume equation (y axis). The solid black line represents a hypothetical 1:1 relationship between the two variables.

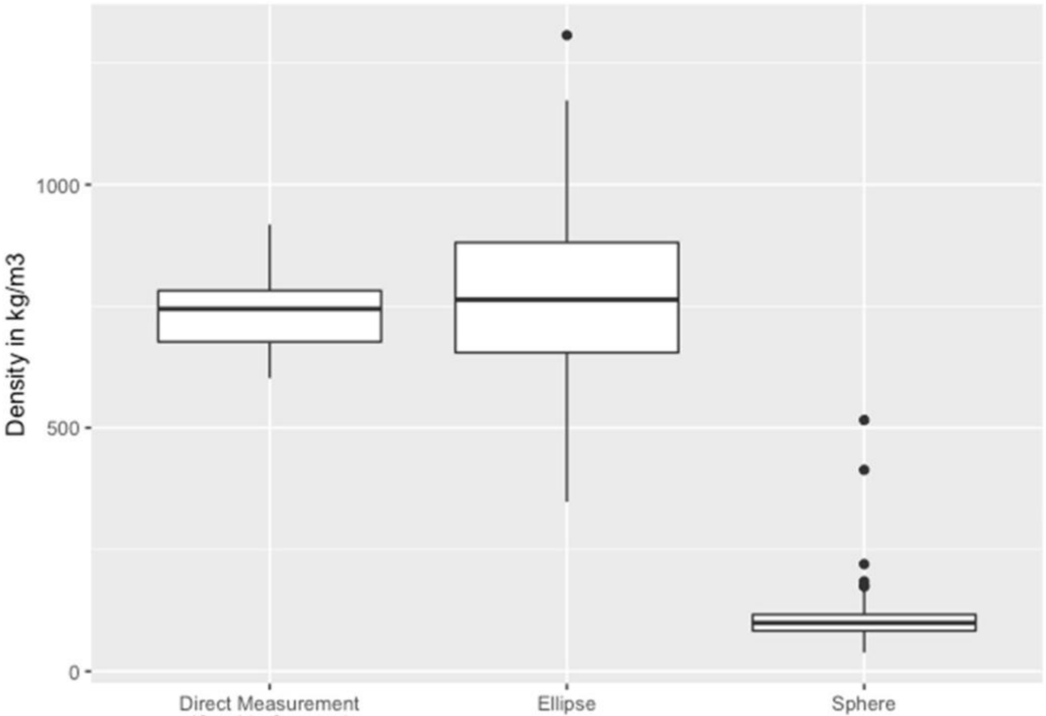

Figure 3-2 Body densities calculated for each species measured in this study using the ellipsoid equation (middle) and the sphere equation (right) (n = 154 species). Densities calculated from direct measurement (left) were gathered from published studies (n = 15 species; a subset of the species we assessed). There was no significant difference between the pre-measured densities

and the densities calculated using the ellipsoid volume equation (Welch Two Sample t-test, t = − 1.37, df = 25.95, Bonferroni- corrected p = 0.35). Densities calculated using the sphere volume equation were significantly smaller than the pre-measured densities (Welch Two Sample t-test, t = 27.58, df = 13.88, Bonferroni-corrected p < 0.001).

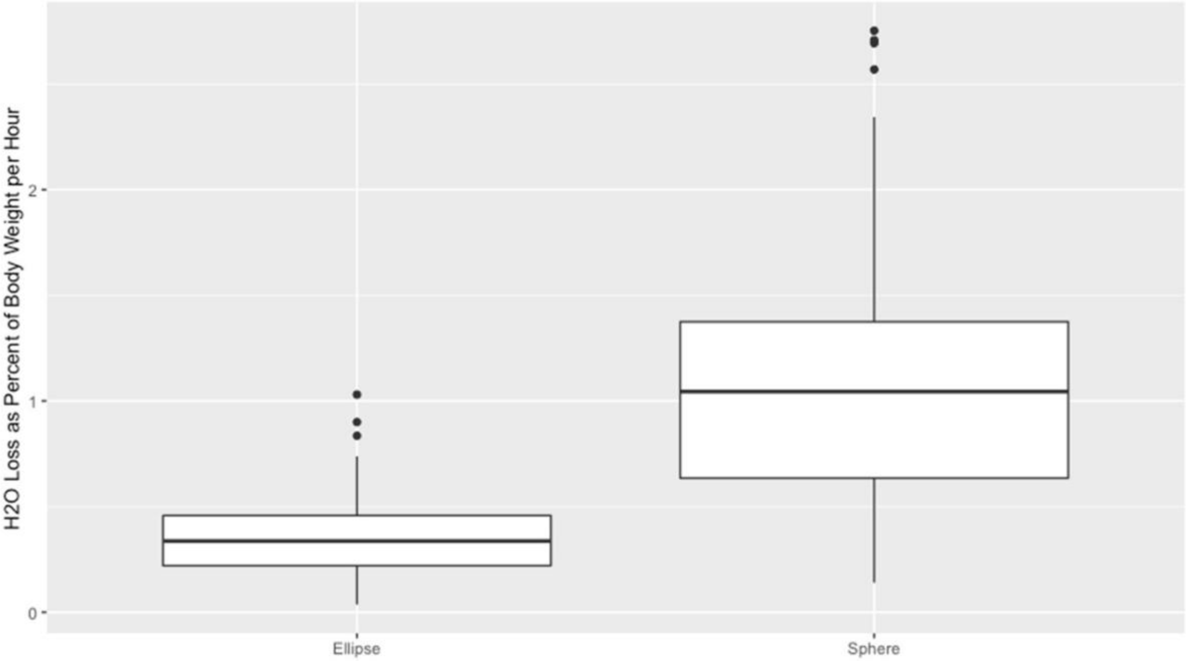

Figure 3-3 Estimated evaporative water loss for 154 bird species where body densities were calculated using two different models for estimating body volume (paired *t*- test, t = − 22.5, p < 0.001).

Chapter 4

Using a mechanistic model to assess thermal vulnerabilities of Mojave Desert birds (Adam J. Eichenwald, J. Michael Reed). In Review at Journal of Thermal Biology

Abstract

Desert bird populations are increasingly vulnerable to rising temperatures driven by climate change, with implications for their survival, behavior, and distributions. We used a mechanistic model to estimate thermal vulnerability, defined as the minimum percent shade a species requires to survive given a specific combination of solar radiation and air temperature, for 151 bird species in the Mojave Desert. This model was parameterized with data collected from museum specimens and the primary literature. We found that bird species differed significantly in their relative susceptibilities to temperature, with an almost 30% spread between the lowest and highest amount of shade required to survive desert thermal conditions. Species sorted optimally by thermal risk into 18 clusters. The marginal effect of thermal vulnerability revealed that species require an average of 79.7 ± 5.3% shade to survive (holding temperature and solar radiation at 50°C and 1400 watts/m2, or full sun). The least thermally vulnerable species were approximately 16% different than the average of all species, and 35.7% different than the most vulnerable species. Reflectance from body feathers explained 21% of the variation in thermal vulnerability; dorsal reflectance was significantly negatively associated with thermal vulnerability, as was body mass. The estimated amount of shade required to survive, according to the mechanistic model, will change given different combinations of temperature and solar radiation, but the relative vulnerabilities between species would not change. Our findings expand understanding of avian thermal properties and can contribute efforts aimed at predicting and mitigating the adverse effects of climate warming on desert bird communities.

Introduction

Desert birds are facing increasing risks from rising temperatures due to climate change (McKechnie et al., 2012; Murali et al., 2023). For example, heat waves are becoming more frequent and intense, posing a significant threat by increasing evaporative water loss and the possibility of lethal dehydration (Albright et al., 2017; Cabello-Vergel et al., 2022). In addition, rising cooling costs and water requirements driven by climate change can further threaten desert bird populations (Riddell et al., 2019), and have already been linked to population declines and mass die-off events in arid regions (McKechnie et al., 2012; McKechnie et al., 2021b; Pattinson et al., 2022). As a further concern, only a fraction (20%) of desert areas with high diversities of birds and low predicted impact of climate change are in protected areas (Ma et al., 2023). While desert birds have evolved various heat dissipation mechanisms and behaviors to regulate their body and brain temperatures, there are physical limits to the effectiveness of these adaptations (Albright et al., 2017; Baker, 1982; Pessato et al., 2020). It remains uncertain whether these strategies can sufficiently mitigate the risks of surpassing avian physiological limits under unprecedented climate conditions (Pessato et al., 2020). Therefore, identifying species most vulnerable to rising temperatures can improve predictions of the ecological impact of climate warming (Seebacher et al., 2023).

Mechanistic thermal models have proven valuable in understanding avian vulnerabilities to increasing heat (Albright et al., 2017; Ma et al., 2023), as they allow researchers to simulate the physiological responses of organisms to changing thermal conditions and predict how these responses may impact their survival, behavior, and distribution (Gates, 1980; Kearney et al., 2010). For instance, these types of models were used to uncover an energetic bottleneck as a potential cause for recurring winter mass-mortality events among North Atlantic seabirds (Fort et al., 2009), and pinpointed sites where Chihuahuan Desert lizards are projected to become extirpated under climate change (Lara-Reséndiz et al., 2015). These models can also be adjusted to incorporate behavioral mechanisms that allow for species to overcome physiological thermal limits, such as shade seeking, posture adjustments, climbing, or retreating underground (Kearney and Porter, 2020). A great deal of information is required for mechanistic thermal models, such as pelage/plumage reflectance, evaporative water loss, and critical thermal limits, which can be difficult to measure (e.g., McKechnie et al., 2021a; Smith et al., 2017; Talbot et al., 2017), especially for species that are not easily kept in captivity (Dudley et al., 2016). Efforts to accurately measure and derive these physiological parameters, particularly for species that are challenging to study in controlled environments, can provide important information for improving the predictive power of mechanistic thermal models, improving assessments of species' susceptibilities to rising temperatures (e.g., Riddell et al., 2019).

Here we measure and derive physiological parameters for 151 species of birds from the Mojave Desert that we use to estimate their physiological limits to temperature. We selected Mojave Desert birds because their historical distributions are well-researched, and observed declines are proposed to be caused by increased cooling requirements from climate change (Iknayan and Beissinger, 2018; Riddell et al., 2021; Riddell et al., 2019). To obtain the parameters required to estimate physiological limits to thermal vulnerability, we employed a combination of methods including derivation from equations based on species body mass, measurements from museum specimens, and interpolated from published data on taxonomically related species. Using this information, we estimated the thermal vulnerabilities of bird species that breed in the Mojave Desert.

Methods

Selection of Species

Species were included in the study if they appeared in the Mojave Desert surveys conducted by Iknayan and Beissinger (2018), or if their distributions as calculated by Fink et al. (2020) cross into the Mojave Desert. The Mojave Desert spans broad latitudinal (34.8° to 36.2°), longitudinal (-117.2° to -115.8°), and elevational ranges (-82m to 3367m). Waterbirds were excluded from these assessments unless the species was specifically surveyed for by Iknayan and Beissinger (2018). As in Eichenwald and Reed (2023), we obtained 5 specimens each (3 males and 2 females) for 151 species of birds at the Harvard Museum of Comparative Zoology (MCZ).

Deriving, calculating, and measuring parameters for NicheMapR

There are several different types of mechanistic models that have been developed (e.g., Kearney and Porter, 2020; Stevenson and Kearney, 2020), each of which requires a related but different subset of parameters depending on the model's purpose. Here we used NicheMapR, a suite of programs in R that calculates heat and water exchange of an organism and the microclimates to which said organism is exposed (Kearney et al., 2021; Kearney and Porter, 2017, 2020). We use NicheMapR because the program is readily available (Taylor et al., 2021) and has explicit instructions for its application (Kearney et al., 2021; Kearney and Porter, 2017, 2020). Calculations for NicheMapR's endotherm function (without incorporating Dynamic Energy Budgets) require data for many (41) input parameters, which are described in Table 1.

We followed Riddell et al. (2019) by setting emissivity (the relative power of a surface to emit heat by radiation) equal to 0.96; animal emissivity is generally assumed to be between 0.95-1.0 (Hammel, 1956). Bird masses were averaged by species from values in VertNet (Chamberlain, 2021), and bird volumes and densities were calculated from our own measurements of museum specimens (Eichenwald and Reed 2023). Some parameters required for the thermal models are derivable from body mass (grams). We used the equation from Riddell et al. (2019) to calculate feather density, with a density cap of 11600, as they suggest. We also fit two linear models with log(body mass) to Riddell et al.'s (2019) measured values for ventral ($R^2 = 0.51$, $F(1, 48) = 50.84$, $p<0.001$) and dorsal feather length ($R^2 = 0.51$, $F(1, 48) = 49.59$, $p<0.001$), and used the fitted regression equations to extrapolate dorsal and ventral feather lengths for all of our species. We used the same approach, using Riddell et al.'s (2019) data, to determine ventral ($R^2 = 0.13$, $F(1, 48) = 7.41$, $p = 0.009$) and dorsal depth of the insulative layer ($R^2 = 0.34$, $F(1, 48) = 24.19$, $p < 0.001$). We calculated metabolic rates and multipliers for evaporative water loss for all species using equations from McKechnie et al. (2021a). Q10 (temperature coefficient) was set as 1 for all species with mass less than 100 grams (Weathers, 1981) but set at the default of 2 for larger species. Bird resting body temperatures and maximum possible body temperatures were taken from McKechnie et al. (2021a).

Not all thermal-based parameters can be derived from body mass, such as feather reflectance. Birds with black feathers will have low reflectance and white feathers will have high reflectance, regardless of body mass. We measured feather reflectance of birds from specimens at the Harvard Museum of Comparative Zoology (Cambridge, Massachusetts, USA), following the methods of Riddell et al. (2019). We used an ASD FieldSpec 4 Max spectrometer over the wavelength range from 350 to 2500 nm using a contact probe for illumination and Spectralon disk for reference. We measured reflectance from five locations on each of the dorsal and ventral surfaces of each body for 2 female and 3 males per species: the crown, throat, and four measurements each spread across the breast and the mantle. Ultimately, each bird species had two reflectance measures included in the model, one dorsal one ventral, where each was the average of 25 measurements. These measurements were made with pure white light and therefore are different than what we would expect under sunlight. Therefore, as with Riddell et al. (2019), we corrected the reflectance curves for solar radiation using the ASTM G-172 standard irradiance spectrum for dry air provided by SMARTs v. 2.9.2 (Gueymard, 2001). The corrected value was calculated by multiplying the intensity of solar radiation by the empirical reflectance, integrating across all wavelengths, and dividing by the total intensity of solar radiation.

Assessment of species thermal vulnerability

NicheMapR allows users to calculate thermal constraints of environmental conditions on most animals (Kearney et al., 2021; Kearney and Porter, 2020); however, ectotherms and endotherms have different biophysical reactions. We used NicheMapR's endoR function, as it is specifically designed to model thermal responses of endotherms (Kearney et al., 2021). We first determined the relative thermal vulnerability of each species under the combinations of air temperature (30 to 45 °C in increments of 1), solar radiation (0 to 1400 W/m^2 in increments of 10), and shade (0 to 100% shade in increments of 5, where 0% is full sun exposure and 100% is perfect shade from direct sun) that are most likely found in the Mojave Desert during the summer. We assumed that a species "dies" if NicheMapR is unable to calculate a solution for species survival for the given environmental conditions, or if predicted water loss is greater than 15% of total body mass per day (Albright et al., 2017). The minimum percent shade a species requires to survive given a specific combination of solar radiation and air temperature was used as a proxy for thermal vulnerability. All other environment-based parameters in the endoR function were left at their default values.

To infer the vulnerability of each species to solar radiation and air temperature, we fit a generalized additive model predicting minimum required shade with solar radiation and air temperature as smooth terms and species as a fixed term. We then used the ggeffects R package to find the marginal effect of species on minimum required shade (i.e., thermal vulnerability), enabling us to create a ranked list of birds based on their thermal vulnerability.

To further explore the relationship between species and thermal vulnerability, we employed silhouette analysis with the cluster package in R (Rousseeuw, 1987). Silhouette analysis is a method used in machine learning to assess the grouping quality of data points. It measures the similarity of a data point to its own cluster compared to other clusters, providing insights into the distinctiveness and separation of clusters. By conducting silhouette analysis, we determined the optimal number of clusters needed for performing K-means clustering, a technique for grouping similar data points together. This analysis allowed us to define species groupings based on their thermal vulnerability, ensuring that species with similar values were grouped. Subsequently, we performed optimal univariate K-means clustering (MacQueen, 1967) using the Ckmeans.1d.dp R package (Wang and Song, 2011) with the identified number of clusters.

Finally, we constructed a linear regression model to actively investigate the influence of reflectance variation or body mass on the thermal vulnerability cluster of birds. The prediction of the thermal vulnerability cluster was based in part on the dorsal and ventral reflectance measurements of the birds. While our mechanistic model for determining thermal vulnerability considered a range of variables, these specific linear models targeted the extent to which reflectance variation or variation in body mass contributed to the classification of birds into their respective thermal vulnerability clusters. Body mass was placed on a log scale.

Results

We present all the parameters gathered for generating mechanistic thermal models of each Mojave bird species in Table 2. The 151 bird species differed in their relative susceptibilities to heat, with a spread of 29.5% between the lowest and highest amount of shade required to survive desert thermal conditions. All species thermal vulnerabilities were significantly predicted by the GAM, which was expected (since thermal vulnerabilities were derived from the species parameters). When examining the marginal effect of thermal vulnerability (the minimum percent shade a species requires to survive given a specific combination of solar radiation and air temperature) by holding temperature and solar radiation at fixed, extreme values (50°C and 1400 watts/m^2, or full sun), species required an average of 79.7 ± 5.3% shade to survive (Fig. 1, Suppl. Material Table S1). The least thermally vulnerable species were LeConte's thrasher (*Toxostoma lecontei*) and Abert's towhee (*Melozone aberti*), which were approximately 16% less vulnerable than the average of all species, and 35.7% less than the most vulnerable species (*Fig. 1*). The most vulnerable species was the golden-crowned kinglet (*Regulus satrapa*), which was approximately 20% more vulnerable than the average. The estimated amount of shade required to survive, according to the mechanistic model, will change given different combinations of temperature and solar radiation, but the relative vulnerabilities between species would not change (all other things being equal). Species sorted optimally by thermal risk into 18 clusters (*Fig. 1*), with on average 8.4 ± 4.2 species per cluster. Clusters were separated from one another by on average 1.7 ± 1.0 percent shade required for species survival given equivalent thermal conditions (*Fig. 1*, Supplementary Table S1).

Dorsal reflectance was generally lower and had less variation across species (0.24 ± 0.05 on average for all specimens) compared to ventral reflectance (0.39 ± 0.10 on average) (Figure 2,

Table 1). This pattern of variation in ventral reflectance compared to dorsal reflectance was consistent even when we grouped the reflectance data by family (Figure 2a). Cluster number was statistically significantly predicted by reflectance ($F = 20.46$, $df = 148$, $R^2 = 0.21$, $p < 0.001$). Dorsal reflectance was found to be significantly negatively associated with the thermal vulnerability cluster; note in Fig 2b that as cluster number increases, thermal vulnerability decreases ($\beta = 42.51$, standard error = 7.61, t-value = 5.59, $p < 0.001$). On the other hand, ventral reflectance was not statistically significantly associated with thermal vulnerability cluster ($\beta = -2.34$, standard error = 3.68, t-value = -0.64, $p = 0.53$) (Figure 2b). Thermal vulnerability was statistically significantly predicted by reflectance ($F= 18.57$, $df = 148$, $R^2 = 0.19$, $p < 0.001$). Increasing dorsal reflectance was statistically significantly predictive of vulnerability ($\beta = -53.00$, standard error = 10.31, t-value = -5.14, $p < 0.001$), but ventral reflectance was not ($\beta = 1.22$, standard error = 4.99, t-value = 0.25, $p = 0.81$) (*Figure 3*). Log-scaled body mass was found to be significantly positively associated with thermal vulnerability cluster (i.e., negatively associated with vulnerability), although with low fit ($F = 8.4$, $df = 300$, $R^2 = 0.03$, $\beta = 0.46$, standard error = 0.16, t-value = 2.90, $p = 0.004$). Increasing log-scaled body mass also was significantly predictive of decreasing thermal vulnerability at the same low level of fit ($F = 10.77$, $df = 300$, $R^2 = 0.03$, $\beta = -0.70$, standard error = 0.21, t-value = -3.28, $p = 0.001$).

Discussion

Mechanistic models play important roles in scientific research. While correlative models describe patterns without necessarily explicitly considering underlying processes, mechanistic models are derived from theoretical assumptions and incorporate the fundamental principles governing the phenomenon (Buckley et al., 2010; Kearney, 2021). By directly linking the parameter values for the variables to these theoretical constructs, mechanistic models offer physically interpretable parameters with meaningful dimensions (Kearney, 2021). Such knowledge provides the basis for predicting wildlife sensitivity to climate change across their distributions, a requirement for informed adaptive conservation of species (Johnston and Schmitz, 1997; Kearney et al., 2010). We collected data to populate mechanistic thermal model parameters for 151 birds in the Mojave Desert, allowing us to identify the species potentially most at risk to increased temperatures associated with climate change. We use the term "potentially at risk" to indicate that species-specific behaviors that can mitigate heat load (e.g., shade-seeking, climbing, burrowing (Kearney and Porter, 2020)) are not included in our model. However, these behaviors could be incorporated if the behaviors and their thermoregulatory effects are known or hypothesized, such as Kearney et al. (2018) including fossorial behavior in models of the fundamental niche of the sleepy lizard *Tiliqua rugosa*.

It is well known that bird species differ in their capacity to tolerate high temperatures (McKechnie et al., 2017). The wide range of bird responses to external temperature exposure from our analysis aligns with findings from the application of other mechanistic models of desert avifauna. For instance, Albright et al. (2017) calculated that climate change negatively impacted the survival of five bird species to different degrees across the entire American southwest, while Ma et al. (2023) reported that the global effects of increased heat on desert birds is heterogeneous even within the same desert system. In these papers, we note that body mass appears often as a key variable influencing survival; indeed, McKechnie et al. (2012) suggest that birds with larger masses may face higher direct risk of hyperthermia due to their relatively smaller surface area. Riddell et al. (2019) calculated with mechanistic models that cooling costs were likely responsible for changes in bird size, an assertion that is supported by a systematic analysis showing that warming temperatures are driving reductions in avian mass (Weeks et al., 2022). In our study, body mass was significantly associated with vulnerability, although at a low degree of fit (although this may be because many of our other parameters were derived from body mass).

In addition to size, results of our analyses showed a strong relationship between dorsal feather reflectance and thermal vulnerability. Countershading (Thayer's law) is typical of birds, though its function and effectiveness is debated (Ruxton et al., 2004).In our study, dorsal reflectance of birds explained approximately 21% of the variation in thermal vulnerability, and as might be expected, the association was negative – birds with lower reflectance had higher thermal vulnerability. Ventral reflectance, in contrast, had no significant influence, demonstrating the importance of collecting accurate reflectance data to parameterize the models. The importance of dorsal reflectance data to calculate thermal vulnerability is supported by empirical evidence, as arid birds tend to reflect higher amounts of near-infrared light from the dorsal area than tropical birds as a biophysical adaptation to heat and direct sunlight (Medina et al., 2018) and avian dorsal reflectance decreases over time when their environment changes from desert to agricultural fields (Mason and Unitt, 2018). Furthermore, the color of feathers influences birds' energy budgets, with darker colors increasing heat absorption in relation to lighter colors, thereby impacting the spatial distribution of species in extreme ecosystems (Rogalla et al., 2022).

For some species, we were not able to measure certain input parameters directly or estimate them allometrically. One such example is the critical thermal maximum (the thermal point at which an animal's motor functions break down, eventually leading to death), which is an important parameter in thermal models (Kearney et al., 2021). Although there have been studies that directly measured such parameters with no long-term damage to a live specimen (e.g., Smith et al., 2017; Talbot et al., 2018), it can present challenges in practice. Obtaining accurate measurements of the critical thermal maximum can sometimes led to lethal outcomes, which may not be feasible or ethically desirable (Lutterschmidt and Hutchison, 1997). Therefore, we relied instead on more approximate parameters based on known measurements from taxonomically related species, which can introduce uncertainties and potential inaccuracies in model predictions. Consequently, models using our parameter values for some of the species should exercise caution when making predictions about desert bird spatial distributions.

As we stated earlier, it is possible for animals to thrive in otherwise unsurvivable environments via behavioral adaptations despite physical limits to surviving high temperatures (Kearney et al., 2018). The population stability of small mammals in the Mojave Desert, for example, has been attributed to their fossorial behaviors (Riddell et al., 2021). Furthermore, some species of Mojave Desert birds are reported to wedge themselves into microsites such as knotholes and crevices in trees and rocks to escape from extreme temperatures (Wolf et al., 1996), and there is anecdotal evidence of them utilizing underground burrows, possibly as a thermal refuge (Puffer et al., 2022). Burrows are also known to be used as thermal refugia by birds in other deserts (Dawson et al., 2019; Williams et al., 1999). Although these behaviors can allow animals to extend their distributions into otherwise lethal environments, they also may result in negative trade-offs that impact survival in other ways (Guo et al., 2020). For example, behaviors that limit heat exposure such as increasing time spent in cooler, shaded microclimates reduces avian foraging efficiency, negatively impacting energy intake and possible even breeding success (van de Ven et al., 2019). Therefore, projections of the potential impacts of climate change on birds using our parameters that do not take these behaviors and trade-offs into account will likely underestimate persistence likelihood.

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Table 4-1 The parameters used in our NicheMapR analysis, including the parameter name as found in NicheMapR, its description, and the units that NicheMapR requires (a dash indicates a unitless metric). Parameter values are given in Table 2, except for those that are not species-specific, such as the animal's current orientation in reference to the sun.

Parameter	Description	Units
ANDENS	Body density	kg/m3
AMASS	Body mass	kg
REFLD	Dorsal feather reflectivity	fractional, 0-1
REFLV	Ventral feather reflectivity	fractional, 0-1
LHAIRV	Ventral feather length	m
LHAIRD	Dorsal feather length	m
ZFURD	Dorsal feather depth	m
ZFURV	Ventral feather depth	m
PANT_MAX	Maximum breathing rate multiplier (panting)	-
RHOD	Dorsal feather density	1/m2
RHOV	ventral feather density	1/m2
TC_MAX	Maximum core temperature	°C
TC	Core temperature	°C
PANT_MULT	multiplier on basal metabolic rate at maximum panting level	-
QBASAL	Basal heat generation	W
Q10	Factor for adjusting BMR for TC	-
SHAPE_B	Ratio between long and short axis	-
SHAPE_B_MAX	Maximum ratio between long and short axis (curling/uncurling)	-
EMISAN	Emissivity	-
TA	Air temperature	°C
TGRD	Ground temperature	°C
TSKY	Sky temperature	°C
VEL	Wind speed	m/s
RH	Relative humidity	%
QSOLR	Solar radiation	Watts/m2
Z	Zenith angle of sun	° from overhead
SHAPE	Animal shape	Cylinder, sphere, plate, or ellipsoid
ORIENT	Orientation in reference to sun (Perpendicular, parallel, vertical, or average of parallel/perpendicular)	--
PCTEYES	Surface area made up by eyes	%
KHAIR	Feather thermal conductivity	Watts/m°C
ELEV	Elevation	m
PCTWET	Percent of skin surface that is wet (sweating)	%
PCTWETMAX	Maximum percent surface area that can be wet (sweating)	%
SUBQFAT	Is subcutaneous fat present? (Yes/No)	--
FLYHR	Is flight occurring this hour? (Yes/No)	--

PCOND	Fraction of surface area that is touching the substrate	--
FATPCT	Percent body fat	%
EXTREF	Oxygen extraction efficiency	%
ABSSB	Solar absorptivity of the substrate	fractional, 0-1
THERMOREG	Should the animal thermoregulate	Yes/no
RESPIRE	Should the animal respire	Yes/no

Table 4-2 Parameter values for each species' input into NicheMapR mechanistic thermal model; parameters that are not species-specific are excluded. Variables in the column names match those in Table 1, where units also can be found.

Scientific Name	Common Name	ANDENS	AMASS	REFLD	REFLV	FV	FD	I.D	I.V	PANT_MAX	RHOD	RHOV	TC_MAX	TC	PANT_MULT	QBASAL	Q10	Shape.B
Accipiter cooperii	Cooper's Hawk	429.589	338.427	0.216	0.527	0.031	0.034	0.008	0.006	8.209	11600.000	11600.000	43.800	39.900	1.891	1.642	2.000	2.835
Accipiter gentilis	Northern Goshawk	576.210	867.981	0.226	0.387	0.036	0.039	0.009	0.006	8.026	11600.000	11600.000	43.800	39.900	2.001	3.138	2.000	3.128
Accipiter striatus	Sharp-shinned Hawk	527.458	128.074	0.210	0.393	0.026	0.029	0.008	0.006	8.403	10427.349	10427.349	43.800	39.900	1.784	0.841	2.000	2.526
Aeronautes saxatalis	White-throated Swift	1000.000	32.855	0.157	0.342	0.019	0.021	0.006	0.005	8.682	5117.083	5117.083	43.800	39.900	1.644	0.330	1.000	2.489
Agelaius phoeniceus	Red-winged Blackbird	1000.000	61.408	0.173	0.214	0.023	0.025	0.007	0.005	8.552	6709.439	6709.439	44.500	40.700	1.591	0.732	1.000	2.620
Aimophila ruficeps	Rufous-crowned Sparrow	1000.000	18.914	0.230	0.372	0.017	0.018	0.006	0.005	8.797	4339.612	4339.612	44.500	40.700	1.529	0.315	1.000	2.887
Alectoris chukar	Chukar	1000.000	475.673	0.253	0.352	0.033	0.036	0.009	0.006	8.142	11600.000	11600.000	43.800	39.900	1.930	2.075	2.000	3.074
Amphispiza bilineata	Black-throated Sparrow	782.332	13.169	0.296	0.400	0.015	0.016	0.006	0.005	8.874	4019.232	4019.232	44.500	40.700	1.510	0.243	1.000	2.387
Aphelocoma woodhouseii	Woodhouse's Scrub-Jay	718.405	78.803	0.241	0.304	0.024	0.026	0.007	0.005	8.501	7679.566	7679.566	44.500	40.700	1.605	0.875	1.000	2.654
Aquila chrysaetos	Golden Eagle	502.801	3727.768	0.178	0.197	0.044	0.047	0.011	0.007	7.750	11600.000	11600.000	43.800	39.900	2.184	8.554	2.000	2.383
Archilochus alexandri	Black-chinned Hummingbird	1000.000	3.039	0.226	0.354	0.007	0.008	0.004	0.004	9.192	3454.260	3454.260	43.800	39.900	1.425	0.064	1.000	3.148
Artemisiospiza nevadensis	Sagebrush Sparrow	777.017	18.179	0.272	0.386	0.016	0.018	0.006	0.005	8.806	4298.640	4298.640	44.500	40.700	1.527	0.307	1.000	2.380
Athene cunicularia	Burrowing Owl	594.673	138.347	0.331	0.421	0.027	0.029	0.008	0.006	8.387	11000.271	11000.271	43.800	39.900	1.792	0.887	2.000	2.406
Auriparus flaviceps	Verdin	1000.000	6.798	0.267	0.412	0.011	0.013	0.005	0.004	9.016	3663.940	3663.940	44.500	40.700	1.477	0.152	1.000	2.768
Baeolophus inornatus	Oak Titmouse	1000.000	15.993	0.254	0.424	0.016	0.017	0.006	0.005	8.833	4176.695	4176.695	44.500	40.700	1.520	0.280	1.000	2.448
Baeolophus ridgwayi	Juniper Titmouse	970.059	16.149	0.240	0.331	0.016	0.017	0.006	0.005	8.831	4185.409	4185.409	44.500	40.700	1.521	0.282	1.000	2.942
Bubo virginianus	Great Horned Owl	426.216	1246.541	0.282	0.410	0.038	0.041	0.010	0.007	7.956	11600.000	11600.000	43.800	39.900	2.045	4.026	2.000	2.720
Buteo jamaicensis	Red-tailed Hawk	427.872	911.708	0.251	0.524	0.037	0.039	0.009	0.006	8.016	11600.000	11600.000	43.800	39.900	2.007	3.246	2.000	2.805
Buteo swainsoni	Swainson's Hawk	535.704	738.183	0.225	0.469	0.035	0.038	0.009	0.006	8.057	11600.000	11600.000	43.800	39.900	1.982	2.807	2.000	3.012

Callipepla californica	California Quail	965.000	162.729	0.219	0.305	0.028	0.030	0.008	0.006	8.355	11600.000	11600.000	43.800	39.900	1.810	0.992	2.000	3.040
Callipepla gambelii	Gambel's Quail	880.858	158.257	0.291	0.446	0.028	0.030	0.008	0.006	8.360	11600.000	11600.000	43.800	39.900	1.807	0.973	2.000	3.174
Calypte anna	Anna's Hummingbird	965.873	3.970	0.203	0.262	0.009	0.010	0.005	0.004	9.133	3506.218	3506.218	43.800	39.900	1.449	0.077	1.000	2.965
Calypte costae	Costa's Hummingbird	1000.000	2.912	0.232	0.290	0.007	0.008	0.004	0.004	9.201	3447.220	3447.220	43.800	39.900	1.422	0.062	1.000	3.298
Campylorhynchus brunneicapillus	Cactus Wren	993.817	38.684	0.281	0.435	0.020	0.022	0.007	0.005	8.648	5442.150	5442.150	44.500	40.700	1.567	0.526	1.000	2.739
Cathartes aura	Turkey Vulture	801.109	1597.071	0.115	0.150	0.039	0.042	0.010	0.007	7.909	11600.000	11600.000	43.800	39.900	2.076	4.774	2.000	3.697
Catharus guttatus	Hermit Thrush	558.836	26.685	0.233	0.405	0.018	0.020	0.006	0.005	8.725	4773.010	4773.010	44.500	40.700	1.547	0.403	1.000	2.516
Catharus ustulatus	Swainson's Thrush	554.342	30.129	0.232	0.461	0.019	0.021	0.006	0.005	8.700	4965.070	4965.070	44.500	40.700	1.553	0.440	1.000	2.471
Catherpes mexicanus	Canyon Wren	871.783	11.592	0.248	0.329	0.014	0.016	0.005	0.005	8.901	3931.287	3931.287	44.500	40.700	1.504	0.222	1.000	2.610
Certhia americana	Brown Creeper	853.123	7.846	0.236	0.474	0.012	0.014	0.005	0.004	8.985	3722.383	3722.383	44.500	40.700	1.484	0.168	1.000	2.629
Chamaea fasciata	Wrentit	573.993	14.532	0.210	0.305	0.015	0.017	0.006	0.005	8.853	4095.217	4095.217	44.500	40.700	1.515	0.261	1.000	2.250
Charadrius vociferus	Killdeer	634.928	79.850	0.247	0.604	0.024	0.026	0.007	0.005	8.499	7737.941	7737.941	43.800	39.900	1.734	0.608	1.000	2.420
Chondestes grammacus	Lark Sparrow	784.106	28.003	0.282	0.487	0.019	0.020	0.006	0.005	8.715	4846.522	4846.522	44.500	40.700	1.550	0.418	1.000	2.489
Chordeiles acutipennis	Lesser Nighthawk	566.112	46.690	0.270	0.318	0.021	0.023	0.007	0.005	8.609	5888.653	5888.653	42.500	42.500	1.679	0.420	1.000	2.299
Chordeiles minor	Common Nighthawk	653.933	68.732	0.216	0.296	0.023	0.025	0.007	0.005	8.529	7117.924	7117.924	42.500	42.500	1.719	0.548	1.000	2.610
Cistothorus palustris	Marsh Wren	830.935	11.042	0.242	0.432	0.014	0.015	0.005	0.005	8.912	3900.580	3900.580	44.500	40.700	1.501	0.215	1.000	2.691
Colaptes auratus	Northern Flicker	659.535	140.452	0.258	0.358	0.027	0.029	0.008	0.006	8.384	11117.684	11117.684	43.800	39.900	1.794	0.896	2.000	2.387
Colaptes chrysoides	Gilded Flicker	858.854	102.642	0.322	0.401	0.025	0.027	0.007	0.005	8.447	9009.063	9009.063	43.800	39.900	1.761	0.722	2.000	2.828
Columba livia	Rock Pigeon	1000.000	296.875	0.341	0.255	0.031	0.033	0.008	0.006	8.235	11600.000	11600.000	43.400	38.500	1.877	1.523	2.000	2.672
Columbina inca	Inca Dove	736.992	46.217	0.280	0.534	0.021	0.023	0.007	0.005	8.611	5862.288	5862.288	43.400	38.500	1.678	0.327	1.000	1.822
Contopus cooperi	Olive-sided Flycatcher	650.078	32.700	0.211	0.350	0.019	0.021	0.006	0.005	8.683	5108.435	5108.435	44.500	40.700	1.558	0.467	1.000	2.598
Contopus sordidulus	Western Wood-Pewee	675.715	13.557	0.247	0.401	0.015	0.016	0.006	0.005	8.868	4040.883	4040.883	44.500	40.700	1.512	0.249	1.000	2.919
Corvus brachyrhynchos	American Crow	413.998	393.927	0.125	0.144	0.032	0.035	0.009	0.006	8.179	11600.000	11600.000	44.500	40.700	1.695	2.765	2.000	2.820
Corvus corax	Common Raven	742.339	1151.909	0.140	0.146	0.038	0.040	0.009	0.006	7.971	11600.000	11600.000	44.500	40.700	1.758	5.955	2.000	2.575

Cyanocitta stelleri	Steller's Jay	784.222	113.632	0.211	0.219	0.026	0.028	0.007	0.006	8.427	9621.929	9621.929	44.500	40.700	1.625	1.137	2.000	2.767
Dryobates pubescens	Downy Woodpecker	736.884	46.190	0.239	0.459	0.021	0.023	0.007	0.005	8.611	5860.771	5860.771	43.800	39.900	1.678	0.417	1.000	2.526
Dryobates scalaris	Ladder-backed Woodpecker	725.457	34.884	0.246	0.429	0.020	0.022	0.006	0.005	8.669	5230.226	5230.226	43.800	39.900	1.650	0.344	1.000	2.488
Dryobates villosus	Hairy Woodpecker	856.527	77.715	0.214	0.464	0.024	0.026	0.007	0.005	8.504	7618.861	7618.861	43.800	39.900	1.732	0.597	1.000	2.436
Empidonax difficilis	Pacific-slope Flycatcher	1000.000	10.602	0.268	0.412	0.014	0.015	0.005	0.005	8.921	3876.038	3876.038	44.500	40.700	1.499	0.209	1.000	2.480
Empidonax oberholseri	Dusky Flycatcher	664.830	11.513	0.266	0.442	0.014	0.016	0.005	0.005	8.903	3926.867	3926.867	44.500	40.700	1.503	0.221	1.000	2.592
Empidonax occidentalis	Cordilleran Flycatcher	734.682	11.615	0.242	0.341	0.014	0.016	0.005	0.005	8.901	3932.575	3932.575	44.500	40.700	1.504	0.223	1.000	2.714
Empidonax traillii	Willow Flycatcher	784.119	12.510	0.237	0.480	0.015	0.016	0.006	0.005	8.885	3982.497	3982.497	44.500	40.700	1.508	0.235	1.000	2.824
Empidonax wrightii	Gray Flycatcher	917.607	12.181	0.264	0.448	0.014	0.016	0.006	0.005	8.891	3964.115	3964.115	44.500	40.700	1.506	0.230	1.000	2.373
Eremophila alpestris	Horned Lark	840.145	31.633	0.304	0.461	0.019	0.021	0.006	0.005	8.690	5048.958	5048.958	44.500	40.700	1.556	0.456	1.000	2.850
Euphagus cyanocephalus	Brewer's Blackbird	798.055	64.200	0.200	0.231	0.023	0.025	0.007	0.005	8.543	6865.173	6865.173	44.500	40.700	1.594	0.756	1.000	2.711
Falco mexicanus	Prairie Falcon	560.031	548.934	0.326	0.623	0.034	0.036	0.009	0.006	8.114	11600.000	11600.000	43.800	39.900	1.947	2.290	2.000	2.659
Falco peregrinus	Peregrine Falcon	638.477	696.142	0.254	0.473	0.035	0.038	0.009	0.006	8.068	11600.000	11600.000	43.800	39.900	1.975	2.696	2.000	2.703
Falco sparverius	American Kestrel	567.851	97.876	0.313	0.464	0.025	0.027	0.007	0.005	8.457	8743.253	8743.253	43.800	39.900	1.756	0.699	1.000	2.302
Geococcyx californianus	Greater Roadrunner	614.860	271.747	0.252	0.412	0.030	0.033	0.008	0.006	8.252	11600.000	11600.000	43.800	39.900	1.867	1.412	2.000	3.360
Geothlypis tolmiei	MacGillivray's Warbler	790.447	10.800	0.191	0.384	0.014	0.015	0.005	0.005	8.917	3887.096	3887.096	44.500	40.700	1.500	0.211	1.000	3.582
Geothlypis trichas	Common Yellowthroat	788.170	10.011	0.226	0.435	0.013	0.015	0.005	0.005	8.933	3843.106	3843.106	44.500	40.700	1.496	0.200	1.000	3.122
Gymnorhinus cyanocephalus	Pinyon Jay	481.777	102.143	0.196	0.229	0.025	0.027	0.007	0.005	8.448	8981.195	8981.195	44.500	40.700	1.619	1.053	2.000	2.051
Haemorhous cassinii	Cassin's Finch	711.977	26.129	0.236	0.361	0.018	0.020	0.006	0.005	8.729	4741.980	4741.980	44.500	40.700	1.546	0.397	1.000	2.469
Haemorhous mexicanus	House Finch	831.347	23.798	0.265	0.374	0.018	0.020	0.006	0.005	8.749	4611.976	4611.976	44.500	40.700	1.541	0.372	1.000	2.386
Hirundo rustica	Barn Swallow	779.441	17.322	0.159	0.378	0.016	0.018	0.006	0.005	8.816	4250.827	4250.827	44.500	40.700	1.524	0.296	1.000	2.953
Icteria virens	Yellow-breasted Chat	758.977	25.945	0.215	0.529	0.018	0.020	0.006	0.005	8.731	4731.751	4731.751	44.500	40.700	1.546	0.395	1.000	2.719
Icterus bullockii	Bullock's Oriole	849.507	35.079	0.226	0.463	0.020	0.022	0.006	0.005	8.668	5241.139	5241.139	44.500	40.700	1.561	0.491	1.000	3.295

Icterus cucullatus	Hooded Oriole	807.293	25.493	0.315	0.436	0.018	0.020	0.006	0.005	8.735	4706.539	4706.539	44.500	40.700	1.545	0.390	1.000	2.728
Icterus parisorum	Scott's Oriole	896.817	37.010	0.239	0.346	0.020	0.022	0.006	0.005	8.657	5348.811	5348.811	44.500	40.700	1.564	0.510	1.000	2.578
Junco hyemalis	Dark-eyed Junco	689.802	18.375	0.209	0.342	0.016	0.018	0.006	0.005	8.804	4309.566	4309.566	44.500	40.700	1.528	0.309	1.000	2.552
Lanius ludovicianus	Loggerhead Shrike	669.989	46.627	0.269	0.473	0.021	0.023	0.007	0.005	8.609	5885.139	5885.139	44.500	40.700	1.577	0.601	1.000	2.130
Leiothlypis celata	Orange-crowned Warbler	728.230	8.760	0.238	0.412	0.013	0.014	0.005	0.005	8.961	3773.360	3773.360	44.500	40.700	1.490	0.182	1.000	2.481
Leiothlypis luciae	Lucy's Warbler	1000.000	6.539	0.254	0.532	0.011	0.013	0.005	0.004	9.025	3649.493	3649.493	44.500	40.700	1.475	0.148	1.000	2.853
Leiothlypis virginiae	Virginia's Warbler	755.896	7.392	0.249	0.411	0.012	0.013	0.005	0.004	8.998	3697.044	3697.044	44.500	40.700	1.481	0.161	1.000	2.726
Loxia curvirostra	Red Crossbill	954.602	31.974	0.201	0.235	0.019	0.021	0.006	0.005	8.687	5067.953	5067.953	44.500	40.700	1.557	0.459	1.000	2.933
Megascops kennicottii	Western Screech-Owl	742.784	141.548	0.276	0.325	0.027	0.029	0.008	0.006	8.383	11178.817	11178.817	43.800	39.900	1.795	0.901	2.000	2.331
Melanerpes uropygialis	Gila Woodpecker	479.256	50.110	0.280	0.393	0.022	0.023	0.007	0.005	8.594	6079.357	6079.357	43.800	39.900	1.687	0.441	1.000	2.160
Meleagris gallopavo	Wild Turkey	621.431	4674.828	0.183	0.228	0.045	0.048	0.011	0.007	7.708	11600.000	11600.000	43.800	39.900	2.214	9.995	2.000	2.889
Melospiza melodia	Song Sparrow	851.782	23.660	0.248	0.461	0.018	0.019	0.006	0.005	8.750	4604.309	4604.309	44.500	40.700	1.541	0.370	1.000	2.863
Melozone aberti	Abert's Towhee	934.355	46.630	0.327	0.481	0.021	0.023	0.007	0.005	8.609	5885.323	5885.323	44.500	40.700	1.577	0.601	1.000	2.361
Melozone crissalis	California Towhee	997.042	50.089	0.248	0.384	0.022	0.023	0.007	0.005	8.594	6078.213	6078.213	44.500	40.700	1.580	0.633	1.000	2.402
Mimus polyglottos	Northern Mockingbird	794.517	49.815	0.269	0.505	0.022	0.023	0.007	0.005	8.595	6062.953	6062.953	44.500	40.700	1.580	0.630	1.000	2.479
Molothrus ater	Brown-headed Cowbird	895.304	42.074	0.233	0.271	0.021	0.023	0.007	0.005	8.630	5631.236	5631.236	44.500	40.700	1.571	0.559	1.000	2.934
Myadestes townsendi	Townsend's Solitaire	500.247	33.861	0.262	0.325	0.020	0.021	0.006	0.005	8.675	5173.205	5173.205	44.500	40.700	1.560	0.478	1.000	2.791
Myiarchus cinerascens	Ash-throated Flycatcher	684.611	27.613	0.274	0.473	0.019	0.020	0.006	0.005	8.718	4824.733	4824.733	44.500	40.700	1.549	0.413	1.000	2.584
Nucifraga columbiana	Clark's Nutcracker	614.785	131.308	0.276	0.313	0.027	0.029	0.008	0.006	8.398	10607.716	10607.716	44.500	40.700	1.633	1.261	2.000	2.373
Oreortyx pictus	Mountain Quail	794.688	216.652	0.258	0.283	0.029	0.031	0.008	0.006	8.297	11600.000	11600.000	43.800	39.900	1.841	1.208	2.000	3.631
Oreoscoptes montanus	Sage Thrasher	910.942	42.597	0.315	0.462	0.021	0.023	0.007	0.005	8.628	5660.413	5660.413	44.500	40.700	1.572	0.564	1.000	2.542
Passer domesticus	House Sparrow	917.994	29.363	0.207	0.334	0.019	0.021	0.006	0.005	8.705	4922.318	4922.318	44.500	40.700	1.552	0.432	1.000	2.696

Passerella iliaca	Fox Sparrow	880.987	32.903	0.224	0.391	0.019	0.021	0.006	0.005	8.681	5119.765	5119.765	44.500	40.700	1.558	0.469	1.000	2.615
Passerina amoena	Lazuli Bunting	720.970	14.472	0.222	0.390	0.015	0.017	0.006	0.005	8.854	4091.890	4091.890	44.500	40.700	1.515	0.260	1.000	2.976
Passerina caerulea	Blue Grosbeak	755.871	27.682	0.239	0.302	0.019	0.020	0.006	0.005	8.717	4828.588	4828.588	44.500	40.700	1.549	0.414	1.000	2.952
Passerina cyanea	Indigo Bunting	833.733	14.138	0.207	0.269	0.015	0.017	0.006	0.005	8.859	4073.269	4073.269	44.500	40.700	1.514	0.256	1.000	2.714
Patagioenas fasciata	Band-tailed Pigeon	804.928	310.935	0.210	0.446	0.031	0.033	0.008	0.006	8.226	11600.000	11600.000	43.400	38.500	1.882	1.583	2.000	2.510
Petrochelidon pyrrhonota	Cliff Swallow	786.400	20.786	0.195	0.403	0.017	0.019	0.006	0.005	8.778	4444.038	4444.038	44.500	40.700	1.534	0.337	1.000	2.508
Phainopepla nitens	Phainopepla	717.384	25.340	0.165	0.153	0.018	0.020	0.006	0.005	8.736	4698.012	4698.012	44.500	40.700	1.544	0.389	1.000	2.636
Phalaenoptilus nuttallii	Common Poorwill	597.288	43.449	0.285	0.279	0.021	0.023	0.007	0.005	8.624	5707.903	5707.903	42.500	42.500	1.672	0.400	1.000	2.557
Pheucticus melanocephalus	Black-headed Grosbeak	687.620	42.952	0.285	0.497	0.021	0.023	0.007	0.005	8.626	5680.179	5680.179	44.500	40.700	1.572	0.567	1.000	2.488
Pipilo chlorurus	Green-tailed Towhee	938.904	28.427	0.271	0.395	0.019	0.020	0.006	0.005	8.712	4870.158	4870.158	44.500	40.700	1.550	0.422	1.000	2.947
Pipilo maculatus	Spotted Towhee	1000.000	40.472	0.175	0.359	0.021	0.022	0.007	0.005	8.638	5541.896	5541.896	44.500	40.700	1.569	0.543	1.000	2.689
Piranga ludoviciana	Western Tanager	638.021	29.926	0.255	0.426	0.019	0.021	0.006	0.005	8.701	4953.726	4953.726	44.500	40.700	1.553	0.438	1.000	2.647
Piranga rubra	Summer Tanager	767.879	30.765	0.314	0.455	0.019	0.021	0.006	0.005	8.695	5000.546	5000.546	44.500	40.700	1.555	0.447	1.000	2.809
Poecile gambeli	Mountain Chickadee	902.382	11.329	0.178	0.251	0.014	0.016	0.005	0.005	8.906	3916.597	3916.597	44.500	40.700	1.503	0.219	1.000	2.663
Polioptila caerulea	Blue-gray Gnatcatcher	751.699	5.640	0.233	0.445	0.010	0.012	0.005	0.004	9.057	3599.334	3599.334	44.500	40.700	1.467	0.133	1.000	2.591
Polioptila melanura	Black-tailed Gnatcatcher	485.385	5.272	0.183	0.339	0.010	0.011	0.005	0.004	9.071	3578.834	3578.834	44.500	40.700	1.464	0.127	1.000	1.882
Pooecetes gramineus	Vesper Sparrow	817.409	24.433	0.278	0.402	0.018	0.020	0.006	0.005	8.744	4647.422	4647.422	44.500	40.700	1.542	0.379	1.000	2.700
Psaltriparus minimus	Bushtit	670.167	5.717	0.186	0.309	0.010	0.012	0.005	0.004	9.054	3603.620	3603.620	44.500	40.700	1.468	0.134	1.000	2.090
Pyrocephalus rubinus	Vermilion Flycatcher	990.639	24.334	0.336	0.471	0.018	0.020	0.006	0.005	8.744	4641.877	4641.877	44.500	40.700	1.542	0.378	1.000	2.747
Quiscalus mexicanus	Great-tailed Grackle	1000.000	146.397	0.158	0.242	0.027	0.029	0.008	0.006	8.376	11449.241	11449.241	44.500	40.700	1.639	1.363	2.000	2.736
Regulus calendula	Ruby-crowned Kinglet	558.713	7.608	0.223	0.399	0.012	0.013	0.005	0.004	8.992	3709.074	3709.074	44.500	40.700	1.482	0.164	1.000	2.039
Regulus satrapa	Golden-crowned Kinglet	347.613	5.876	0.176	0.303	0.011	0.012	0.005	0.004	9.048	3612.519	3612.519	44.500	40.700	1.469	0.137	1.000	2.129

Salpinctes obsoletus	Rock Wren	844.399	16.371	0.290	0.516	0.016	0.018	0.006	0.005	8.828	4197.779	4197.779	44.500	40.700	1.522	0.284	1.000	2.246
Sayornis nigricans	Black Phoebe	743.487	17.840	0.218	0.345	0.016	0.018	0.006	0.005	8.810	4279.700	4279.700	44.500	40.700	1.526	0.303	1.000	2.611
Sayornis saya	Say's Phoebe	538.462	21.589	0.295	0.362	0.017	0.019	0.006	0.005	8.770	4488.779	4488.779	44.500	40.700	1.536	0.347	1.000	2.651
Selasphorus platycercus	Broad-tailed Hummingbird	1000.000	3.103	0.213	0.301	0.007	0.009	0.004	0.004	9.187	3457.850	3457.850	43.800	39.900	1.427	0.065	1.000	3.093
Setophaga graciae	Grace's Warbler	741.424	8.065	0.192	0.376	0.012	0.014	0.005	0.004	8.979	3734.580	3734.580	44.500	40.700	1.485	0.171	1.000	2.907
Setophaga nigrescens	Black-throated Gray Warbler	743.574	9.142	0.192	0.352	0.013	0.014	0.005	0.005	8.952	3794.665	3794.665	44.500	40.700	1.492	0.188	1.000	2.885
Setophaga occidentalis	Hermit Warbler	836.334	9.174	0.192	0.400	0.013	0.014	0.005	0.005	8.952	3796.441	3796.441	44.500	40.700	1.492	0.188	1.000	2.729
Setophaga petechia	Yellow Warbler	864.870	9.806	0.286	0.489	0.013	0.015	0.005	0.005	8.937	3831.678	3831.678	44.500	40.700	1.495	0.197	1.000	3.224
Sialia currucoides	Mountain Bluebird	521.647	28.168	0.222	0.318	0.019	0.020	0.006	0.005	8.714	4855.719	4855.719	44.500	40.700	1.550	0.419	1.000	2.501
Sialia mexicana	Western Bluebird	526.989	25.876	0.224	0.314	0.018	0.020	0.006	0.005	8.732	4727.894	4727.894	44.500	40.700	1.545	0.395	1.000	2.643
Sitta carolinensis	White-breasted Nuthatch	1000.000	18.197	0.205	0.398	0.016	0.018	0.006	0.005	8.806	4299.630	4299.630	44.500	40.700	1.527	0.307	1.000	2.909
Sitta pygmaea	Pygmy Nuthatch	1000.000	10.441	0.159	0.320	0.014	0.015	0.005	0.005	8.924	3867.105	3867.105	44.500	40.700	1.498	0.206	1.000	2.438
Sphyrapicus nuchalis	Red-naped Sapsucker	667.356	48.487	0.209	0.338	0.021	0.023	0.007	0.005	8.601	5988.847	5988.847	43.800	39.900	1.683	0.431	1.000	2.065
Spinus lawrencei	Lawrence's Goldfinch	660.476	10.164	0.259	0.384	0.013	0.015	0.005	0.005	8.930	3851.631	3851.631	44.500	40.700	1.497	0.202	1.000	2.635
Spinus pinus	Pine Siskin	849.647	12.822	0.273	0.399	0.015	0.016	0.006	0.005	8.880	3999.865	3999.865	44.500	40.700	1.509	0.239	1.000	2.317
Spinus psaltria	Lesser Goldfinch	672.635	9.103	0.202	0.495	0.013	0.014	0.005	0.005	8.953	3792.461	3792.461	44.500	40.700	1.491	0.187	1.000	2.444
Spizella atrogularis	Black-chinned Sparrow	614.799	11.448	0.235	0.327	0.014	0.016	0.005	0.005	8.904	3923.247	3923.247	44.500	40.700	1.503	0.220	1.000	2.503
Spizella breweri	Brewer's Sparrow	850.250	10.784	0.284	0.481	0.014	0.015	0.005	0.005	8.917	3886.217	3886.217	44.500	40.700	1.500	0.211	1.000	2.381
Spizella passerina	Chipping Sparrow	898.769	15.966	0.246	0.369	0.016	0.017	0.006	0.005	8.833	4175.210	4175.210	44.500	40.700	1.520	0.279	1.000	2.436
Stelgidopteryx serripennis	Northern Rough-winged Swallow	823.572	15.257	0.211	0.449	0.016	0.017	0.006	0.005	8.843	4135.662	4135.662	44.500	40.700	1.518	0.271	1.000	2.630
Streptopelia decaocto	Eurasian Collared-Dove	627.323	156.180	0.321	0.527	0.027	0.030	0.008	0.006	8.363	11600.000	11600.000	43.400	38.500	1.806	0.896	2.000	2.365

Sturnella neglecta	Western Meadowlark	853.015	94.269	0.287	0.574	0.025	0.027	0.007	0.005	8.465	8542.109	8542.109	44.500	40.700	1.615	0.995	1.000	2.437
Sturnus vulgaris	European Starling	918.280	82.733	0.137	0.142	0.024	0.026	0.007	0.005	8.491	7898.714	7898.714	44.500	40.700	1.608	0.906	1.000	3.078
Tachycineta thalassina	Violet-green Swallow	714.162	14.603	0.147	0.460	0.015	0.017	0.006	0.005	8.852	4099.189	4099.189	44.500	40.700	1.516	0.262	1.000	2.295
Thryomanes bewickii	Bewick's Wren	1000.000	10.042	0.182	0.304	0.013	0.015	0.005	0.005	8.932	3844.852	3844.852	44.500	40.700	1.496	0.201	1.000	3.024
Toxostoma bendirei	Bendire's Thrasher	566.152	57.344	0.273	0.443	0.022	0.024	0.007	0.005	8.566	6482.818	6482.818	44.500	40.700	1.588	0.697	1.000	2.487
Toxostoma crissale	Crissal Thrasher	628.455	62.321	0.276	0.385	0.023	0.025	0.007	0.005	8.549	6760.360	6760.360	44.500	40.700	1.592	0.740	1.000	2.594
Toxostoma curvirostre	Curve-billed Thrasher	656.667	79.343	0.285	0.399	0.024	0.026	0.007	0.005	8.500	7709.659	7709.659	44.500	40.700	1.605	0.879	1.000	2.429
Toxostoma lecontei	Le Conte's Thrasher	847.531	61.008	0.366	0.483	0.023	0.025	0.007	0.005	8.554	6687.161	6687.161	44.500	40.700	1.591	0.729	1.000	2.397
Toxostoma redivivum	California Thrasher	907.785	90.108	0.249	0.439	0.025	0.027	0.007	0.005	8.474	8310.060	8310.060	44.500	40.700	1.612	0.963	1.000	2.766
Troglodytes aedon	House Wren	930.824	10.822	0.211	0.387	0.014	0.015	0.005	0.005	8.916	3888.343	3888.343	44.500	40.700	1.500	0.212	1.000	2.847
Turdus migratorius	American Robin	586.298	77.281	0.238	0.373	0.024	0.026	0.007	0.005	8.505	7594.699	7594.699	44.500	40.700	1.604	0.863	1.000	2.428
Tyrannus verticalis	Western Kingbird	908.158	40.445	0.280	0.525	0.021	0.022	0.007	0.005	8.638	5540.393	5540.393	44.500	40.700	1.569	0.543	1.000	3.316
Vireo bellii	Bell's Vireo	738.531	9.283	0.219	0.489	0.013	0.014	0.005	0.005	8.949	3802.477	3802.477	44.500	40.700	1.492	0.190	1.000	2.886
Vireo gilvus	Warbling Vireo	672.628	11.980	0.230	0.493	0.014	0.016	0.005	0.005	8.894	3952.936	3952.936	44.500	40.700	1.505	0.228	1.000	2.214
Vireo plumbeus	Plumbeous Vireo	572.645	16.708	0.230	0.462	0.016	0.018	0.006	0.005	8.824	4216.604	4216.604	44.500	40.700	1.523	0.289	1.000	2.356
Vireo vicinior	Gray Vireo	830.111	12.368	0.244	0.486	0.014	0.016	0.006	0.005	8.888	3974.575	3974.575	44.500	40.700	1.507	0.233	1.000	2.716
Xanthocephalus xanthocephalus	Yellow-headed Blackbird	735.174	70.412	0.199	0.283	0.023	0.025	0.007	0.005	8.524	7211.619	7211.619	44.500	40.700	1.599	0.807	1.000	2.771
Zenaida asiatica	White-winged Dove	785.383	147.918	0.263	0.490	0.027	0.029	0.008	0.006	8.374	11534.014	11534.014	43.400	38.500	1.800	0.856	2.000	2.585
Zenaida macroura	Mourning Dove	656.821	106.418	0.291	0.536	0.026	0.028	0.007	0.006	8.440	9219.604	9219.604	43.400	38.500	1.764	0.652	2.000	1.886
Zonotrichia leucophrys	White-crowned Sparrow	705.660	26.622	0.243	0.361	0.018	0.020	0.006	0.005	8.726	4769.466	4769.466	44.500	40.700	1.547	0.403	1.000	2.455

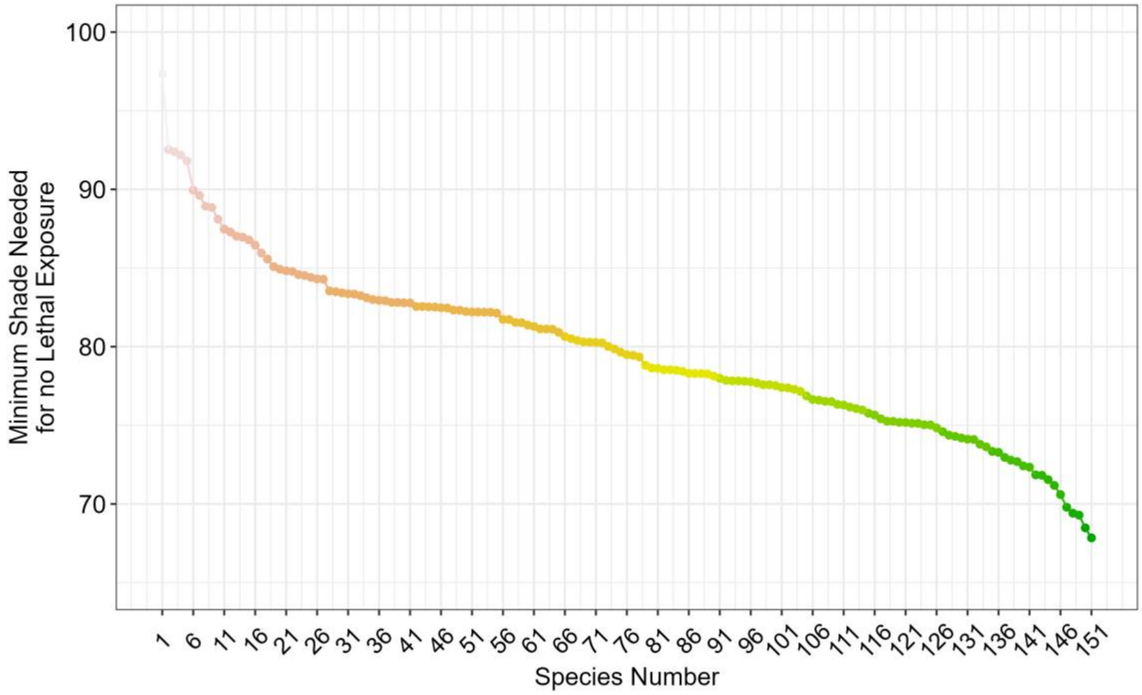

Figure 4-1 Thermal vulnerabiity (y-axis), defined as the minimum percent shade a species requires to survive (avoid lethal exposure) given a specific combination of solar radiation and air temperature. Species are ranked in order of highest (left) to lowest (right) thermal vulnerability. Values and species names are found in Supplemental Table S1. Representation of the K-means clusters, with each column representing a bird species, and colors representing each of the 18 resulting clusters. Absolute thermal vulnerabilities will change based on differences in solar radiation and temperature, but the relative vulnerability of one species to another will remain the same. Values above are from a model of possible combinations of solar radiation and temperature, but are presented as the marginal (or partial) effect, where temperature and solar radiation are held constant. Species numbers correspond to species numbers in Supplemental Table S1.

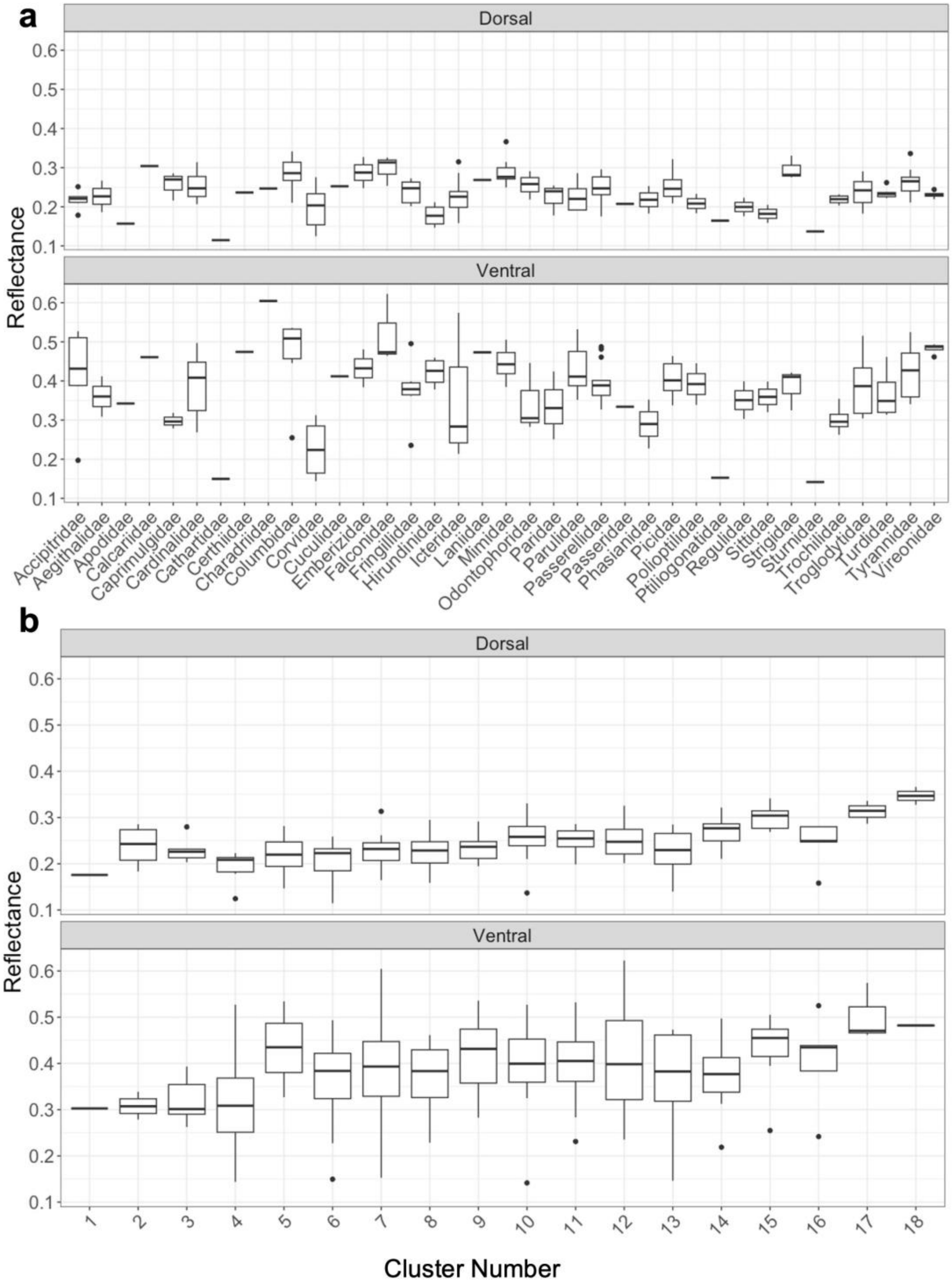

Figure 4-2 Measured dorsal and ventral reflectances, grouped by bird taxonomic family (a) and by our calculated thermal vulnerability clusters (b). Cluster numbers on the x-axis match cluster

colors in Figure 1 (1 is most vulnerable species cluster and 18 is least vulnerable). Reflectance at 0 is total absorptance (black), while reflectance at 1 is total reflectance (white).

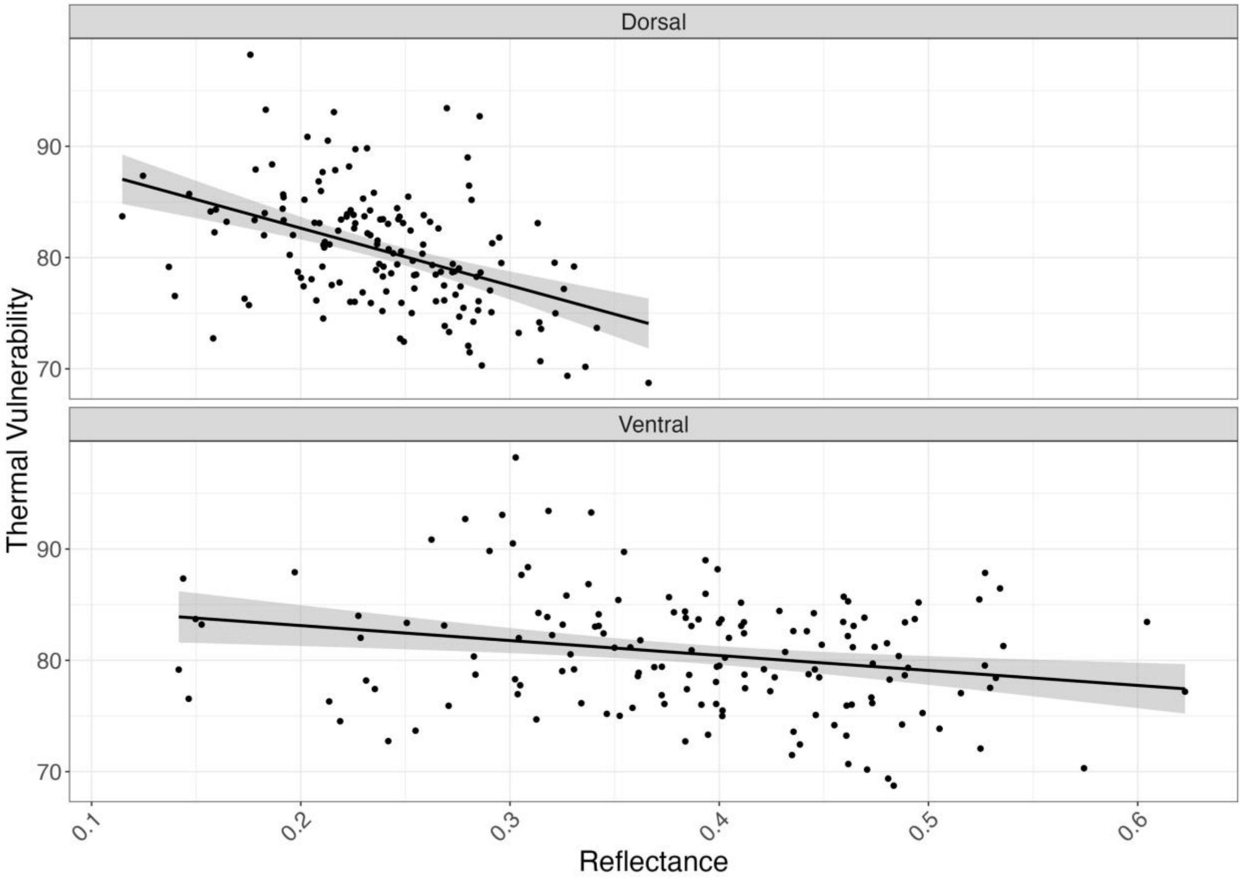

Figure 4-3 Linear regression between thermal vulnerability from dorsal (top) and ventral (bottom) reflectance. Dorsal reflectance is statistically significantly associated with thermal vulnerability, while ventral reflectance is not.

Chapter 5

Indirect evidence of underground thermal refugia modifying desert bird communities in the face of climate change (Adam J. Eichenwald, J. Michael Reed).

Abstract

Models projecting the impacts of climate change on animal distributions have been criticized for assumptions that limit their predictive capabilities. Such forecasting, however, is useful when examining plausible alternative scenarios for species responses to such external pressures. We apply a community viability analysis (CVA) in the form of a series of projections that considered the effect of multispecies interactions on a declining Mojave Desert bird community. Our alternative models include various types of access to above- and below-ground thermal refugia. Conventional wisdom suggests that birds do not utilize underground burrows dug by other animals as thermal refugia, which has led to their decline with increased temperatures. We used a thermal model to assess multiple site-specific scenarios of avian burrow use under various microclimate conditions for 151 bird species. To avoid a "just-so story" narrative, we compared model outcomes with published data, our own field surveys, and data from a citizen science project (eBird). Our field surveys offered precise pattern detection but limited spatial coverage, while citizen science data provided broader geographical and temporal context. We calculated that birds having no access to underground refugia should have resulted in instability in bird community composition over the course of the 20th and 21st centuries in the face of climate change, with a greater loss of species than has been observed. However, thermal model output for scenarios in which burrow use is an existing but uncommon behavior are more consistent with real world observations. Furthermore, field surveys consistently indicate a positive link between bird richness and abundance and the use of underground burrows. Our analysis of eBird

data showed that this relationship was strongest in areas with lowest amounts of aboveground vegetative shade – consistent with a scenario where birds fall back on burrows as thermal refugia due to a lack of protection aboveground. Therefore, even if underground thermal refugia use was not a historic behavior for birds, published and field results are consistent either with birds currently adopting this behavior or, alternatively, birds using as-yet-unidentified thermal refugia with similar properties. Such scenarios must be regarded as speculative based only on existing anecdotal evidence, but it suggests further field experiments that can inform ecosystem management and policies.

Introduction

Climate change effects on animal distributions have been projected for many species (e.g., Pearson and Dawson 2003, Pecchi et al. 2019). Many of these projections are derived from co-associations between current distributions and climate variables, and they often incorporate physical landscape features and habitat. This type of forecasting has been criticized for its restrictive assumptions, such as assuming that current distributions are limited by the factors being investigated, that these factors will continue to limit the species' distribution under future conditions, not incorporating adaptations (Dormann 2007, Austin and Van Niel 2011), not allowing for behavioral plasticity and acclimatization (Willis and Bhagwat 2009, Austin and Van Niel 2011), and assuming biotic interactions will remain constant despite changing conditions (Austin and Van Niel 2011, Trainor and Schmitz 2014). Indeed, forecasting distributions is notoriously difficult due to the rise of climatic conditions with no modern analog (Fitzpatrick and Hargrove 2009) and limited experimental confirmation of models (Dormann 2007, Austin and

Van Niel 2011, Boettiger 2022). Therefore, results from these and similar models should be treated as hypotheses to be tested.

Even within these limitations, forecasting is an important tool for addressing conservation questions. One of the most common forecasting tools in species conservation is stochastic demographic population projections, referred to as population viability analyses. These are used to estimate relative extinction risks under alternative future environmental conditions or management scenarios, i.e., to compare alternative hypotheses using a model (Beissinger and Westphal 1998, Reed et al. 2002, Lacy 2019). Such analyses have been used to predict how predator reintroduction might be economically beneficial to local cattle farmers (Prowse et al. 2015), whether increases in grizzly bear predation following shifts in prey availability are sufficient to account for elk population declines (Middleton et al. 2013), or which age class of loggerhead sea turtles are predicted to have the greatest population impact in response to protective management (Crouse et al. 1987). In some cases, they can even provide information on systems where testable data is difficult or even impossible to collect (e.g., Prowse et al. 2013), making viability analyses important tools for developing ecological hypotheses under climate change (Selwood et al. 2015).

Historically, population viability analyses (PVA) have predominantly centered on single species (Beissinger 2002). However, a growing awareness of the need for a multi-species, ecosystem-focused perspective (Sabo 2008) has led to the emergence of community viability analysis (CVA), an group of approaches to modeling the persistence and dynamics of communities under various conditions of disturbance or management that accounts for interactions between species (Ebenman and Jonsson 2005, Lacy et al. 2013, Eichenwald and Reed 2021). We can generate evidence-based hypotheses for how climate change may be impacting the survival and distribution of entire communities of species which we can evaluate with CVA, setting a foundation for the subsequent, more systematic experimentation required for confirming the presence and influence of certain interspecific interactions.

Here we conduct a persistence-based CVA of a well-researched bird community in the Mojave Desert, assessing the possibilities that the loss of bird species is driven by thermal vulnerability and that thermal refugia, such as surface shade and burrows, might have influenced or currently influences patterns of avian population persistence. Specifically, we generate hypotheses of different scenarios of bird species persistence over time and species loss related to thermal vulnerability and refuge from the threat of heat. Over the last century, Mojave Desert birds have suffered notable declines that are hypothesized to be caused by climate change (Iknayan and Beissinger 2018, Riddell et al. 2019, Riddell et al. 2021), while the mammal community has remained relatively stable (Riddell et al. 2021). Although birds in desert environments utilize microclimates such as vegetative shade or crevices in trees and rock as thermal refugia (Rundel and Gibson 1996a, Wolf et al. 1996), it has been proposed that birds may be particularly vulnerable to increasing temperatures because they, unlike mammals, are unable to construct their own microclimates in the form of underground burrows (Riddell et al. 2021), which provide thermal refugia for wildlife because of their relatively cooler and more stable temperature compare to the surface (Rundel and Gibson 1996a). In the Mojave Desert, shallow burrows are created by small mammals and lizards (Laundré and Reynolds 1993, Van Vuren and Ordeñana 2012), and the Mojave Desert tortoise (*Gopherus agassizii*) digs deep burrow systems (Hansen 1963, Rundel and Gibson 1996a). The Mojave Desert tortoise, along with its relatives in other arid habitats, are thought of as ecosystem engineers because of these burrows and their potential benefits to the biotic community (Walde et al. 2009, Pike and Mitchell 2013).

Prevailing wisdom is that birds generally do not utilize underground burrows as thermal refugia in desert environments (Austin and Smith 1974, Dean and Vickery 2003), although this may be because it can be time consuming and costly to document avian burrow use (Dean and Vickery 2003). However, birds are well-known as secondary cavity users (e.g., Brush 1983), and there are some that do nest underground, taking advantage of existing burrows and crevices (Crowe and Longshore 2013). Use of burrows by local wildlife has not been studied systematically, but there is anecdotal evidence of some bird species utilizing burrows in the Mojave and elsewhere (Pittman Jr. 1960, Austin and Smith 1974, Bowers and Dunning 1985, Coate 1994, Dean and Vickery 2003, Pike and Mitchell 2013, Puffer et al. 2022). Considering the strong selective pressure of high temperatures exacerbated by climate change, we suggest that the use of burrows as thermal refugia would likely be favored for enhancing bird survival.

In the absence of systematic study of burrow use by birds, we generated a suite of hypotheses (models) to predict current and past bird species richness in the Mojave Desert, based on species-specific vulnerability to temperature and predilection for utilizing underground thermal refugia. Biophysical models differed in the degree to which species have access to refuge from the heat, ranging from the equivalent protection provided by above-ground vegetation, and burrows of different depths and availability. We modeled hourly microclimate data at each of 1494 sites, and its thermal suitability for each of 151 species, daily for 5 summer months, for 20 years from 1959 and 2019. Projections of species richness from these biophysical models were compared to published data on historic bird richness. Data on species-specific thermal vulnerabilities for the 151 bird species we evaluated came from mechanistic physiological models of avian thermal properties (Eichenwald and Reed In review). Finally, we tested whether observable patterns in avian species distributions (as seen in citizen science bird sighting data (eBird) and to our own field survey data of birds and burrows) were consistent with model outcomes, even after we controlled for the potential confounding effect of habitat. Evidence consistent with the premise that underground burrows (or their thermal equivalents) influence bird richness and abundance would lay a foundation for future targeted, manipulative experiments, while contrary results would negate the need to implement such a time-consuming assessment.

Methods

Study System

The Mojave Desert covers one-tenth of the desert area in the contiguous United States and Mexico, spanning broad latitudinal (34.8° to 36.2° N), longitudinal (117.2° to 115.8°W) and elevational ranges (-82m to 3367m) (Rundel and Gibson 1996c). Temperatures are generally warm, and the desert holds the record for the highest measured air temperature on the planet (El Fadli et al. 2013). The desert has experienced a rise in mean annual air temperature by approximately 2°C since the early 20th century (Bai et al. 2011). Vegetation is dominated by creosote (*Larrea spp.*), which covers nearly two-thirds of the total desert area (Rundel and Gibson 1996c). In some cases, the iconic and Mojave-restricted Joshua tree (*Yucca brevifolia*) creates woodlands with a variety of codominant shrubs with increased cover (Rundel and Gibson 1996c).

Overview

We adopted a multifaceted approach to thoroughly investigate our alternative hypotheses. Initially, we utilized a pre-published mechanistic thermal model to assess the consistency of avian burrow use (Eichenwald and Reed In review). These models were applied to spatial and time specific data under a variety of microclimate conditions to evaluate the plausibility of avian burrow use (see next section, Figure 1). We were cautious of the potential pitfall of constructing a narrative to fit the results (a "just-so story"), which can occur if one relies only on computational models to examine questions of community ecology (Hubálek 2021). To counter this limitation, we compared the modeling outcomes with empirical data published by Iknayan and Beissinger (2018) as well as data derived from our own field surveys conducted during our research and data contributed by citizen scientists (eBird, Sullivan et al. 2014). Our field surveys offered higher precision in pattern detection, although they were limited in spatial coverage. Conversely, the citizen science data sacrificed some pattern precision but contributed information from a broader geographical area and over a more extended period.

Mechanistic Model

We divided the Mojave Desert into a grid of 1494 square cells ("sites") measuring 8890m on each side. We then modeled the responses of 151 bird species to the microclimate estimates at each site using the R package NicheMapR (Kearney and Porter 2017, Kearney et al. 2021), which calculates an organism's heat and water exchange based on the corresponding microclimates and a suite of biophysical characteristics of the species (Kearney and Porter 2017, Kearney et al. 2021). The biophysical parameters for each bird were taken from Eichenwald and

Reed (In review). To obtain hourly microclimate data at each site, we utilized the ERA5 hourly climate reanalysis for 20 years in four time blocks that spanned 60 years: 1959-1962, 1980-1983, 1990-1993, 2001-2004, and 2016-2019. We employed the mcera5 R package (Klinges 2022) to acquire these data. Although other climate models are availabe for a section of the desert during this period, we used ERA5 because it is compatible with NicheMapR. Due to limitations of computer memory and computation time on the Tufts high-performance computing cluster, we did not download and analyze all available months and years. Instead, we focused on data from April 1 to September 1, which encompasses the critical months for bird survival during spring and summer. We selected four consecutive years for each time block and introduced a gap of 10-20 years before proceeding to the next block, which allowed us to mitigate any influence of single-year anomalous weather phenomena on our values. Among the available options, we chose 1959 as our baseline year as it was the earliest year of accessible ERA5 data and aligned with the period when the Grinnell bird surveys ended (1908-1968). To ensure consistency in date tracking, NicheMapR employs the day of the year; we addressed leap years by excluding the leap day. For instance, day 100 of the year was consistently represented as April 10.

Hourly microclimate data for each year were calculated using NicheMapR's micro_era5 function, which employs methods described in Kearney et al. (2020) to estimate microclimate at fine time scales. We assumed birds were positioned 1.5 meters above the ground (per Riddell et al. 2019) and incorporated the effect of surrounding topology at each site; this means direct sunlight could be blocked if the angle was occluded by higher ground. Additionally, the NicheMapR microclimate functions include a "warm" parameter that adjusts calculations based on a shifted temperature. For our analyses, we computed the median temperature increase (x°C) from 2016 to 2090 at specific locations in Google Earth Engine and used x as our warming parameter when accessing ERA5 data from 2016. To account for abnormal weather phenomena, we repeated this process with 2017, 2018, and 2019 baselines, resulting in four estimates for the year 2090. We utilized the CNRM-CM5 climate change model, known for its applicability over land(Kamworapan and Surussavadee 2019), considering the rcp45 (probable baseline) and rcp85 (worst-case) climate scenarios (van Vuuren et al. 2011).

We used a proxy measurement (plant cover) to determine shade availability in the Mojave Desert. At bird survey sites, we measured sunlight intensity under the most prevalent plant species using a LX1330B Digital Illuminance Light Meter. Lux measurements were taken in 10 spots per plant: 5 under the canopy and 5 in adjacent sunny areas. We calculated percent shade by comparing average lux values in shade and full sunlight. Creosote and white bursage (*Ambrosia dumosa*) were common but provided minimal shade (around 50% shade), while Joshua trees and Mojave yucca (*Yucca schidigera*) offered substantial shade but were patchily distributed (around 90% shade). Therefore, we predicted that low-shade areas were those with low percentages of plant cover dominated by creosote and white bursage, while high shade areas would be dominated by Joshua trees and higher densities of plant cover. If true, we could use measures of NDVI to determine percent plant cover and use it as a proxy variable for shade.

To assess cover distribution, we employed high-resolution satellite imagery from the National Agriculture Imagery Program (NAIP). Analyzing data acquired between Jan 2019 and Dec 2021, we used Google Earth Engine to access red, green, blue, and near-infrared band information with a one-meter ground sample distance. Developed impervious surfaces were removed by creating a masking layer based on the National Land Cover Database (NLCD). The NDVI was calculated from the NAIP raster layer, and cells with NDVI values less than or equal to 0 were excluded. This resulted in a raster layer classifying plants at the one-square-meter level. The percent plant cover per site was determined by dividing the number of plant-representing raster cells by the total number of cells in that site.

We classified areas as low or high shade using maximum likelihood classification in ESRI ArcMap. Groundtruthed locations, which we visited across the Mojave Desert, were independently classified as low or high shade. We then buffered each location 1km and calculated the percent plant cover in each zone. A one-tailed Welch's two-sample t-test with heterogeneous variances supported our prediction that low-shade areas have lower plant cover compared to high-shade areas (t = 2.08, df = 14.51, p-value = 0.03). This validation allows us to use the percent plant cover raster as a proxy for shade types across the Mojave Desert. For our analyses, we assumed high-shade, yucca-dominated areas provided approximately 90% protection from sunlight, while low-shade creosote-dominated areas provided approximately 60% protection from sunlight.

Birds' migratory and breeding patterns result in partial summer (April through August) presence in the Mojave Desert, providing some relief from extreme heat. Therefore, we analyzed bird presence data using the ebirdst R package (Fink et al. 2020) to categorize temporal use into pre-breeding migration, breeding, and year-round presence. Prefabricated distribution models from the Cornell Lab of Ornithology (Fink et al. 2020) were downloaded for each species, representing weekly ranges. Shapefiles representing species' ranges in each season were created using R code (Strimas-Mackey et al. 2021), including estimated end dates for associated seasons.

The temporal and spatial distributions obtained were applied to our mechanistic models of species-specific thermal vulnerability by excluding days when bird species were not present. For instance, if a species was found only at a specific location in the Mojave Desert during the pre-breeding migration season, we removed all subsequent days from the model after confirming the final date of that season. Conversely, if a species was present year-round at a location, we ran the model for all hours/days for the target time frame. Species present year-round were evaluated during breeding and pre-breeding seasons; species present during the breeding season were also regarded as present during the pre-breeding season. It is important to note that this analysis assumes stability in species presence/absence distributions and season end dates based on eBird surveys from 1959 to 2090, although actual changes over a century are difficult to precisely map due to data limitations.

Using the temporal distributions described above, we ran endoR for each of our sites, years, and species, for a total of 18 modeled scenarios (Figure 2). Furthermore, we calculated how increasing shade from 0-100% (increments of 5) affected bird thermal responses using the *shade* parameter in the endoR function. Degree of thermal vulnerability of each species, per site, per year was defined by the minimum required shade in which there are no hours where the model was unable to calculate a solution (i.e., how much shade was required for a bird to survive all hours in a day) or to prevent the species from losing 15% or more of its body mass in water (Albright et al. 2017, Eichenwald and Reed In review). Finally, we calculated median thermal vulnerabilities of birds within each 4-year block. We used the Tufts University High Performance Compute Cluster to run our models to shorten the substantial computation times.

We also examined bird thermal responses in underground burrows at depths of 200 (tortoise burrow, Hansen 1963), 50, 20, and 5 cm (mammal burrows, Laundré and Reynolds 1993, Van Vuren and Ordeñana 2012), representing the available microhabitat. Burrows were assumed to have no direct exposure to solar radiation or wind. Median thermal vulnerabilities were calculated as previously described. Note that these refugia were evaluated in addition to available shade from vegetation.

It is important to note that not all bird species can fit inside mammal burrows, although tortoise burrow entrances are much larger. To determine species capable of fitting through both types of burrow entrances, we measured the vertical and cross-sectional lengths of 10 mammal burrow entrances at each of the 42 sites we used for our field surveys (see below). The cross-sectional area of the openings was calculated using the ellipse area formula. One-sample t-tests with Bonferroni corrections compared the distribution of burrow entrance areas with the average cross-sectional area of each bird species, obtained from measurements of bird width and height from Eichenwald and Reed (2023). Species with significantly smaller cross-sectional areas than the burrow openings were considered capable of entering. Only species meeting this criterion were included in subsequent analyses of burrows and their associated underground microclimates.

To determine how thermal vulnerability of bird species in the Mojave Desert has changed over time, we fit two linear mixed models to our data using REML and the nloptwrap optimizer (Makowski et al. 2020) with year as a predictor, species and location as random variables, and thermal vulnerability as a dependent variable. The first model used only aboveground thermal vulnerability data in response to Mojave Desert climate conditions and included results from all species, while the second modeled only belowground thermal vulnerability data at all depths and included results only from species capable of fitting in both mammal and tortoise burrows. We then plotted the marginal effect of year on thermal vulnerability in both models.

We analyzed predicted bird community diversity over time using principal coordinates analysis (Gower 1966) and the Jaccard index of dissimilarity in the Vegan R package (Dixon 2003). Each site/year combination was considered separately, considering species presence/absence and their minimum shade requirements for survival. For low-shade sites, species were considered present if their minimum shade requirement was ≤60%, while for high shade sites, it was ≤90%. To handle observations with zero species, we included a dummy species present at all sites. Although excluding locations with zero observed species is common due to undefined calculations with the Jaccard index, we included absence-only observations in our study as they indicate mechanistically calculated lethal environmental conditions. Confidence intervals for PCoA were calculated to assess differences in predicted community types across years.

We also used a negative-binomial mixed model, employing ML and the Nelder-Mead optimizer (Makowski et al. 2020), to analyze species richness (excluding the dummy species), with year and burrow depth (including aboveground data) as predictors. Site (raster cell) was treated as a random variable. In addition, we considered different success rates for birds in securing burrows when needed (75%, 50%, and 25% chance). For each species, we generated uniform-random numbers between 1-100 to determine success or failure. If successful, the bird was classified as "always successful" and its contribution to richness was calculated based on burrow depth. If unsuccessful, the bird was classified as having failed to find burrows when needed, and its contribution to richness was calculated based on aboveground conditions. This process was repeated 50 times per year in a Monte Carlo simulation. We fitted a negative-binomial mixed model, using ML and Nelder-Mead optimizer (Makowski et al. 2020), predicting species richness with year, burrow depth (including aboveground data), and success rate. Site (raster cell) was included as a random variable.

We simulated bird underground refugia use over time using microclimate and shade data solely from survey areas used by Iknayan and Beissinger (2018). Their bird richness survey data at the beginning and end of our prediction timeline were compared to our predicted scenario outcome, excluding climate change scenarios. Birds were assumed to use desert tortoise burrows initially and imperfectly for thermal protection but were forced to switch to imperfect mammal burrows as desert tortoise populations declined over time. Hourly bird behavior calculations determined whether birds sought underground refugia when environmental conditions were lethal despite available shade. Our scenarios considered different probabilities of successfully taking refuge in burrows based on depth and year. A Monte Carlo simulation was performed 100 times per year to gain an understanding of the variation in response. Due to time and computer memory limitations, we were constrained in the number of scenarios we could run. We used a negative-binomial mixed model with ML and Nelder-Mead optimizer (Makowski et al. 2020) to predict species richness with year, including the site as a random variable.

Citizen science data and field surveys

Our field surveys were conducted with a standardized sampling effort (described below) over a relatively limited spatial extent, but they allowed for simultaneous measurements of microhabitat features. In contrast, eBird contains over a decade of survey data from across the entire Mojave Desert, but each survey has different sampling effort and observers report no data on microhabitat features. Therefore, we had to infer features of interest using remote sensing data (see below). Each approach compensates for the weaknesses of the other.

We conducted our surveys in the eastern Mojave Desert in April and May 2023 in the areas surrounding Las Vegas, Nevada. Field surveys were conducted as far north as Coyote Springs, Nevada (36.81° N, 114.94° W), and as far south as the Mojave National Preserve in California (35.06° N, 115.55° W). We performed 129 point-count surveys for birds across 43 sites in the eastern Mojave Desert. Sites were selected to be at least 0.5 km from one another and were usually over 3-5 km from each other. Consecutive points on a transect were 500 m apart, with 3 survey points per transect. Surveys were done between sunrise and 4 hours after sunrise. We conducted bird counts for 10 min at each point, including all species observed or heard within 100 meters of the survey point. Viewshed in the Mojave Desert is vast, even in the most vegetated areas, and we sometimes observed birds outside our survey radius; they were noted, but we did not include these in our counts unless they flew overhead. Birds observed or heard during walks between survey points along a transect were also recorded separately. We also noted birds observed on our return from the farthest survey point along the transect, but only if the species had not yet been recorded in the survey. To be included, these birds also had to be within the 100m of the transect.

When returning from the last point along a transect, we used a tally counter to record the number of burrows within 5 meters on both sides of the transect. Burrows were separated into two categories: 1) tortoise-made burrows, and 2) burrows made by other vertebrates. Burrows made by tortoises are easily recognizable due to their large size and half-dome shape (Rundel and Gibson 1996a). Smaller, circular burrows are made by other reptiles and by rodents but could not be attributed to taxon. There were also shallow excavations made by species such as kit fox (*Vulpes macrotis*) and black-tailed jackrabbit *(Lepus californicus*), but they were excluded from our surveys because they were too shallow to provide refuge from the sun for resident birds.

We downloaded eBird data from the Cornell Lab of Ornithology (https://science.ebird.org/, September 2021) for the years 2009-2021 (2009 is the earliest available year) for April 1 – August 31 (the spring-summer months). We limited this list to the bird species that are resident in, or migrants through, the Mojave Desert during the spring and summer months, limited to the 151 species used in our biophysical model. We followed the protocol of Strimas-Mackey et al. (2020) on how best to prep the data for analysis using the auk package in R (Strimas-Mackey et al. 2018). We limited data to surveys where observers created a "complete checklist" (i.e., where the participant reported all birds that they detected and identified, allowing inference of counts of zero individuals for the species that were not reported). We also removed duplicate lists, where two observers in the same group recorded separate lists. Checklists are generally autocorrelated in space and time; we corrected for autocorrelation by defining an equal-area hexagonal grid across the study region with 5 km between hexagon centers, and then randomly sampling one checklist per hexagon per week (Strimas-Mackey et al. 2020). We used hexagons because they suffer from relatively smaller amounts of spatial distortion than do other common shapes (Sahr 2011).

We developed a raster map of expected counts of tortoises across the Mojave Desert using data on tortoise observations and transect locations collected by the US Fish and Wildlife Service from 2001-2019 (Allison and McLuckie 2018; data provided by Linda Allison, USFWS, pers comm). We used these observations as a proxy for the relative abundance of tortoise-built microclimates (burrows), assuming higher numbers of tortoise observations are indicative of higher numbers of burrows. Under some circumstances, a basic kernel density analysis can be sufficient to calculate the density of features in a neighborhood and provide the necessary raster map. However, USFWS surveys were not spatially unbiased; some areas were more heavily sampled than others. Therefore, an area with a greater number of tortoise observations could be due to higher sampling effort at that site or to a genuine higher abundance of tortoises. Consequently, we adopted the fisheries biology solution of calculating catch per unit effort – or in our case sightings per unit effort – rather than using raw observations (Maunder and Punt

2004). This standardizes the estimates across all surveys and provides a measure of relative abundance for tortoises, and by proxy tortoise-built microclimates, across the Mojave Desert.

We used the Kernel Density tool in ArcMap to calculate the distribution of densities for both tortoise observations and surveys. Kernel density bandwidth was estimated using ArcGIS's default method, which adapts Silverman's Rule-of-thumb bandwidth estimation formula for two-dimensional space. We calculated the expected count of tortoises per raster cell using ArcGIS's kernel density "expected count" setting, and then used the raster calculator to determine expected sightings per unit effort with the following equation (Breen et al. 2014):

$$Expected\ sightings\ per\ unit\ effort\ = \frac{expected\ counts}{density\ of\ sampling\ effort}$$

Tortoises tend to remain within the same home ranges over the course of their lives (Berry 1986); therefore, we created a single tortoise sightings per unit effort raster that compiled all data from the USFWS over the course of their study period. This was by necessity, as the USFWS focused on surveying for tortoises in different areas of the Mojave in different years.

Any analysis regarding the importance of microhabitat to bird presence must include in the analysis a way of controlling for habitat. Objectively "good" habitat should attract all animal species in the desert, including the mammals and reptiles that construct burrows for themselves. Therefore, it is plausible for birds to be associated only with better habitat, and that a correlation between bird presence and burrow density is only a demonstration that all desert animals are converging on the same high-quality areas. To account for this possibility, we developed two habitat quality rasters: a plant cover raster (i.e., vegetative shade) and an NDVI raster. We used NDVI because it is associated with higher quality animal habitat in deserts (Creech et al. 2016). Both rasters were developed with high resolution satellite imagery (Recio et al. 2013) to classify plants at 1m^2 resolution. We used Google Earth Engine to access and analyze data gathered between 01/01/2019 and 12/31/2021 from the National Agriculture Imagery Program (NAIP), which acquires red, green, blue, and near-infrared band data at a one-meter ground sample distance (GSD). We removed developed impervious surfaces such as roads, cities, and solar panels from the dataset by creating a masking layer from the National Land Cover Database (NLCD). Any NLCD raster cell classified as having above 0% coverage by a developed impervious surface was masked out of the NAIP raster. We then calculated the NDVI of the NAIP raster layer and removed all raster cells with NDVI values less than or equal to 0, creating a raster layer classifying plants at the $1m^2$ level.

To analyze the association of non-tortoise burrows with eBird observations, we required a proxy variable that could be developed with satellite imagery. Our field data revealed that the number of burrows along a given transect were highly predicted by the ground type at said site, where ground type was split into 4 qualitative categories based on its firmness and soil type (soft/clay, soft/sandy gravel, hard/clay, hard/sandy gravel). We were unaware at the time that the terms “clay” and “sandy” have their own separate definitions in the field of soil science; for our purposes, we defined “clay” as ground that holds its shape when dug into and has a similar consistency to wet sand, while “sandy” is ground that is drier and loose (akin to that found at a beach). Burrows as predicted by these categories were overdispersed, requiring a quasi-Poisson GLM to model how burrow numbers decline as the ground becomes more difficult to dig into (linear effect of ground type, beta = -0.61, 95% CI [-0.82, -0.41], $t(39) = -5.87$, $p < .001$, McFadden’s pseudo-$R^2 = 0.60$). Therefore, “digging difficulty” of the ground is a viable proxy variable for the number of burrows. The best “digability” variable we found is the presence or absence of desert pavements, which are surfaces covered by closely packed, interlocking rock fragments (Dickerson 2012). Desert pavements are classifiable via remote sensing (Beratan and

Anderson 1998), and although desert tortoises can dig through the hard layer, smaller reptiles and mammals are not (Karl 1980, Dickerson 2012). We confirmed that the presence or absence of desert pavements (described below) were indeed predictive of the number of non-tortoise burrows at our field sites (one-tailed t-test, difference = 21.88, t(34.26) = 3.17, p = 0.002). Therefore, we used a classified desert pavement layer as a proxy variable for the number of non-tortoise burrows near eBird surveys.

We generated this pavement layer with a method created by Beratan and Anderson (1998) for the Landsat 4-5 Thematic Mapper. The Landsat TM was decommissioned in 2011, which is the closest time from which we could determine an image. However, desert pavements develop and change over thousands of years (Dickerson 2012), so their locations in space are likely to have remained static during the time between layer creation and our surveys. We created a composite RGB image in Google Earth Engine (Gorelick et al. 2017) from the 2011 Landsat TM, and then drew training polygons that classified the image into binary categories: "hard pavement" or "softer ground." Polygons were groundtruthed using data collected on soil types during our field research, and we used a random forest classifier with 10 trees (sensu Breiman 2001) to classify our final raster.

We assessed the representation of each environmental variable by calculating its value at each survey site, both ours and those from eBird. We created a buffer around all our field-survey and eBird sites in a circle of 1km radius and calculated the average NDVI within the buffer and the most frequent desert pavement classification value. Finally, to calculate the percent plant cover, we divided the number of 1m^2 raster cells representing plants in a buffer by the total number of all 1m^2 raster cells in said area.

To test whether bird abundances and richness from our field surveys are associated with estimated burrow abundance, we fitted multiple Poisson linear models (estimated using ML) predicting bird counts with varying combinations of NDVI, number of burrows, number of tortoise burrows, and percent shrub cover. As we only had 43 survey points of our own, we could not confidently use more than 4 predictors in a model. If the resulting model was overdispersed (violating Poisson assumptions) we re-ran the model using a negative binomial distribution. We then followed guidelines from Arnold (2010) to select the best model. Models with the lowest AICc are generally considered top-ranking . However, it has been the case where multiple models are within 2 AICc from one another and, therefore, are both considered "empirically supported" – even if one model has an uninformative parameter with model deviance that does not overcome the +2 AICc penalty for additional parameters. Therefore, we discarded models with uninformative parameters (with slopes close to 0), even if they had lower AICc values (Arnold 2010).

We repeated this modeling procedure with eBird data. We used a mixed model to account for surveys that were performed in the same location in space at different times; these are autocorrelated, which must be accounted for to not violate modeling assumptions. The Cornell Lab of Ornithology classifies all surveys by their location in space, grouping those that were performed in approximately the same place. We used this grouping as a random effect.

In the suite of tested models with eBird data, we included one that used only variables of survey effort (i.e., number of surveyors, amount of time a survey was conducted, distance traveled in a survey) as a null model. If this null model were the best fit model, it would show that the best predictors of bird presence in eBird surveys is merely how much effort went into the survey. However, all models included all effort variables, allowing us to control for effort as a potential covariate. Model selection with AICc was the same as with models from our field data. 95% Confidence Intervals (CIs) and p-values were computed using a Wald z-distribution approximation.

Results

Mechanistic Model

We predicted, and found, a quadratic relationship between bird shade requirements for survival above ground (i.e., without access to underground refuge from the heat) and time (across decades), with shade requirements for birds to survive increasing over time (conditional R2 = 0.76). Within this model, the effect of year as a quadratic ordinal predictor is statistically significant and positive (beta = 4.12, 95% CI [4.06, 4.18], t(517299) = 131.04, $p < .001$) (Figure3a). That is, years (year groups) differed significantly from each other, with the earliest years (1959-1962) requiring the least amount of shade for bird survival, and subsequent years exhibiting steadily increasing shade required, as expected under climate change.

The generalized linear mixed model predicting the total number of hours a species would be exposed to lethal temperatures over time when they had access to below-ground refugia showed strong effects of both year and burrow depth (conditional $R^2 = 0.71$) (Figure 3b). Burrows at depths of 5 cm and 20 cm significantly and quadratically increased in number of hours exposure to lethal temperatures over time (decades) (5 cm beta = 7.44, 95% CI [6.49, 8.38], $p < 0.001$, 20 cm beta = 7.44, 95% CI [6.49, 8.38], $p < 0.001$). However, the model's intercept, to which all other burrow predictors are compared statistically, corresponding to burrow depths of 200cm, is at 0.01 (95% CI [-0.02, 0.05], $p = 0.49$), showing that birds are unlikely to be at risk of exposure to lethal temperatures at such depths. Furthermore, there is no significant difference at depths of 50 cm over time (beta = 0.23, 95% CI [-0.71, 1.18], p = 0.63) Indeed, the effect of rising temperatures on bird thermal vulnerability decreased as burrow depth increased. These differences demonstrate the increasing thermal risk to birds as they take refuge closer to the surface, although the difference in effect size is much larger at a depth of 5 cm. In fact, our models predict that birds at 5cm depths will generally be exposed to over 150 total hours of lethal temperatures in a summer, which is significantly worse than burrows at any other depth (Figure 3b). Standardized parameters were obtained by fitting the model on a standardized version of the dataset; 95% Confidence Intervals (CIs) and p-values were computed using a Wald t-distribution approximation (Figure 3b).

Aboveground shade-driven bird community composition as calculated with principal coordinates analysis is increasingly dissimilar over time from the original composition in 1959-1962 over time (i.e., associated with increasing temperatures) (Figure 4). Community compositions in 2001-2004 and 2016-2019 are similar, but composition is predicted to shift even further from the mid-20th century baseline under both the rcp45 and rcp85 climate change scenarios. Community composition when birds are allowed access to underground refugia at depths of 5cm is like that aboveground, but differences are increasingly less pronounced with access to increasingly deeper burrows. At depths of 20cm, community composition is similar between most years prior to 2016-2019. Finally, composition shifts under both climate scenarios, with a pronounced difference under the rcp85 projection. If birds are allowed access to burrow depths of 50cm and 200cm, we no longer see any discernible differences in community composition regardless of year (Figure 4).

Predicted species richness differed significantly over both time and available burrow depths, and there was an interaction (Figure 5). Species richness was by far the highest in scenarios with access to desert tortoise burrows (200cm depth), and lowest for the scenario with no access to burrows. In contrast, there was virtually no difference in predicted species richness for communities with access to burrows of 50cm and 20 cm depth except under future scenarios of climate change (beta = -0.01, 95% CI [-0.06, 0.04], p = 0.69). There was little to no difference in predicted species richness between communities with no access to burrows, and access to only 5cm-deep burrows in all years and climate change scenarios (Figure 5a). The model's total explanatory power was substantial (conditional R2 = 0.70). Aboveground, 5 cm, and 20 cm depths follow significantly negative, quadratic patterns (aboveground beta = -0.76, 95% CI [-0.80, -0.71], p < 0.001, 5 cm beta = -0.82, 95% CI [-0.87, -0.78], p < 0.001, 20 cm beta = -0.22, 95% CI [-0.27, -0.16], p < 0.001). This means that species richness declines over time regardless of burrow access at these three depths; however, richness at the beginning of the study is higher when there is access to greater depths, while refugia closer to the surface result in greater declines to richness with increased temperatures.

Furthermore, restricting access to burrows (i.e., situations where burrow use is not common or bird access to burrows is imperfect) leads to a systematic decrease in predicted species richness as access decreases (Figure 5b). Although access to deep (200cm) burrows consistently results in significantly greater species richness, the richness expected for the other burrow depths becomes progressively lower and more similar because only the most thermally resistant species persist. The linear effect of success rate is statistically significant and negative (beta = -1.03, 95% CI [-1.03, -1.03], p < 0.001, conditional R2 = 0.49). All depths follow significantly negative and quadratic patterns over time (5 cm beta = -0.67, 95% CI [-0.68, -0.67], p < 0.001, 20 cm beta = -0.21, 95% CI [-0.22, -0.21], p < 0.001, 50 cm beta = -0.02, 95% CI [-

0.03, -0.02], $p < 0.001$), showing how the combined effect of increasing temperatures and imperfect refugia access results in declines to species richness.

Finally, our simulated burrow availability scenario (where there was declining tortoise burrow availability over time, with increased dependence on mammal burrows) replicated species richness observations from Iknayan and Beissinger (2018) in 1959-1962 and 2016-2019. Our confidence intervals of species richness for the year 1959-1962 overlap with confidence intervals of richness measured by Iknayan and Beissinger (2018) at that time, as do confidence intervals of species richness in 2016-2019. The total explanatory power of the model itself is substantial (conditional R2 = 0.90), and the year 2016-2019 is significantly different from 1959-1962 (beta = -0.57, 95% CI [-0.57, -0.56], $p < 0.001$, intercept = 3.85 (95% CI [3.62, 4.08], $p < 0.001$) (Figure 6).

Citizen Science Lists and Field Surveys

Both species richness and bird abundance were consistently low during our field surveys. We recorded an average of 5.1 ± 0.9 species and 8.6 ± 1.7 individual birds within the formal survey period. Notably, we also observed a relatively higher occurrence of small burrows dug by mammals and reptiles (60.4 ± 8.3 burrows per transect) compared to the relatively rare occurrence of burrows dug by desert tortoises (2.2 ± 0.6 burrows per transect). Citizen scientists' eBird surveys showed a similar number of species (8.3 ± 0.3 species) but recorded significantly higher bird abundances (27.0 ± 1.4 individuals), likely due to the longer survey durations permitted in eBird (recommended 5 km of survey length for modeling (Strimas-Mackey et al. 2020)).

Our analyses utilizing Poisson models revealed valuable insights into the factors associated with bird abundance in our field surveys. The best-fit model included the number of non-tortoise burrows, NDVI, and percent shrub cover as predictors (Figure 7a). This model demonstrated high explanatory power (Nagelkerke's R2 = 0.93) and indicated a significant positive relationship between non-tortoise burrows and bird abundance (beta = 0.02, 95% CI [0.01, 0.02], p < .001). Additionally, percent shrub cover showed a significantly positive association with bird abundance (beta = 0.82, 95% CI [0.18, 1.42], p = 0.009). However, mean NDVI had no statistically significant explanatory power (beta = 4.50, 95% CI [-4.98, 14.20], p = 0.36). The model predicting bird richness with the lowest AICc was within 0.39 of the next closest model and was a nested version of the higher AIC model. We therefore selected the model with the second-lowest AIC as our best model; this model included the number of non-tortoise burrows as the sole predictor (Figure 7b). This model demonstrated a statistically significant positive relationship between non-tortoise burrows on bird richness (beta = 0.01, 95% CI [0.01, 0.02], p < .001, Nagelkerke's R2 = 0.70).

When analyzing the eBird data, negative binomial mixed models were employed due to overdispersion in the Poisson models. The two best-fit models included distance traveled, number of observers, survey start time, survey duration, percent shrub cover, NDVI, and ground hardness (negatively indicative of mammal burrows). The best-fit model additionally incorporated the estimated number of tortoises per unit area and the moderating effect (or interaction) of percent shrub cover (Figure 8a, conditional R2 = 0.69). The second-best model according to AICc did not include the tortoise effect but incorporated the moderating effect of percent shrub cover on desert pavement (Figure 8b, conditional R2 = 0.70). In the best-fit model, percent shrub cover (beta = 0.34, 95% CI [0.30, 0.39], p < .001), NDVI (beta = 1.15, 95% CI [0.53, 1.76], p < .001), desert pavement (beta = 4.98, 95% CI [3.75, 6.21], p < .001), and tortoises per unit area (beta = 0.22, 95% CI [0.06, 0.38], p = 0.008) all had significant positive associations. The moderating effect of percent shrub cover on tortoises per unit area was significantly negative (beta = 2.00, 95% CI [0.95, 3.06], p < .001).

In the second model, desert pavement had a significant positive association (beta = 0.34, 95% CI [0.30, 0.39], p < .001), as did percent shrub cover (beta = 0.63, 95% CI [0.36, 0.90], p < .001) and NDVI (beta = 1.30, 95% CI [0.63, 1.96], p < .001). The moderating effect of percent shrub cover on desert pavement was also significant (beta = 4.65, 95% CI [3.43, 5.88], p < .001). These findings indicate that the influence of shrub cover on bird abundance is negligible in areas with softer ground, which generally exhibit high abundances of birds. However, shrub cover becomes increasingly important in areas with hard desert pavement, with low abundances in areas of low cover and higher abundances in areas of higher cover. The effect of NDVI in this model was not significant, as in the first model.

Multiple models were assessed for predicting species richness from eBird data, with some models showing minimal differences in AIC scores. The selected model, with the lowest AIC and the least-nested structure (conditional R2 = 0.62), incorporated percent shrub cover, NDVI, tortoises per unit area, and the moderating effect of percent shrub cover on tortoises per unit area (Figure 8c). In this model, percent shrub cover (beta = 0.25, 95% CI [0.22, 0.28], p < 0.001; Std. beta = 0.10, 95% CI [0.06, 0.14]), NDVI (beta = 1.05, 95% CI [0.65, 1.45], p < .001), and tortoises per unit area (beta = 3.59, 95% CI [2.81, 4.37], p < .001) all had significant positive effects. The moderating effect of percent shrub cover on tortoises per unit area was significantly negative (beta = 1.21, 95% CI [0.52, 1.89], p < .001).

Discussion

Results from our mechanistic model, published data, our field research, and eBird data consistently indicated a positive relationship between bird populations and thermal refugia consistent with use of underground burrows. Taken together, our results are consistent with three plausible scenarios: 1) increased pressures of climate change on bird populations have selected for individuals that utilize burrows as thermal refugia; 2) bird use of burrows as thermal refugia has been a present behavior but is not necessarily common, resulting in larger levels of heat exposure; or 3) that there are currently unidentified, or unappreciated above-ground thermal refugia or thermoregulatory behavior with similar properties to those found in burrows. Such scenarios must be regarded as speculative in the absence of empirical evidence from predictive studies (Gould 1978). However, these scenarios can serve as valuable foundations for conducting testable and systematic studies, offering insights for future research programs that will inform ecosystem management and policies (Currie 2023).

It is true that results from our model are inconsistent with the supposition that birds can always rely on underground burrows for thermal regulation. Indeed, we calculated that perfect access to deeper underground refugia would have resulted in stability in bird community composition from the 20th to the end of the 21st century, even in the face of climate change. Of course, Mojave birds are declining, which falsifies this scenario. However, scenarios in which birds need to search for underground refugia and often fail to locate them, or where avian burrow use is an existing but relatively uncommon behavior, are consistent with our model output. Results from our model also imply that the decline of Mojave Desert tortoise may have had a negative impact on birds by limiting the best-available thermal refugia. Tortoises once existed in densities ranging from 40 and 150 individuals per square kilometer (Averill-Murray et al. 2012), but currently densities seldom rise above 10 individuals per square kilometer (Allison and McLuckie 2018) (Allison and McLuckie 2018) (Allison and McLuckie 2018). Therefore, the most likely scenario is one in which burrow use by birds is not a common behavior, along with a concurrent decrease in the availability of tortoise burrows over time. This, however, should be considered a new hypothesis that requires further testing.

Interestingly, analyses of data gathered from both eBird and our own field surveys independently highlight the presence of underground refugia on the landscape as the most important predictor of both bird richness and abundance. Even after controlling for the effect of habitat, the association of underground refugia on bird richness and abundance remains evident, particularly in areas with low percent shrub cover. Our field surveys further indicate that birds exhibit a stronger response to the shallower burrows constructed by small mammals and reptiles compared to tortoise burrows, although the presence of tortoise burrows still has a discernible effect on bird populations. The relative importance of tortoise in comparison to small mammal burrows is less clear in the analysis of eBird data, possibly due to our use of a coarse environmental proxy variable.

Our best-fit models of species richness and abundance from eBird data further suggest that the effect of vegetation cover is mitigated by the presence of either tortoise or small mammal/reptile burrows. We predicted that percent vegetation cover is critically important for birds in areas where the presence of burrows is low; however, in areas with burrows, the effect of cover is statistically negligible. Such a pattern is illustrative of an environment where the increased presence of burrows as thermal refugia on the landscape removes vegetative shade from acting as a limiting variable for bird richness and abundance. Even if the results from our model are incorrect and underground thermal refugia use was not a historic behavior, results from our field survey are consistent with the scenario that birds are currently adopting this behavior. Environmental pressures such as climate change are known to result in dramatic alterations to animal behavior as they search for ways to reduce negative impacts (Beever et al. 2017, Gunn et al. 2022). Therefore, it is plausible that birds in the Mojave Desert have recently adopted a new response to rising heat by relying on secondary use of underground thermal refugia.

Although we accounted for NDVI and vegetative shade, it is important to acknowledge that the observed patterns in our data may be influenced by unknown behaviors and mechanisms other than secondary utilization of burrows. Water, for example, is fundamental for the survival of desert animals (Gurera and Bhushan 2020), Rundel and Gibson 1996a). Therefore, we would expect areas where birds have greater access to water to have higher concentrations of all animals, which could result in a correlation between burrows and bird populations that we did not account for. Such a variable would likely not be in the form of groundwater or precipitation, as both variables positively impact desert vegetation "greenness" (Rundel and Gibson 1996b) and would be controlled for by our high-resolution NDVI coefficient. The manipulative experiments we recommend as next steps are designed to address such uncertainties: if an experiment disproves the notion that birds use burrows as thermal refugia, it will indicate the presence of another confounding variable associated with both Mojave Desert bird distributions and burrows, or that there are fundamental problems with the physiological models of NicheMapR (Kearney and Porter 2017, Kearney et al. 2021), or the parameter values we used in our models (Eichenwald and Reed in review).

If Mojave Desert birds have indeed started relying on burrows as thermal refugia, it may not reverse their observed population declines. There is a cost to behavioral thermoregulation, as behaviors critical for survival, growth, and reproduction can be either partially or completely incompatible with the need to avoid or dissipate heat (Cunningham et al. 2021). For example, a bird forced underground will have reduced foraging time and potentially limited energy intake (Cunningham et al. 2015, Pattinson and Smit 2017), which can have a negative effect on offspring production (Cunningham et al. 2021). Retreating into thermal refugia also could reduce the opportunity for birds for territorial displays (Santee and Bakken 1987). Each of these costs could have a continuing negative effect on bird populations, which will likely intensify as heat exposure from climate change increases the period of forced microclimate use. Without additional field data, it is not possible to predict accurately the difference in expected population declines between the two scenarios: 1) where there is no underground burrow use, and 2) where underground thermal refugia use occurs with associated behavioral costs. However, it is plausible that the effects of avian declines will have a limited impact on the rest of the ecosystem in the form of extinction cascades compared to the loss of other vertebrate taxa from the Mojave Desert food web (Eichenwald et al. In Review).

Systematic experiments to test between these two scenarios will be crucial in shaping appropriate and tailored conservation strategies for the birds in the Mojave Desert. If heat exposure is the primary concern, conservation efforts should focus on mitigating the impacts of climate change, such as by implementing habitat restoration measures that provide shade and cooling spaces (Mawdsley et al. 2009). However, if our results are indeed representative of increased avian reliance on underground refugia, we may instead see reduced foraging time as a key challenge. In that case, conservation strategies that focus on long-term bird conservation should prioritize measures to enhance food availability and accessibility for birds within their restricted habitats, such as by implementing targeted strategies like supplementary feeding programs or managing species that compete for food resources (Mawdsley et al. 2009).

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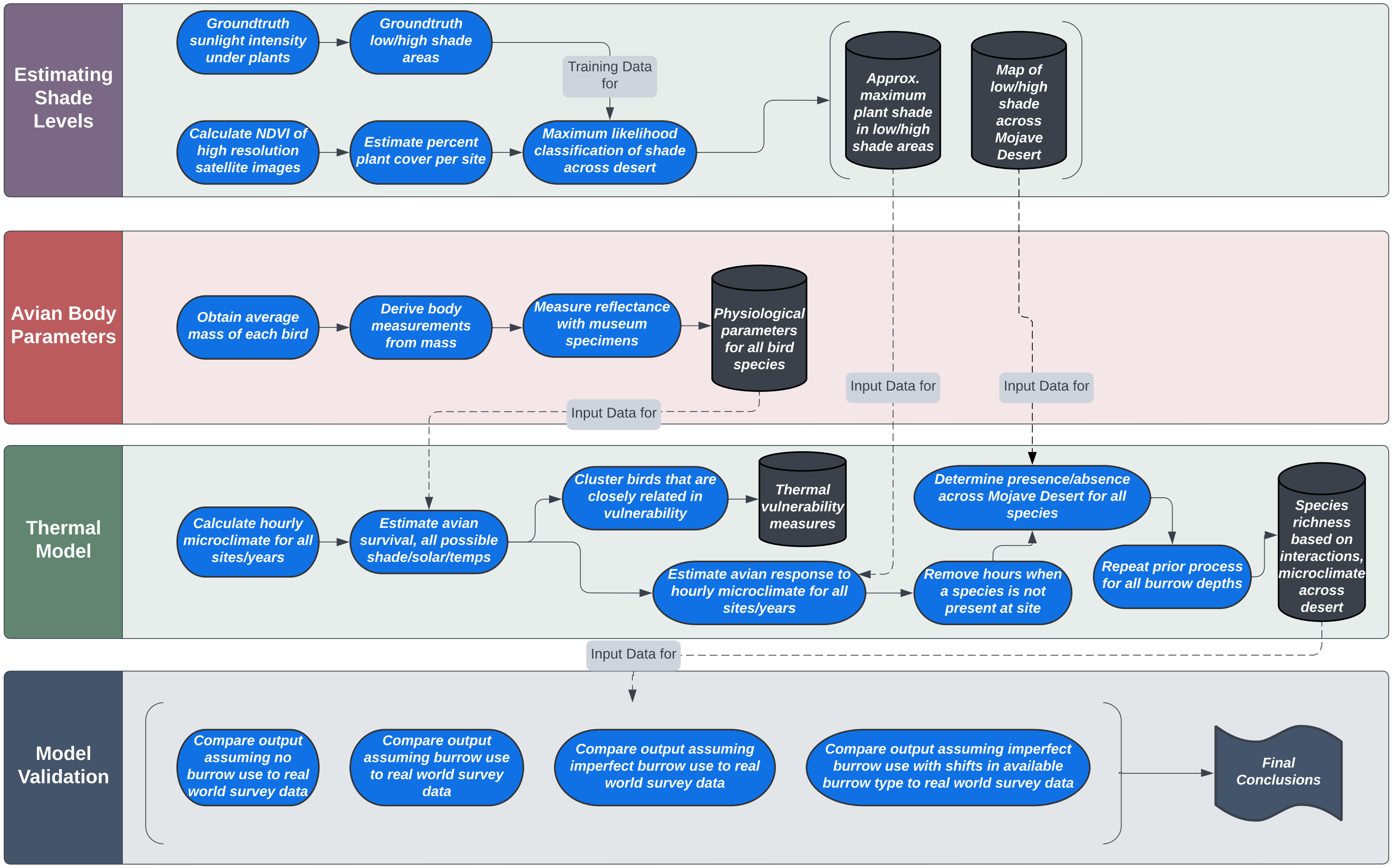

Figure 5-1 Flowchart of the order of steps used in my methods. The workflow can be broadly divided into 4 categories: estimation of real-world shade levels, collection of avian body parameters, implementation of multiple mechanistic thermal models, and validation of mode output. Generally, data collected in categories at the top of the flow chart (e.g., estimating shade levels, avian body parameters) feed into steps in the categories at the bottom.

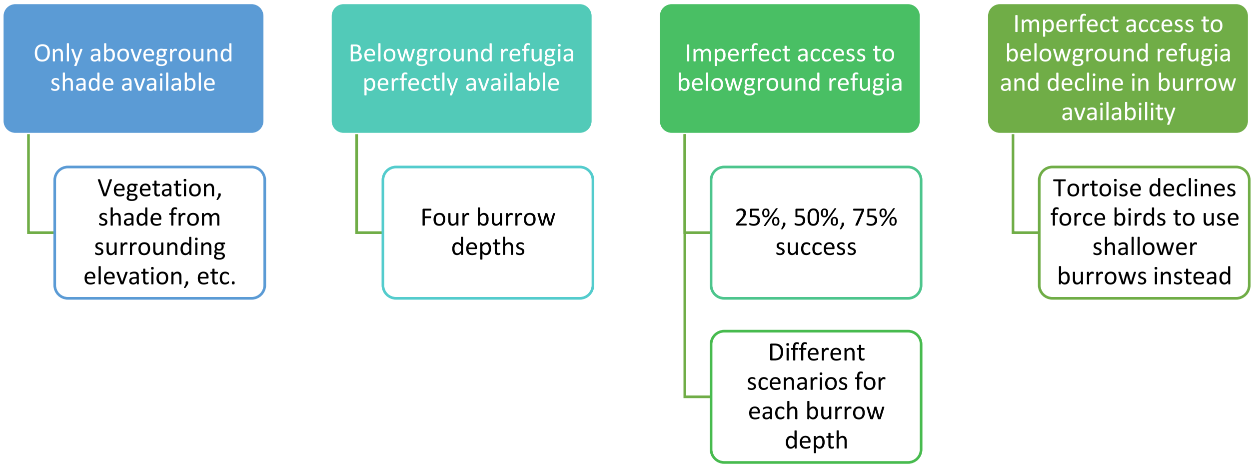

Figure 5-2 Visual representation of the four scenarios and 18 sub-scenarios used in the mechanistic thermal model. The four rectangles at the top are the four main scenarios. From left to right, scenarios were only shade aboveground, birds have perfect access to burrows as thermal refugia, birds use belowground thermal refugia more rarely, and rarer belowground refugia use coupled with a decline in tortoise burrows. Sub-scenarios are listed beneath each scenario. Only one version of the aboveground shade scenario was calculated. However, all belowground scenarios were calculated at four different burrow depths. Furthermore, imperfect burrow access was also calculated for three different levels of “success” at utilizing burrows, for each of the four different burrow depths (total of 12 models). Finally, only one sub-scenario was calculated for the tortoise decline and imperfect use scenario

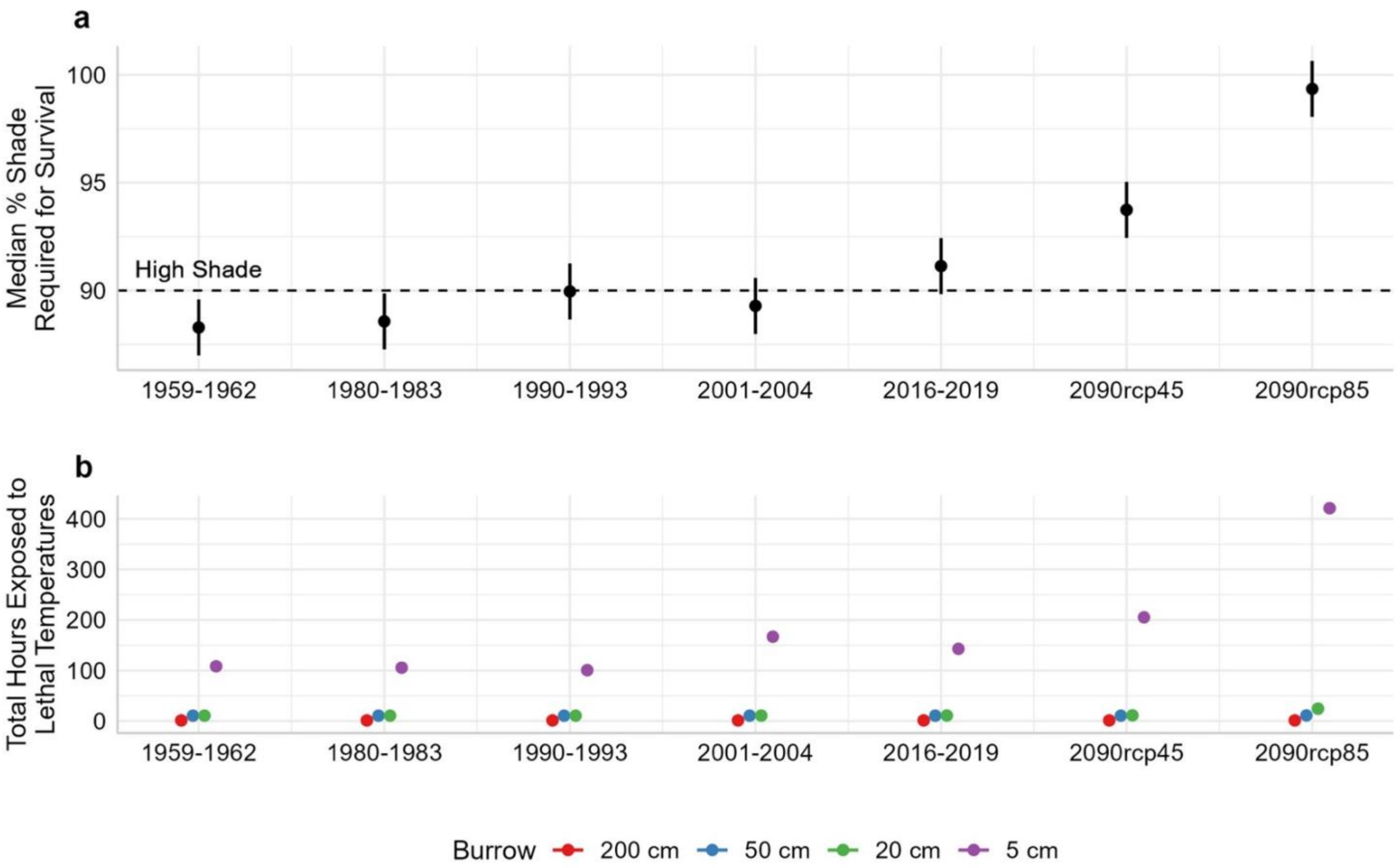

Figure 5-3 Graphs of the thermal vulnerability of aboveground bird species (a) and the total hours a bird is exposed to lethal temperatures even if underground refugia are available (b), where all other variables are controlled (i.e., marginal effects). Confidence intervals in (a) are 83.4%, which provides an approximate $\alpha=0.05$ test (Payton et al. 2003).

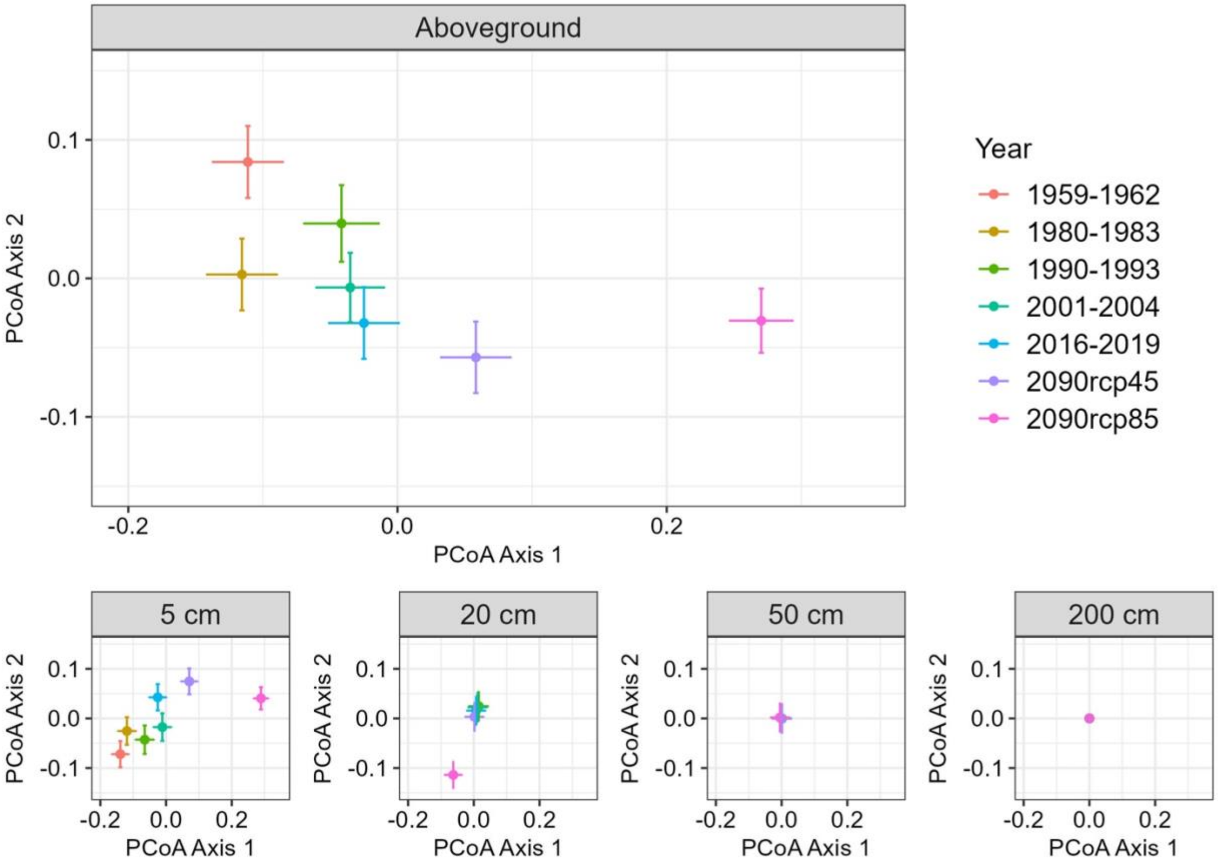

Figure 5-4 Principal coordinates analysis of the differences in bird community composition (i.e., species richness, using the Jaccard Similarity Index) assuming that birds are only found only aboveground or at the varying burrow depths. Years closer together are more similar in composition, while years farther apart are less alike in composition. Bars represent 95% confidence intervals.

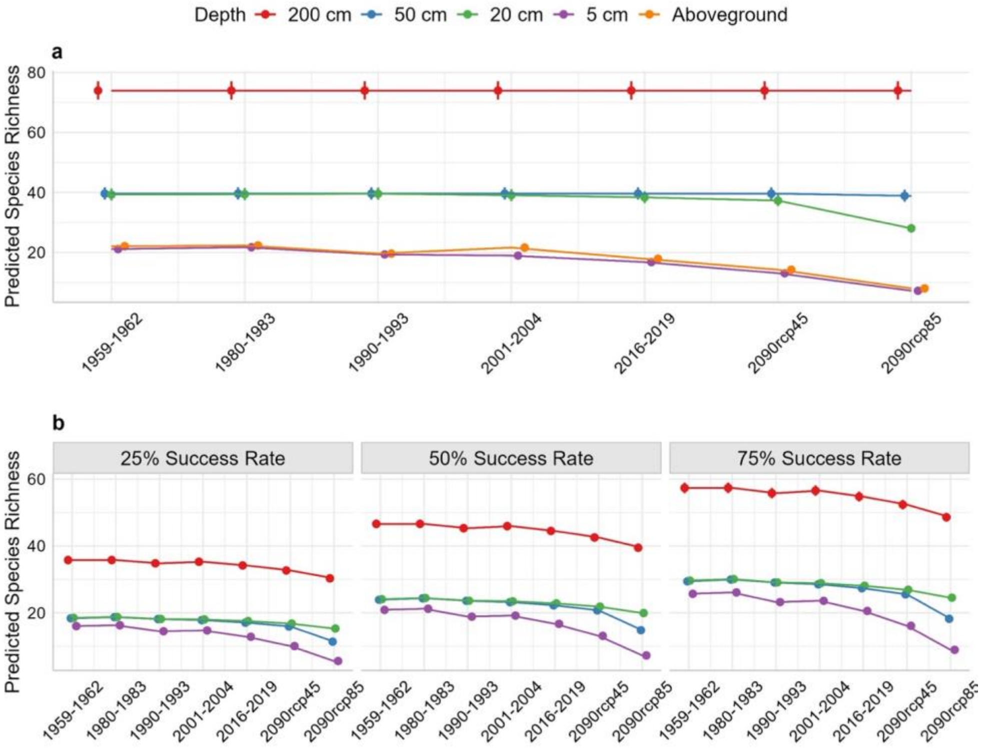

Figure 5-5 Predictions of species richness over time based on available burrow depth, where species have a 100% success rate of finding and using burrows of various depths (a) or where species have a given success rate (b). Species capable of fitting into mammal burrows were assumed to have perfect access to each depth when needed for survival, while species incapable of fitting into mammal burrows were assumed to only have access to shade. Aboveground predictions assume that no species was able to find shelter in a burrow.

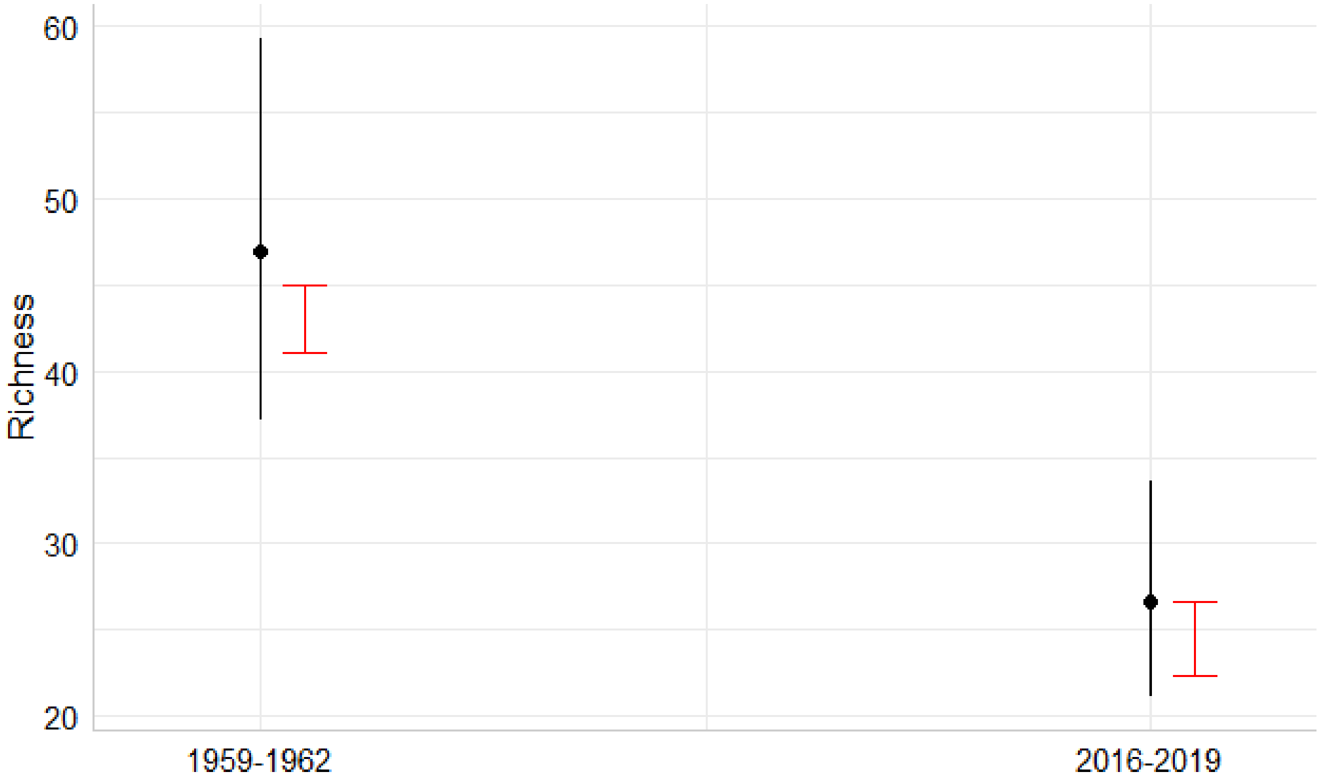

Figure 5-6 Predictions of species richness over time in a hypothetical scenario where desert tortoise burrows decline in availability and birds are instead forced into mammal burrows of varied depths. Black points and line (95% confidence interval) represent output from our model. Red error bars represent the confidence intervals of observed species richness reported by Iknayan and Beissinger (2018); estimated from their Figure 1B.

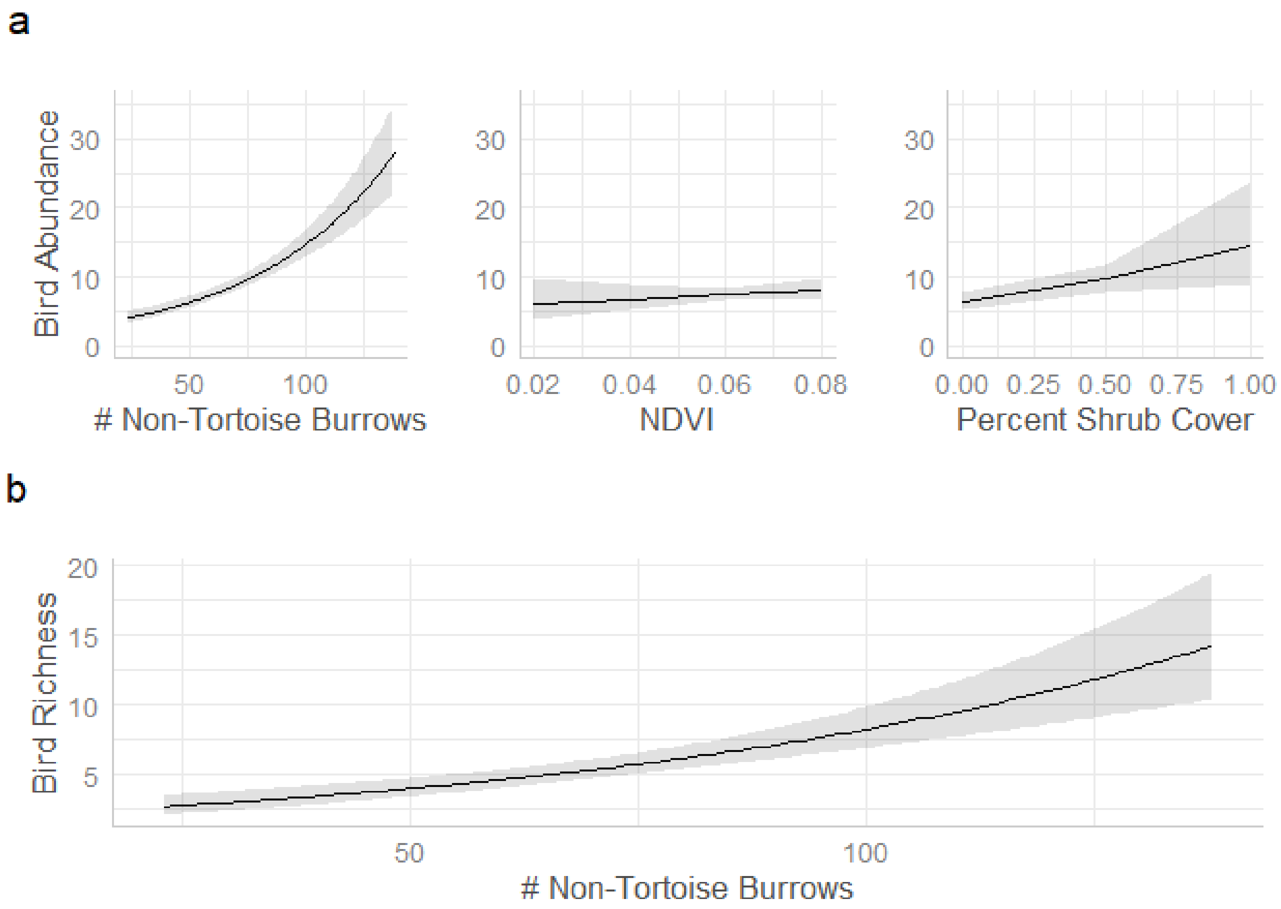

Figure 5-7 Marginal effect plots representing bird abundance (a) and richness (b) to predictor variables in the best selected models of our own field surveys. Bird abundance was highly dependent on the number of non-tortoise burrows, with comparatively minor effects of NDVI and percent shrub cover (a). Models with interacting effects of NDVI or shrub cover on burrows were less fit. The best fit model for bird richness had number of non-tortoise burrows as the only predictor (b), and burrow numbers had a strong positive effect on richness.

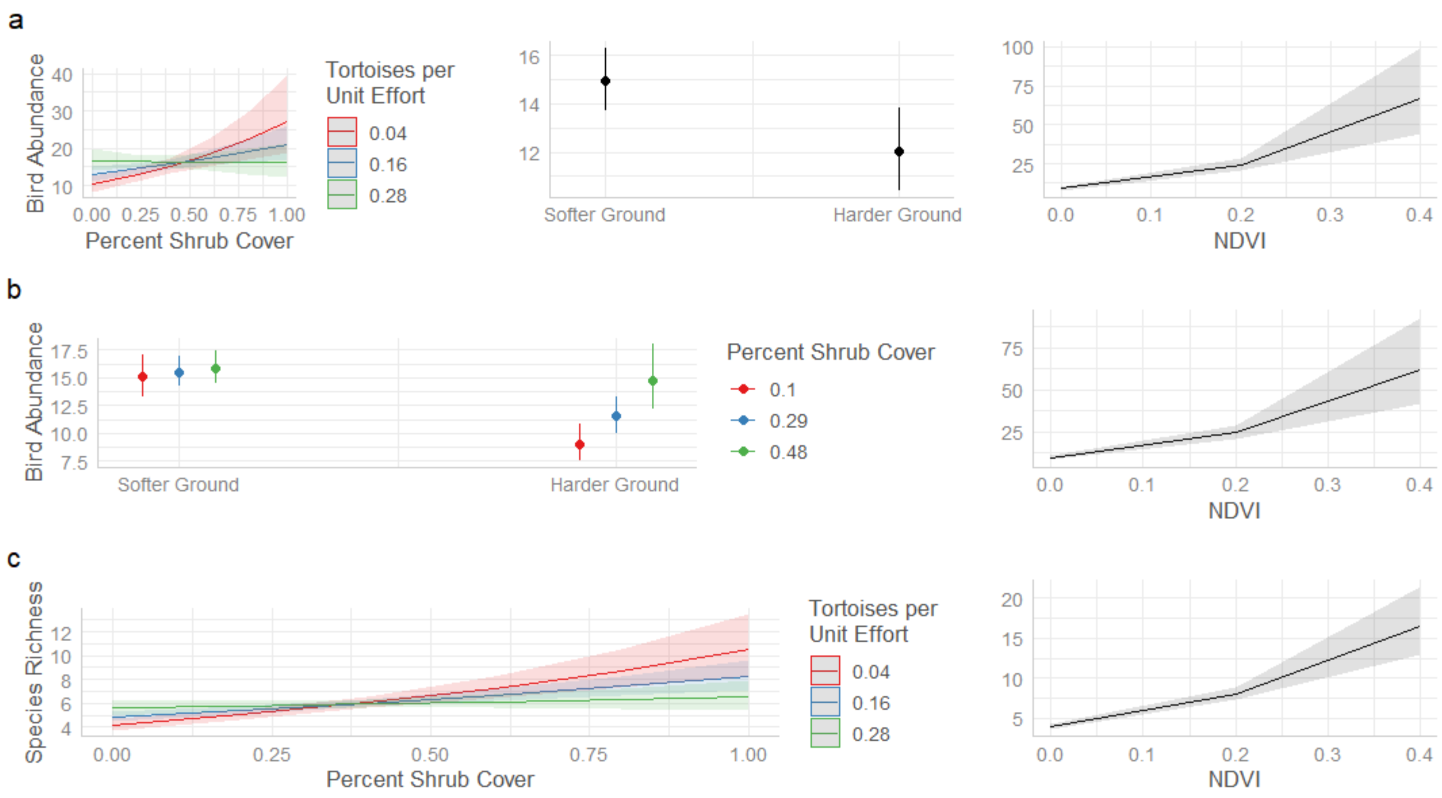

Figure 5-8 Marginal effect plots representing bird abundance to predictor variables in the two best fitting models (a,b) and representing bird richness to predictor variables in the best fitting model (c) from eBird surveys. In the best fitting model (a), abundance was predicted by an interaction between tortoises per unit effort and percent shrub cover, in addition to desert pavement presence (harder vs softer ground) and NDVI. Softer ground and higher NDVI resulted in increases to bird abundance. In addition, percent shrub cover was only important for bird abundance when tortoises per unit effort was low. In the second-best fitting model (b)

abundance was predicted by an interaction between desert pavement presence and percent shrub cover in addition to NDVI. Percent shrub cover was only important for abundance in areas where the ground was too hard for small mammals and reptiles to dig burrows. Richness (c)was predicted by an interaction between tortoises per unit effort and percent shrub cover in addition to NDVI. Higher NDVI resulted in increases to bird abundance. In addition, percent shrub cover was only important for bird abundance when tortoises per unit effort was low.

Chapter 6

Potential extinction cascades in a desert ecosystem: linking food web interactions to community viability (Adam J. Eichenwald, Nina H. Fefferman, J. Michael Reed). In Review at Ecology and Evolution

Abstract

Desert communities are threatened with species loss due to climate change, and their resistance to such losses is unknown. We constructed a food web of the Mojave Desert terrestrial community (300 nodes, 4080 edges) to examine the potential cascading effects of bird extinctions on the network, compared to losses of mammals and lizards. We focused on birds because they are already disappearing from the Mojave, and their relative thermal vulnerabilities are known. We quantified bottom-up secondary extinctions and evaluated the relative resistance of the community to losses of each vertebrate group. The impact of both random and vulnerability-based bird species loss was relatively low compared to the consequences of mammal (causing the greatest number of cascading losses) or reptile loss, and birds were relatively less likely to be in trophic positions that could drive top-down effects in apparent competition and tri-tropic cascade motifs. An avian extinction cascade with year-long resident birds caused more secondary extinctions than the cascade involving all bird species, for both randomized and thermal vulnerability-based ordered extinctions. Notably, we also found that relatively high interconnectivity among avian species has formed a subweb, enhancing network resistance to bird losses.

Introduction

Investigating the interactions between species can be a key aspect of safeguarding biodiversity and promoting effective conservation efforts (Eichenwald and Reed 2021, Sabo 2008, Soulé, Estes, Miller and Honnold 2005). The functional loss of even a single species can have far-reaching and sometimes unforeseen consequences for entire ecosystems (Paine 1974, Terborgh, Lopez, Nunez, Rao, Shahabuddin, Orihuela, Riveros, Ascanio, Adler, Lambert and Balbas 2001), in some cases resulting in extinction cascades via secondary extinctions (Brodie, Aslan, Rogers, Redford, Maron, Bronsteire and Groves 2014, Säterberg, Sellman and Ebenman 2013). For example, the loss of sea otters (*Enhydra lutris*) famously resulted in the catastrophic collapse of biodiverse kelp forests into urchin barrens (Estes and Palmisano 1974). The effects of species loss may pose threats to human health (Markandya, Taylor, Longo, Murty, Murty and Dhavala 2008), or to ecosystem services (Pike and Mitchell 2013). As such, conservation efforts often must go beyond focusing on individual species and instead incorporate an understanding of their interactions within a community (Soulé, Estes, Miller and Honnold 2005, White, Zipkin, Manley and Schlesinger 2013, Zipkin, Andrew Royle, Dawson and Bates 2010). Doing so can enable us to better predict the effects of environmental perturbations (e.g., Jönsson and Thor 2012), mitigate the spread of introduced, invasive species (Galiana, Lurgi, Montoya and López 2014), promote ecosystem services (Buechley and Şekercioğlu 2016), and rehabilitate degraded landscapes (Soulé, Estes, Berger and Del Rio 2003). Neglecting to consider the sometimes intricate and indirect relationships between species can lead to management approaches that are ineffective or even detrimental to an ecosystem (Bowen and Lidgard 2013, Johst, Drechsler, Thomas and Settele 2006, Letnic and Koch 2010, McDonald-Madden, Sabbadin, Game, Baxter, Chades and Possingham 2016, Muggleton and Benham 1975).

One promising approach to addressing these challenges is through community viability analysis (CVA) (Ebenman and Jonsson 2005, Ebenman, Law and Borrvall 2004, Eichenwald and Reed 2021). CVA encompasses a variety of approaches to quantifying community structure, composition, and function in response to perturbations or management actions. For instance, by representing a community as a network of species interactions, researchers can identify species that play a significant role in community stability or resilience (Eichenwald and Reed 2021, Jönsson and Thor 2012), or identify effective management interventions (McDonald-Madden, Sabbadin, Game, Baxter, Chades and Possingham 2016).

Here we conduct a resistance-based community viability analysis (Eichenwald and Reed 2021) of the terrestrial community of the Mojave Desert, a well-studied ecosystem in the southwest United States (e.g., Iknayan and Beissinger 2018, Kissel, Wallace, Anderson, Dickson, Van Neste, Landau, Averill-Murray, Allison and Fesnock 2023, Rundel and Gibson 1996). We did this by first constructing a food web and then examining the potential cascading loss of species following initial species losses. Specifically, we assess the impact of bird loss compared to losses of mammals and lizards, which have been found to be more resistant to the effects of climate change (Riddell, Iknayan, Hargrove, Tremor, Patton, Ramirez, Wolf and Beissinger 2021). The Mojave Desert bird community has suffered notable declines over the last century that have been attributed to climate change (Iknayan and Beissinger 2018, Riddell et al. 2019, Riddell et al. 2021). In contrast, mammal species in the Mojave have remained relatively stable despite increasing heat, presumably because they dig burrows, which function as thermal refugia (Riddell et al. 2021). Despite a century of research in this ecosystem, there has been limited investigation into the extent to which the loss of different species may affect the persistence of others.

To investigate the vulnerability of the Mojave Desert community to bird loss compared to losses of other vertebrates, we constructed a food web for the terrestrial community and conducted network analyses. Network analyses can be used to map and model interspecific relationships (Borrett, Moody and Edelmann 2014) such as food webs, where links between species indicate one consuming the other (de Visser, Freymann and Olff 2011, McDonald-Madden, Sabbadin, Game, Baxter, Chades and Possingham 2016). We quantified bottom-up secondary extinctions to capture potential cascading effects of the increasing frequency of primary extinctions of birds, mammals, and reptiles on other species in the food web (Dunne and Williams 2009). Because birds are declining in the Mojave, and an analysis of relative vulnerability of birds in that region to increased temperatures is available (Eichenwald and Reed In review), we analyzed the effects of bird loss in order of thermal vulnerability compared to random loss of species. These analyses provided insights into the relative importance of each vertebrate group in maintaining community structure and stability in the face of species loss. Additionally, we tested for the prevalence of each vertebrate group within patterns in the food web that are known for causing top-down secondary extinctions (Baiser, Elhesha and Kahveci 2016). Through these analyses, we assessed one aspect of the relative importance of each vertebrate group within specific subgraphs, as well as changes in connectivity patterns, providing further understanding of their potential impacts on the community.

Methods

The Mojave Desert spans broad latitudinal (34.8° to 36.2°), longitudinal (-117.2° to -115.8°), and elevational ranges (-82m to 3367m), and tends to share much of its biota with the neighboring Sonoran Desert to the south and the Great Basin to the north (Rundel and Gibson 1996). Daytime temperatures are generally warm, and the desert holds the record for the highest measured air temperature on the planet (El Fadli, Cerveny, Burt, Eden, Parker, Brunet, Peterson, Mordacchini, Pelino and Bessemoulin 2013). However, the Mojave may experience cool Arctic air masses during the winter rainy season and hence receives some snow (Rundel and Gibson

1996). The desert has experienced a rise in mean annual air temperature by approximately 2°C since the early 20th century (Bai, Scott, Chen, Minnich and Chang 2011). We developed our particular CVA of the Mojave Desert biotic community following the overarching guidelines proposed by Eichenwald and Reed (2021): 1) delineate the focal community, 2) decide on viability measures and questions, 3) enact calculations, and 4) address uncertainty.

Delineating the Focal Community

Food webs have been generated for some communities in the Mojave Desert, such as soil nematodes (Ferris 2010) and aquatic systems (Wilson and Blinn 2007). However, we needed to create a food web containing the terrestrial vertebrate community of the Mojave Desert for our analyses. The first step was to assemble the most complete list of taxa available for the study region. Historically, such a task was performed by consulting with local experts (Martinez 1991), an approach that could result in incomplete webs with missing species (Polis 1991). More recently, online databases collated from large-scale citizen science observations can allow construction of more thorough taxa lists, although such catalogs still tend to be deficient when it comes to insect and plant species. We constructed our taxa list by downloading observation data from the Global Biodiversity Information Facility (GBIF, gbif.org, April 2023) within the geographical limits of the Mojave Desert. We limited data to observations only; although GBIF includes museum specimens in its database, the latitude and longitude associated with these records sometimes are of the museum that currently holds the specimen instead of where the specimen was collected. We then culled the taxa list further by examining the resulting species list one at a time and removing species if they did not actually appear in the Mojave Desert, based on species-specific distributional accounts. There is a variety of reasons for these species being incorrectly included in the Mojave Desert in the GBIF database, such as mapping or identification errors (Roberts, Elphick and Reed 2010, Zizka, Carvalho, Calvente, Baez-Lizarazo, Cabral, Coelho, Colli-Silva, Fantinati, Fernandes and Ferreira-Araújo 2020). For example, the white-tailed antelope ground squirrel (*Ammospermophilus leucurus*) looks very similar to the San Joaquin antelope squirrel (*A. nelsoni*); however, the latter has a restricted range that does not include the Mojave Desert, while the former is ubiquitous in the Mojave. Consequently, when the San Joaquin antelope squirrel appeared in our first-pass taxa list, we culled it on the assumption that it was a misidentification or misapplied location. We did not have to rely on this method to obtain a list of bird species, as we had already created this list in previous papers (Eichenwald and Reed 2023, Eichenwald and Reed In review) (although we did remove the hairy woodpecker *Leuconotopicus villosus*, although its range covers some of the Mojave, it is so scarce within that range that we could not justify including it in the web). We classified birds into two categories for the extinction cascade (see below): non-residents and residents. We classify resident birds are present year-round in the Mojave Desert, while we classify non-resident birds are present only during the pre-breeding (migration) or breeding season, as classified by the Cornell Lab of Ornithology's ebirdst models (Strimas-Mackey, Ligocki, Auer and Fink 2021). We focused on birds that are present during the summer, as heat exposure from climate change is thought to be the major driver of Mojave avian species loss (Riddell, Iknayan, Hargrove, Tremor, Patton, Ramirez, Wolf and Beissinger 2021). Therefore, birds that are present only during the winter or in the post-breeding season are not included in our web.

Assigning predation links between species is more time-consuming. In recent years, some researchers have attempted to derive feeding links from patterns of co-occurrence and trophic levels; however, co-occurring species do not necessarily interact with one another in expected ways (Blanchet, Cazelles and Gravel 2020). Alternative methods of inferring feeding links based on predator and prey body mass and trophic level have varying degrees of success but can still result in inaccuracies (Rohr, Naisbit, Mazza and Bersier 2017). To minimize errors of inclusion in food-web links, we chose to include only feeding links that have been confirmed (Martinez 1991) instead of inferring feeding links. For each vertebrate species, we searched the literature, including compendium volumes such as Birds of the World (Billerman, Keeney, Rodewald, Schulenberg and (Editors) 2022) for evidence (e.g., observations of feeding, investigation of stomach contents, eDNA) of its predators and prey. Each species' common and scientific names were used as keywords in Google Scholar, along with the keywords "stomach contents," "food," diet," "predation," "consumption," or "prey." If a species' scientific name was changed in the last few decades, we performed separate searches with older names as keywords as well. We also searched for science-based encyclopedias or compendia on specific taxa (e.g., "reptiles") in the Americas. Finally, we consulted the Global Biotic Interactions database (Poelen, Simons and Mungall 2014) and the Avian Diet Database (Hurlbert, Olsen, Sawyer and Winner 2021), which are archives of consumption links. Observations from these interaction-specific data sources were supplemental; we did not assume that all feeding interactions present in the Mojave Desert were available in such sources.

We did not include generic links, such as if a species is said to consume "mammals," we did not include all mammals in that species' diet. However, if a predator is confirmed to eat animals from a particular genus, we did include links to all species within that genus. Some feeding links were observed but not included in the final network because they were likely atypical events. For instance, a black-chinned hummingbird (*Archilochus alexandri*) was once observed hovering in front of the nose of a captive mountain lion (*Puma concolor*) and the cat consumed the bird (Baltosser and Russell 2020). We considered this unlikely to be relevant in a natural food web. We also scrutinized links attributed via DNA analyses of gut contents or feces. When a predator eats another animal, it is possible for the DNA of anything the prey consumed to also appear in the predator's stomach (Sheppard, Bell, Sunderland, Fenlon, Skervin and Symondson 2005). Alternatively, some herbivores scavenge meat from carcasses or engage in occasional predation (Pietz and Granfors 2000), which can result in particularly strange DNA-verified feeding links. Therefore, if a feeding link appeared unlikely and was verified by DNA, we did not include it in the final web. For example, a known omnivore such as the coyote (*Canis latrans*) consuming plant matter is strange but not unheard of, and so such links were included in the web. Chukar (*Alectoris chukar*), on the other hand, subsist on leaves and seeds and feed their young insects; therefore, predation links suggesting chukar hunt rodents (e.g., Hurlbert, Olsen, Sawyer and Winner 2021) were not included. Although we were able to find data on predators and prey for each vertebrate species, similarly detailed information for insects and plants was less available. We found that data on feeding interactions involving these groups was generally provided at higher taxonomic levels (e.g., order, class), making it impossible to include them in a food web at the species level. Insects and arachnids, therefore, were aggregated at taxonomic orders; this type of aggregation is common in published food webs (Martinez 1991). Plants were aggregated at taxonomic orders for all calculations that did not require interaction strength (see below for explanation on interaction strength) but were aggregated at the taxonomic kingdom level for calculations involving biomass (see below).

Thus, we generated a food web where directed links represent a known consumptive interaction between predator and prey. However, not all interaction links are equivalent; in fact, differences in interaction strength across a web are common based on the percent of a species' diet coming from each prey type (Berlow, Neutel, Cohen, de Ruiter, Ebenman, Emmerson, Fox, Jansen, Jones, Kokkoris, Logofet, McKane, Montoya and Petchey 2004). Even poorly estimated interaction strengths provide greater average certainty in modeled predictions based on the web than does an approach that uses only the presence or absence of each interaction (Novak, Wootton, Doak, Emmerson, Estes and Tinker 2011). Therefore, we estimated interaction strength for all links using the fluxweb package in R, which allows for the calculation of energy fluxes in food webs based on the conceptual framework of the "food web energetics" approach (Gauzens, Barnes, Giling, Hines, Jochum, Lefcheck, Rosenbaum, Wang and Brose 2019). To calculate energy fluxes between predator and prey, the package's functions require three variables: 1) species biomasses in mass per unit area, 2) metabolic rates, and 3) feeding efficiencies. Metabolic rates and feeding efficiencies are calculatable from body mass and species type (vertebrate endotherm, vertebrate ectotherm, invertebrate, plant) of the species in question (plant metabolic rates are considered non-existent) using equations in the fluxweb package (Gauzens, Barnes, Giling, Hines, Jochum, Lefcheck, Rosenbaum, Wang and Brose 2019). Estimations of species biomass (g/km^2) are more difficult, requiring estimations of both individual body mass and number per unit area. Calculating the average mass of each species is straightforward, as the masses of museum specimens are often measured before they are taxidermied. We obtained average vertebrate masses from rvertnet (Chamberlain 2021). It is also possible to obtain an estimation of species densities (number of individuals per km^2) allometrically, as Damuth (1981) reported a size-density relationship (SDR) following a power law with a scaling exponent close to –0.75 (Isaac, Storch and Carbone 2013). This relationship is less accurate at the local scale (White, Ernest, Kerkhoff and Enquist 2007), but is still a suitable way of approximating species density other than the time-consuming method of surveying the abundance of each species individually. We allometrically calculated the densities of all vertebrates and multiplied by their masses to obtain species-by-species biomass.

Calculating insect and plant biomasses are more difficult due to the aggregation of their nodes, wide variation in masses (for invertebrates), lack of research on allometric relationships, and unclear total numbers of species. Fortunately, there has been a prior survey of arthropod biomasses in some parts of the Mojave Desert, where the results were aggregated by taxonomic order (Rundel and Gibson 1996). We collected biomass information from this source; however, not all arthropod taxa in our food web had corresponding biomasses in the surveys. Therefore, we used the Rphylopars package in R (Goolsby, Bruggeman and Ané 2017) to infer missing biomass data. Rphylopars uses statistical models to predict what a missing trait of a species might be based on information about related species, analyzing the evolutionary relationships between species and the traits they possess. The package considers the phylogenetic relationships between species, which helps to account for the fact that closely related species are likely to have relatively similar traits. We constructed a phylogenetic tree using taxize (Chamberlain and Szöcs 2013) to represent the evolutionary relationships among species of interest, then used this tree as input data for the Rphylopars package. We employed a Brownian motion evolutionary model to estimate missing trait values for species lacking data, which is the default and most-used method (Goolsby, Bruggeman and Ané 2017). Our method of calculating network extinctions (next section) was insensitive to differences in insect biomass within their confidence intervals (see next section). Therefore, we assumed that each arthropod node had the median biomasses calculated by Rphylopars.

We were unable to find reports that provided above-ground plant biomass in the Mojave Desert, even at a high taxonomic level. However, Rundel and Gibson (1996) provided an equation relating average total aboveground biomass in g/m^2 to the amount of precipitation from September through March in the Mojave Desert:

$$log(Aboveground\ Net\ Production) = 1.976\ log(SepttoMarchPrecip - 26.2) - 2.746$$

We used this equation, including total September-March precipitation across the years of their study (1964-1968, 1971-1976), to estimate above-ground plant biomass.

Viability Measures, Calculations

To investigate the potential for secondary extinctions of vertebrates (where the loss of one species leads to the losses of others), we utilized the NetworkExtinctions package in R (Ávila-Thieme, Kusch, Corcoran, Castillo, Valdovinos, Navarrete and Marquet), which is based on methods originally proposed by Dunne and Williams (2009). The method involves removal of a primary species from the network, followed by a review of the resources remaining for the remaining species. If any of the remaining species lose all their resource species, they are removed from the web, resulting in a secondary extinction. However, species can be forced into extinction after losing even a few of their resources, depending on how reliant the consumer was on said resource (Berg, Pimenov, Palmer, Emmerson and Jonsson 2015). To incorporate the effect of interaction strength in the extinction cascade, we ran the simulation four times for each removal scenario, each with a different threshold value of 0.6, 0.7, 0.8, and 0.9, respectively. This means that a species needed to have a remaining interaction strength between it and all its prey greater than or equal to the threshold value to avoid secondary extinction. For example, a threshold value of 1.0 would cause a predator to go extinct if it lost a single prey species (plants are included as prey), while a threshold of 0.0 would result in a predator never going extinct even after losing all its prey.

To assess the relative importance of birds to the Mojave Desert food web in comparison to other vertebrates, we first conducted three removal experiments based on the predicted order in which Mojave avian species should go extinct due to climate change-induced heat exposure, derived from a mechanistic model (Eichenwald and Reed In review). The first removal experiment included all bird species. In addition, because we suspected that losing year-round resident bird species would have a different effect on the system than would losing birds that lived in the Mojave only part of the year, we conducted two additional removal experiments: removing only non-resident bird species and removing only resident bird species, both done in the order of estimated thermal vulnerability.

In contrast, the predicted extinction orders for Mojave mammals and lizards based on increasing temperatures have not been evaluated. Thus, we randomly sorted the order of mammal removal from the food web, computed the resulting secondary extinctions, and repeated this process 100 times to account for variation in the order of removal. We tested the effect of reptile removal from the community using the same randomization procedure. As the bird extinction order listed above is not validated with field data, we also repeated the randomization procedure for the three bird cascade scenarios (all birds, resident birds removed, non-resident birds removed). We did not include plants and invertebrates in a primary removal cascade due to their aggregation, which would lead to an artificially high change in the number of links and render any comparison incomplete or invalid. We also evaluated the degree to which predicted extinction cascades were sensitive to inferred arthropod biomasses from Rphylopars. For each arthropod with inferred biomasses, we randomly selected biomasses from within the 95%

confidence interval calculated by Rphylopars to parameterize the interaction strengths for the food web and then ran the predetermined climate change-induced primary extinction cascade with all birds. We ran this simulation 100 times with the same bird extinction order, but different arthropod biomass values drawn randomly from their distribution. The resulting secondary extinction cascade for each run was always the same. This was unsurprising, as the extinction cascade method is based on bottom-up effects, and arthropods are on the lower end of the food chain and were not included in primary removal cascades. As randomly choosing biomasses from within the confidence interval did not influence our cascades of interest, we used the median inferred biomass for arthropods as listed above.

To gain a deeper understanding of potential bottom-up secondary extinction cascades within our food web, we examined homophily between nodes within and between different ecological groups (mammals, plants, insects, birds, and reptiles). Homophily helps us see whether species with similar characteristics tend to connect and interact more often than those that are different (e.g., are mammals more likely to interact just with other mammals, or do they link to other animal types as well?). We employed Coleman's Homophily Index (Coleman 1958), which calculates homophily scores within each defined group. The index gives us a number between -1 and 1: a score of 0 means there are equal connections between different groups, 1 means all connections are within the same group, and -1 means all connections are between different groups. As a reminder, our secondary extinction cascades operated from prey to predator, whereas the homophily index traditionally measures connections from predator to prey. Therefore, a homophily index would provide information on a top-down cascade. To obtain information on bottom-up effects, we inverted the links in the graph before calculating the homophily index.

While the NetworkExtinctions approach is valuable for analyzing food webs, it has limitations in accurately predicting the impact of consumer loss on the resources that these consumers utilized. This is because it can capture only extinctions caused by bottom-up effects, such as the primary loss of all or a fraction of a consumer's resources. It does not consider the potential for top-down effects, such as the impact of predators (Berg, Pimenov, Palmer, Emmerson and Jonsson 2015, Terborgh, Lopez, Nunez, Rao, Shahabuddin, Orihuela, Riveros, Ascanio, Adler, Lambert and Balbas 2001). Consequently, methods investigating secondary extinctions in topological food webs may overestimate the network's robustness by overlooking the influence of predators (Curtsdotter, Binzer, Brose, de Castro, Ebenman, Eklof, Riede, Thierry and Rall 2011). However, within food webs, patterns of interactions referred to as motifs or subgraphs (used synonymously here) are observed (McLeod and Leroux 2021). These motifs vary in their characteristics, and some specific subgraphs are facilitative of top-down effects. For instance, apparent competition occurs when two species that do not directly compete for resources affect each other indirectly by acting as prey for the same predator. This interaction forms a triangular motif (Holt and Bonsall 2017) (*Figure 1*). In the event of the extinction of one prey species, the predator may compensate by increasing its consumption of an alternative prey, potentially leading to a secondary extinction. It is worth noting that in some cases, apparent competition might not be strong enough to result in a secondary extinction, particularly if the extinct prey species is a minor or relatively opportunistic component of the predator's diet or if there are many species in the predator’s diet. Nevertheless, within our food web (assuming completeness), the set of all apparent competition-shaped subgraphs A encompasses the number of apparent competition motifs that may lead to secondary extinctions B (B is a proper subset of A, or $B \subsetneq A$). By assuming a proportional relationship between A and B, we can assess the relative importance of a taxon based on the frequency of its species appearing in trophically key positions within subgraphs (McLeod and Leroux 2021). The same logic applies to trophic cascades, where predators can exert indirect effects on species through the control of intermediate consumers (Ripple, Estes, Schmitz, Constant, Kaylor, Lenz, Motley, Self, Taylor and Wolf 2016). Trophic cascades are also characterized in their shape by easily recognizable subgraphs (Ebenman and Jonsson 2005) (*Figure 1*). If an apex predator is removed from the web, the intermediate consumer that it used to control may experience population growth and cause severe depletion of its own prey species.

We identified all apparent competition and trophic cascade subgraphs in our food web using the VF2 algorithm (Cordella, Foggia, Sansone and Vento 2004) in the R iGraph package (Csardi and Nepusz 2006) (this method is also known as subgraph enumeration). We limited trophic cascade subgraphs to tri-trophic food chains, excluding chains where the apex consumer depredated both the intermediate consumer and the prey of the intermediate consumer. We tallied the frequency of subgraphs where birds, mammals, and reptiles were identified as either the apex predator (for trophic cascade motifs) or the prey (for apparent competition motifs). This allowed us to quantify the occurrences of these motifs specifically associated with each taxonomic class. We then compared the occurrences of these motifs per class to Erdős–Rényi algorithm-generated networks, which we used as a null model (sensu Baiser, Elhesha and Kahveci 2016). This algorithm generates random networks where the only constraint is that the randomized network must have the same number of nodes and expected links as the observed network (Erdös and Rényi 1959). We ran the null model 100 times, counting and splitting subgraphs in the same way as with the empirical data. We then compared empirical motif counts to those of the null models using z-scores and p-values (Baiser, Elhesha and Kahveci 2016). We focused on motifs where an animal's removal from the web could result in a top-down secondary extinction. For apparent competition-based subgraphs, for example, the prey positions should be the cause of top-down forced secondary extinctions, due to compensatory predation following the loss of one of the species. For tri-trophic cascade-based subgraphs, the apex predator position should be the cause of top-down forced secondary extinctions from the release of the second-tier consumer from predatory control. We refer to these positions in the motifs as driving positions (or drivers).

Results

Our Mojave Desert food web was comprised of 150 bird species, 43 mammals, 42 reptiles, 26 orders of insects, and 39 orders of plants. There were 4,080 edges in the web (Figure 2; the adjacency matrix and list of predation links are found in Supplemental Tables S1 and S2). The mean number of links a node had for birds was 20.7 ± 17.4 (median 16.0), for mammals it was 23.5 ± 13.3 (median 18.0), 23.0 ± 14.3 (median 18.5) for reptiles, 72.4 ± 69.6 (median 42.5) for invertebrates, and 30.6 ± 24.4 (median 26.0) for plants. For trophic levels of 1 to 4, where 1 is plants and 4 is apex predators, birds had an average trophic level of 3.24 ± 0.10, mammals had an average trophic level of 2.85 ± 0.23, reptiles had an average trophic level of 3.75 ± 0.17, and invertebrates had an average trophic level of 2.96 ± 0.32.

Most consumptive interactions with birds involved other birds, invertebrates, and plants (including interactions where birds were either predator or prey). In contrast, mammals and reptiles exhibited more balanced interactions with other animals in the web. Birds demonstrated a relatively high homophily score of 0.66, indicating a strong inclination for birds to form connections with other birds within the food web. In contrast, the invertebrate and mammal groups exhibited lower homophily scores of 0.02 and 0.07, respectively – values indicative of an even mix of links within and without their groups. The reptile group displayed a homophily score of 0.36, indicating a moderate tendency relative to the other groups for reptiles to be connected to other reptiles within the food web. Plants, as primary producers, did not act as predators or prey for other plants in the food web, resulting in a homophily score of -1.00.

All instances of bird primary extinction cascades resulted in fewer accumulated secondary extinctions than observed from the extinctions of either reptiles or mammals under all threshold (remaining interaction strength) scenarios (*Figure 3 and 4*). In fact, under the 60% and 70% threshold conditions, random loss of bird species did not cause any secondary extinctions until over 50 species were lost from the food web. Mammal extinctions resulted in the most rapidly accumulating number of secondary extinctions, as well as the greatest number of accumulated secondary extinctions in the food web. Extinction of reptiles from the food web resulted in a rate and accumulated number of secondary extinctions that was intermediate between birds and mammals. An avian extinction cascade where only birds that were year-long residents were removed also resulted in greater numbers of accumulated secondary extinctions than did than the cascade from extinctions that included all bird species, both under randomized extinctions (*Figure 3*) and ordered extinctions according to thermal vulnerability (*Figure 4*). However, cascades including only birds that were in the Mojave for part of the year (non-residents) resulted in similar levels of secondary extinctions to the cascade that included all birds except under higher thresholds. At thresholds of 80-90%, randomized order of extinction of bird species resulted in higher numbers of secondary extinctions when all bird species were included compared to the effects of randomized extinctions from only non-residents (*Figure 3*). On the other hand, preset extinctions based on thermal vulnerability resulted in higher numbers of secondary extinctions from non-residents in comparison to thermal vulnerability extinctions from all birds (*Figure 4*).

There were significantly fewer birds than expected in driving positions (i.e., positions that can be the cause of top-down forced secondary extinctions) in apparent competition-based subgraphs when compared to null models, including motifs where only one of the prey species was a bird ($z = -32.1$, $p < 0.001$) and those where both prey species were birds ($z = -15.1$, $p < 0.001$). However, comparing z-scores reveal that mammals and reptiles were approximately equally likely to appear as only one of the prey species, and were much more likely to do so than birds (*Figure 5*). In fact, in motifs where reptiles were both prey species there was no significant difference between real-world data and the null models ($z = -0.7$, $p = -0.23$), while mammals had significantly greater representation than we would expect from null models ($z = 4.74$, $p = 0.001$, *Figure 6*). Motifs where reptiles were only one of the prey species were also found less frequently than in null models ($z = -17.3$, $p < 0.001$), as were mammals ($z = -18.2$, $p < 0.001$, *Figure 5*).

There were also significantly fewer birds than expected in driving positions (i.e., the apex predator) in tri-trophic-based subgraphs when compared to null models ($z = -9.1$, $p > 0.001$, *Figure 5*). There were also significantly fewer mammals than we would expect in the apex position ($z = -13.5$, $p<0.001$), but there was no difference between null model expectations and the number of reptiles in the apex position ($z = -0.73$, $p = 0.23$, *Figure 5*). Birds were more likely to be found in the apex position than were mammals, but they were comparatively less likely to be in the apex position than were reptiles *(Figure 5*).

Discussion

Ecosystems are intricate networks of interactions in which the presence or absence of species has the potential to trigger a chain reaction of cascading secondary extinctions throughout the community (Ebenman, Law and Borrvall 2004). Modeling these cascades in real-world food webs can provide valuable insights for adjusting species management or harvesting strategies (Ávila-Thieme, Corcoran, Pérez-Matus, Wieters, Navarrete, Marquet and Valdovinos 2021, de Visser, Freymann and Olff 2011). Indeed, the economic advantages of the ecological network-based predictive approach has led to its adoption by fisheries scientists (Yun, Hutniczak, Abbott and Fenichel 2017), who not only have developed complex, dynamic representations of marine ecosystems (Fulton, Link, Kaplan, Savina-Rolland, Johnson, Ainsworth, Horne, Gorton, Gamble, Smith and Smith 2011) but have also created bespoke software to analyze such models (Heymans, Coll, Link, Mackinson, Steenbeek, Walters and Christensen 2016). However, studies of this nature in natural terrestrial systems, particularly those that investigate secondary extinction cascades, are rarer despite their potential to predict ecosystem robustness to species loss (Ebenman 2011). Here we constructed the most comprehensive food web available for terrestrial species in the Mojave Desert as of this publication and used it to test scenarios of vertebrate extinction. We found that the impact of bird species loss on the subsequent structure and richness of the food web via secondary extinction cascades was relatively low compared to the potential consequences of removing mammals or lizards.

The homophily indices we calculated offer valuable clues to the underlying reasons behind these findings. A high proportion of bird links in our network are to other birds, while reptiles moderately connected to other reptiles and mammal connections were proportionally equal. The high interconnectivity among avian species has resulted in the formation of a "subweb," a subset of species that are highly connected to prey and/or predators within the same subset (Melián and Bascompte 2004). Such groupings can enhance the network's resilience and protect it from the impacts of losing highly connected species from within the subweb (Melián and Bascompte 2002, Melián and Bascompte 2004), insulating the food web from bird extinctions and demonstrating why other vertebrates have greater import to network persistence in the Mojave Desert.

Evidence from published research corroborates our conclusion. Riddell, Iknayan, Hargrove, Tremor, Patton, Ramirez, Wolf and Beissinger (2021) found that Mojave mammal populations have remained stable despite crashing bird populations, which is suggestive of limited secondary extinctions in this system following avian declines. Furthermore, although there are many examples of cascading effects stemming from apex avian predators around the world (Terraube and Bretagnolle 2018), Estrada and Rodriguez-Estrella (2016) explain that in the Baja California Peninsula desert (neighboring the Mojave) such birds are poor surrogates for other species in the area. In fact, they suggest that there is reduced interaction strength between apex birds and their prey, in this system, which we note would also reduce the probability of secondary extinctions following species loss.

We add to their supposition on interaction strengths with data from our motif analysis: in this system, there may be less of an opportunity for birds to influence the food web from the top. Birds occupied driving positions within apparent competition-based motifs less frequently than mammals or reptiles, suggesting they are less likely to cause secondary extinctions through top-down apparent competition-based effects. On the other hand, birds occupied the apex predator position in a tri-trophic motif more frequently than mammals (but less often than reptiles). Therefore, we assume the extinction of a bird species to have a higher likelihood of causing secondary extinctions through top-down trophic cascade-based effects compared to mammals, but lower than if a reptile were to go extinct. This result is because mammals in the web are less likely to appear at the top of the food chain and initiate top-down control of tri-trophic motifs. Indeed, mammals in our food web are on average 0.5-1.0 trophic levels lower than the other vertebrates.

Despite the concordance between the predictions from our food web and field data, the relative resilience of our network to bird extinctions does not appear to be replicated in other studies. For example, although Brazilian forest webs are robust to random bird extinctions, the avian species at higher extinction risk are critical in maintaining community structure (Vidal, Hasui, Pizo, Tamashiro, Silva and Guimarães Jr. 2014). Indeed, the vulnerability of certain species is often linked to their functional roles and interactions within the network, and random extinctions are less likely to disrupt critical links than when a vulnerable species is lost (Berg, Pimenov, Palmer, Emmerson and Jonsson 2015). This differs from our findings, where losses of birds at high risk of extinction from climate change had limited to no subsequent effects on network composition or structure. The difference in systems may play a role, as deserts were one of the few biomes where a meta-analysis did not find evidence of cascading effects from birds in tri-trophic food chains (Mäntylä, Klemola and Laaksonen 2011). Alternatively, this difference may be attributable to birds having a greater effect on plants and insects through top-down predation (Mäntylä, Klemola and Laaksonen 2011, Vidal, Hasui, Pizo, Tamashiro, Silva and Guimarães Jr. 2014). Since we had to aggregate plants and insects due to limited data availability and were restricted in our capacity to analyze top-down effects, it is possible that we underestimated the capacity of birds to influence this food web. Furthermore, although we focus on predation, there are other interaction types present in the Mojave that could influence secondary extinction cascades. Gopher tortoises (*Gopherus* spp.), for example, are considered as keystone species due to their propensity to dig burrows that other animals could then use as refugia (Catano and Stout 2015), and populations of the Mojave Desert tortoise (*G. agassizii*) have declined dramatically over the course of the late 20th and 21st centuries (Kissel, Wallace, Anderson, Dickson, Van Neste, Landau, Averill-Murray, Allison and Fesnock 2023).

We caution that a community viability analysis based on food webs without dynamics can underestimate the risk and number of secondary extinctions (Ebenman and Jonsson 2005). Indeed, topological analysis always predicts a lower number of secondary extinctions than dynamic analysis, especially for food webs with high connectance (Eklof and Ebenman 2006), while non-standard food sources may be more common during circumstances that would otherwise result in cascading community failure. Our web lacks the parameters and equations required to incorporate population dynamics and is not capable of tracking cascading losses in arthropods except at the level of taxonomic order. Therefore, it is possible that we are underestimating the risk and number of secondary extinctions, particularly since cascading effects from birds often influence arthropods (Murakami and Nakano 2000). Natural and manipulative experiments that examine specific coextinctions from species loss would overcome these limitations, such as how Jönsson and Thor (2012) conducted a CVA predicting the effect of common ash *Fraxinus excelsior* diebacks from disease on affiliated lichen communities. However, obtaining such data is generally difficult and time-consuming.

Finally, our web does not account for birds' abilities to fly large distances, which allows them to be part of multiple food webs in disparate locations in the same period (which is referred to as a *metacommunity*) (Leibold, Holyoak, Mouquet, Amarasekare, Chase, Hoopes, Holt, Shurin, Law, Tilman, Loreau and Gonzalez 2004). Such behavior, as observed in previous studies

(Maron, Estes, Croll, Danner, Elmendorf and Buckelew 2006), can result in significant fluxes of nutrients that have the potential to alter ecosystems. Consequently, the loss of birds from our food web may induce secondary extinction cascades within the desert community via non-consumptive effects (defined as the impact of animals on the growth, behavior, or development of other species, e.g., Peckarsky, Abrams, Bolnick, Dill, Grabowski, Luttbeg, Orrock, Peacor, Preisser, Schmitz and Trussell (2008)). These effects cannot be accounted for in a network based solely on predator-prey interactions (Wooten 2020). Indeed, although researchers have known for years that non-consumptive effects impact population dynamics in food webs (Lima and Dill 1990, Peckarsky, Abrams, Bolnick, Dill, Grabowski, Luttbeg, Orrock, Peacor, Preisser, Schmitz and Trussell 2008) and have conducted manipulative experiments on how they impact smaller webs (Schmitz 2008), such research has only recently been introduced into analyses of full ecological networks (e.g., Ho, Tylianakis, Zheng and Pawar 2019).

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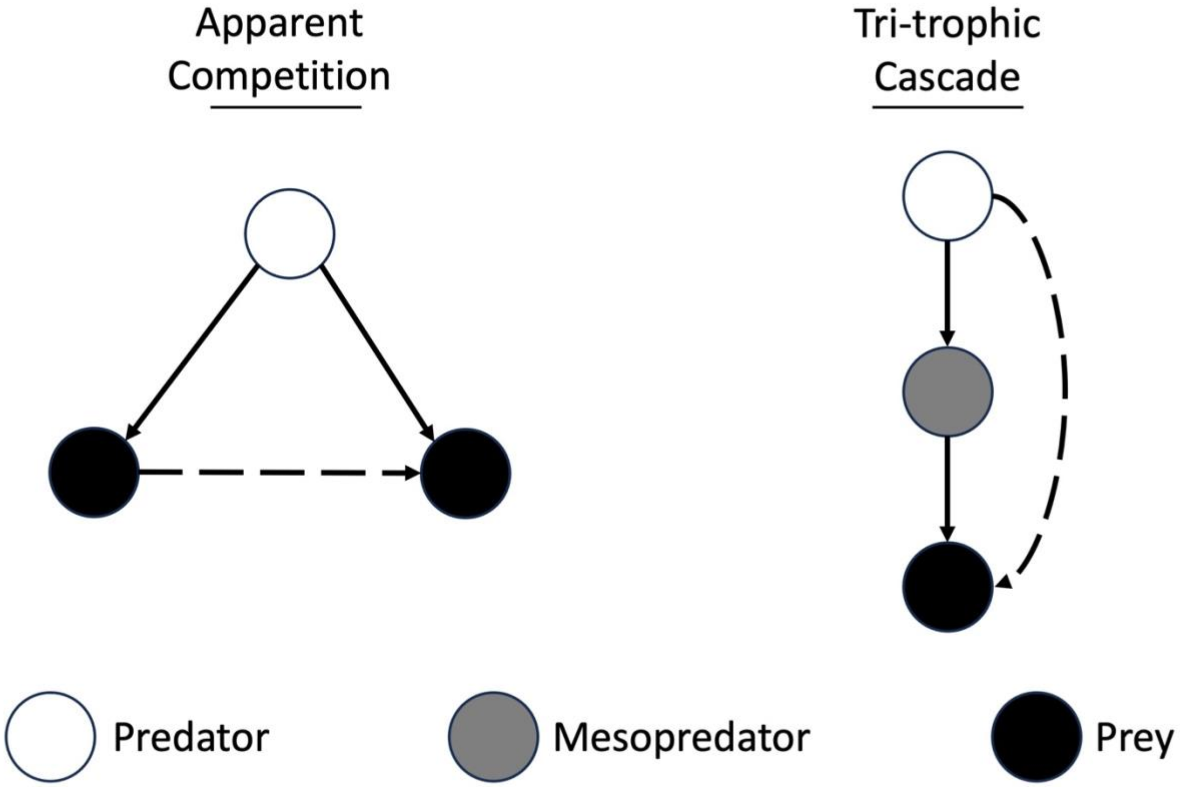

Figure 6-1 Example networks demonstrating the shape of apparent competition and tri-trophic cascade subgraphs. Predator/prey (consumptive) interactions are represented by solid lines, while indirect effects are represented by dashed lines.

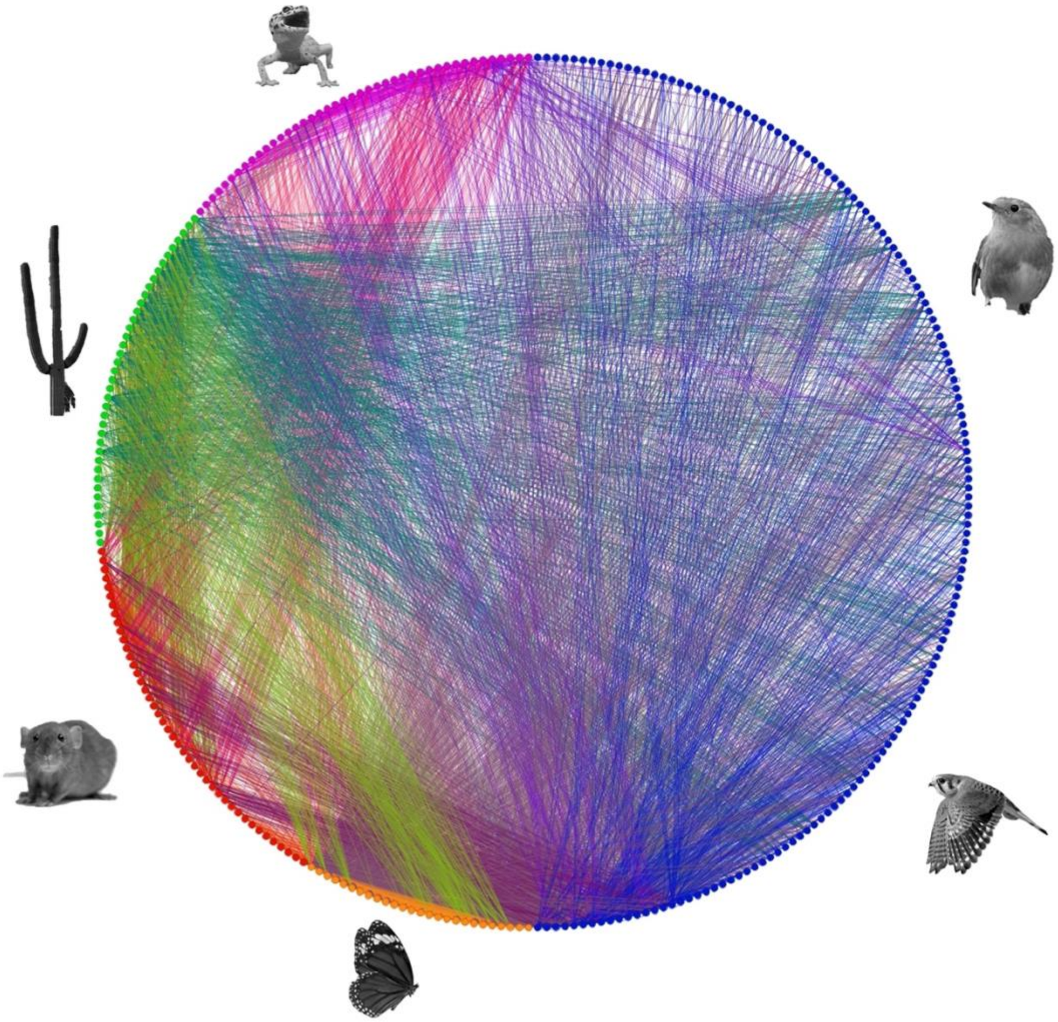

Figure 6-2 The full food web of the Mojave Desert terrestrial community created and used in this study. Plants are shown in green, mammals in red, insects in orange, birds in blue, and reptiles in purple. The color of the line matches that of what is being consumed, (e.g., a bird eating a plant will be joined by a green line). This web has 150 birds, 43 mammals, 42 reptiles, 26 insects (aggregated to order), and 39 plants (aggregated to order). There are 4080 feeding links.

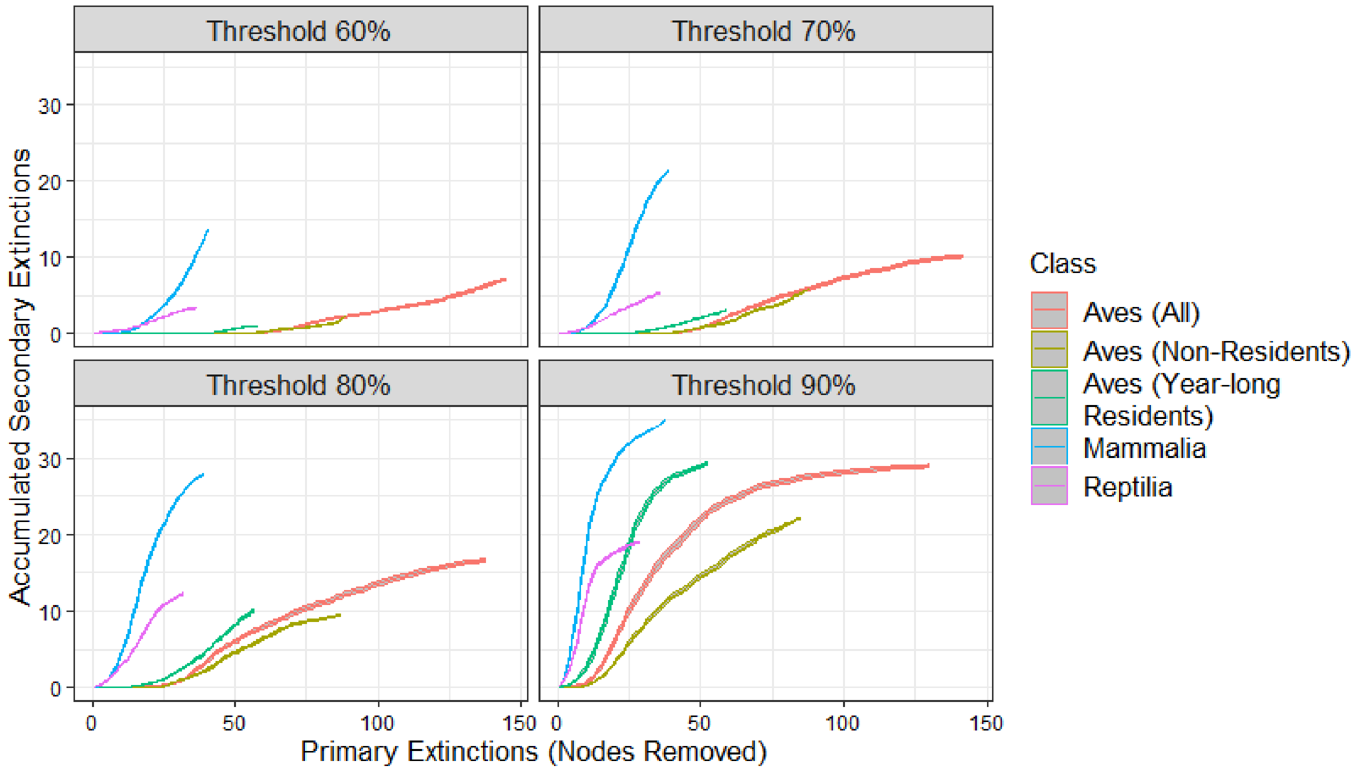

Figure 6-3 Secondary extinction cascades caused by primary extinctions from birds (all species, resident-removals only, and non-resident-removals only (where non-residents are birds that either breed or migrate through the Mojave but are not present year-round)), mammals, and reptiles. All cascade lines represent 95% confidence intervals based on randomized order of species removal from 100 replicates. Threshold percentages means that a species needed to have a remaining interaction strength greater than or equal to the threshold following a primary extinction to avoid secondary extinction (a threshold of 100% would always result in secondary extinctions, while a threshold of 0% never would). Lines for mammals and reptiles are the same as in Figure 4.

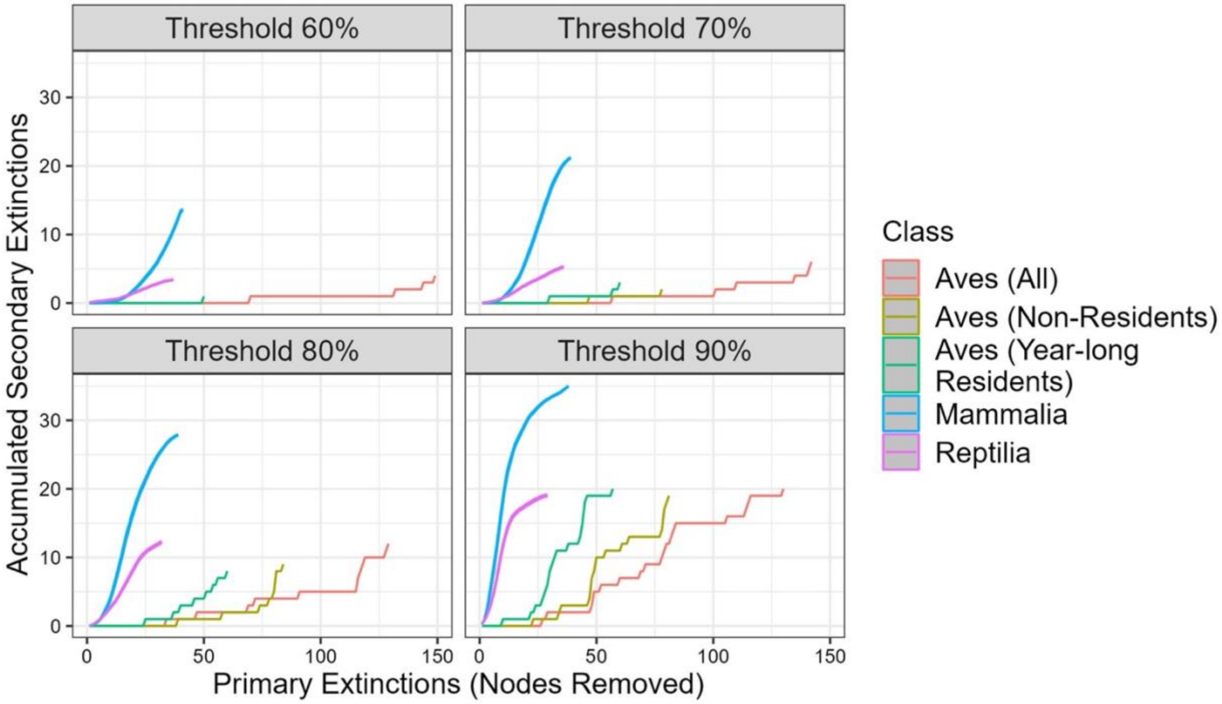

Figure 6-4 Secondary extinction cascades caused by primary extinctions from birds (all species, residents only, and non-residents only), mammals, and reptiles. Bird lines represent a single removal order from most to least vulnerable to temperature increases (from Eichenwald and Reed (In review). Threshold percentages means that a species needed to have a remaining interaction strength greater than or equal to the threshold following a primary extinction to avoid secondary extinction (a threshold of 100% would always result in secondary extinctions, while a threshold of 0% never would). Mammal and reptile cascade lines represent 95% confidence intervals based on randomized order of species removal from 100 replicates and are the same as in Figure 3.

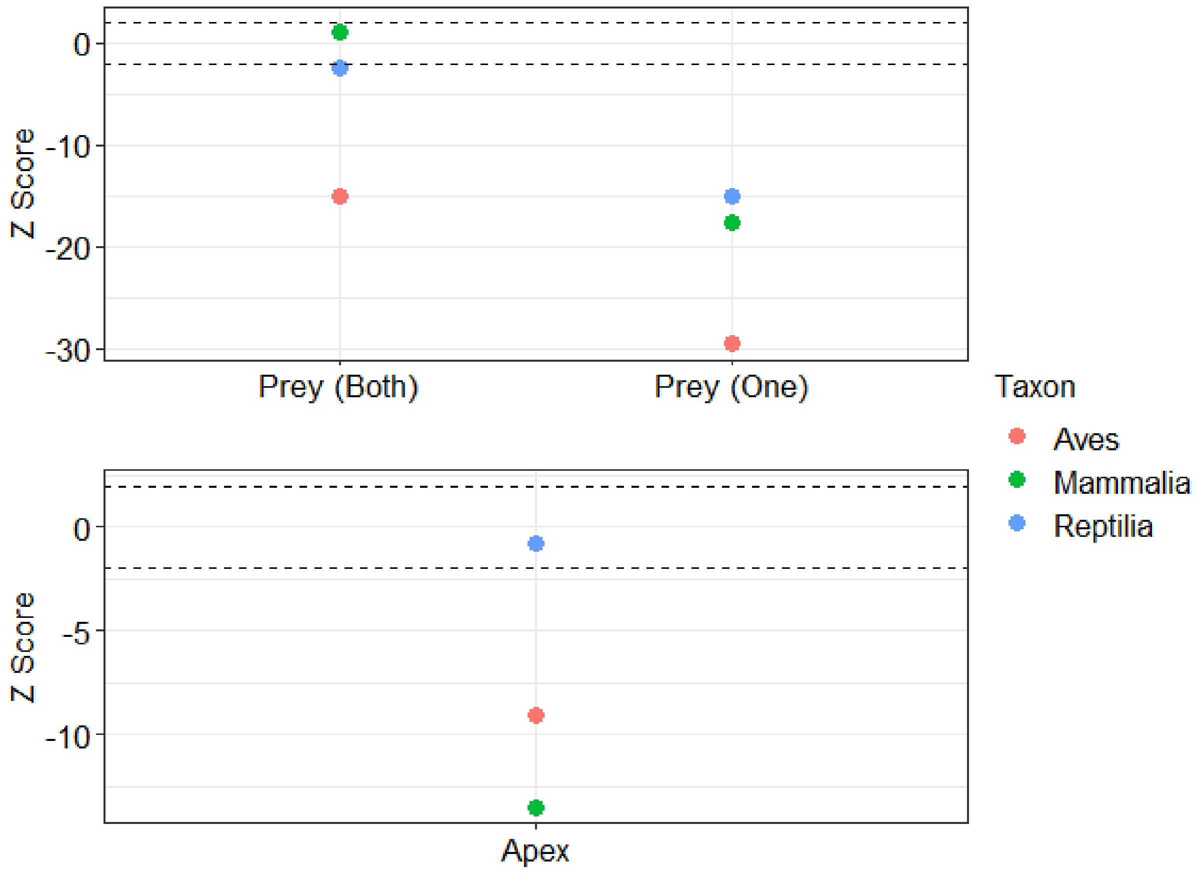

Figure 6-5 Z scores of the number of apparent competition (top) and tri-trophic (bottom) motifs in comparison to null graphs. X-axis labels refer to the driving position (positions that can be the cause of top-down forced secondary extinctions) within the motif (for example, the *Aves* point over *prey (both)* in the top graph refers to the z-score where both prey in the apparent competition motif were birds). We only count motifs where the taxon in question is in driving position, where losing that species could result in top-down driven secondary extinctions. Points between the dashed lines are not significantly different from the null model; points outside the dashed lines are significantly different from the null.

Chapter 7

Conclusions

This Thesis in Context

Incorporating a community perspective into understanding the dynamics and ecology of a suite of species not only allows us to better understand and safeguard species and ecosystems but also provides a broader framework for addressing critical questions, such as predicting the effects of climate change (Soulé et al. 2003, Soulé et al. 2005, Sabo 2008). By recognizing the interconnectedness of species on a landscape and considering the potential cascading effects and feedback loops within ecological networks, we gain insight into the broader implications of threats and proposed management actions (Wittmer et al. 2013, McDonald-Madden et al. 2016). This perspective enables us to identify crucial relationships, vulnerabilities, and key drivers of change, providing a more comprehensive understanding of community dynamics (Säterberg et al. 2013). Additionally, viewing species through a community lens offers valuable insights into alternative conservation regimes, empowering resource managers to evaluate strategies that encompass species interactions, ecological functions, and ecosystem services (e.g., Middleton et al. 2013, Serrouya et al. 2015, Serrouya et al. 2019). By integrating these assessments into decision-making processes, we can more effectively address urgent conservation needs and enhance the resilience of ecosystems in the face of environmental challenges (Heleno et al. 2020). In this thesis I explored community ecology-based responses to climate change. It provides one perspective of how we might approach conservation from this perspective.

Summary of Findings

The most important highlights from my thesis were the creation of a framework for community viability analysis and its implementations. Each approach was designed to answer a different question of import: 1) to identify a potentially important relationship between the observed and expected effects of climate change and secondary use of underground thermal refugia on birds, and 2) to clarify the relative importance of birds in comparison with other vertebrates to ecosystem resistance.

In chapter 2, I introduced an approach to assess the long-term survival (persistence via resistance and resilience to perturbations) of ecological communities. The proposed framework builds upon existing single-species viability analysis methods, incorporating a broader range of factors such as species interactions, food web dynamics, habitat connectivity, and environmental changes. By considering these complex interactions, I aimed to provide a more comprehensive understanding of community viability. The expanded framework enhances the accuracy and relevance of ecological assessments, guiding more effective conservation and management strategies to safeguard biodiversity and ecosystem health in the face of environmental challenges.

In chapter 3, I began preliminary work on the viability analysis of my target ecosystem, the Mojave Desert, by determining how to accurately obtain the necessary parameters for thermal models. Specifically, I first needed to determine relative thermal vulnerabilities of birds using a physical (mechanistic) model. One component of this assessment required input on the density of each bird species because it affects heat loss. The traditional approach to estimating body density in birds was to pull data on mass and length from readily available databases, then to assume the bird was a sphere, and determine density as mass/volume. I found this method to be biased, underestimating density, thereby overestimating thermal vulnerability. I showed that using measurements of the long and short axis and assuming an animal is an ellipsoid provided better density estimations. This required gathering my own data from museum specimens, because the short axis of birds is never reported, but it made a meaningful difference in assessing avian thermal properties of birds, and therefore their vulnerability to climate change impacts.

In chapter 4, I continued collecting biophysical parameters for Mojave Desert birds to further parameterize the thermal vulnerability model (NicheMapR) in preparation for a community viability analysis. I allometrically derived some attributes and directly measured others. Data on feather reflectance was the most difficult (tedious) to obtain, due to the expensive equipment required and the need to take 10 measurements per bird specimen and have 5 replicates for each of 151 species. I also estimated relative thermal vulnerabilities to heat exposure from these data, pinpointing which species were more at risk than others due to climate change in the desert, all other things being equal. The identification of thermal vulnerabilities and the significance of dorsal feather reflectance as a predictor of vulnerability helps to prioritize protection measures for the most at-risk bird populations in desert ecosystems. This also provides a significant dataset that others can use for further investigation of climate change and desert birds.

In chapter 5, I applied the parameters and model from chapters 3 and 4 to conduct a persistence-based CVA across the Mojave Desert ecosystem both spatially and temporally. This CVA is comprised of a mechanistic thermal model, analysis of my own field data, and evaluation of surveys from citizen scientists. I test for the existence of an unconfirmed interaction between birds and underground thermal refugia dug by mammals and reptiles, as such a mechanism should impact the persistence of Mojave Birds under climate change. The scenario with greatest support from our data is that birds do utilize underground thermal refugia, although it is impossible to determine whether this is a historical behavior or a new adaptation. The hypothesis that our model and field data point to as most likely is one where birds incidentally used burrows in the past but may be increasing this behavior in the modern era. Indeed, in all best fit models for our field data, burrow presence was highly predictive of bird richness and abundance, and – most interestingly – our eBird results suggest reduced impact of aboveground shade when burrows are present, with an increasing positive impact of burrows on richness and abundance as shade levels decrease. This chapter does not confirm the existence of this interaction, it only provides evidence that such a mechanism is consistent with collected data. Above all, this chapter illustrates the benefits of conducting predictive studies based on plausible scenarios – particularly using a CVA – as they serve as steps in the scientific method, feeding back and forth between models and predictions, and here it generated what I think are valuable insights to bird vulnerability and potential management actions.

In chapter 6, I conducted a resistance-based CVA of the Mojave Desert ecosystem using a network analysis of cascading extinction risk. I build a food web of the desert based on predator and prey interactions obtained from the primary literature, and I calculated interaction strengths based on theoretical fluxes of energy through the system. I then estimated the relative community resistance to species loss by analyzing the potential cascading impacts on the ecosystem when removing specific groups, such as birds, mammals, and reptiles, from the web. My biggest surprise was the relative lack impact of bird loss relative to other vertebrate taxa on cascading extinctions. Analyses from the chapter shed light on the factors that drive secondary extinction patterns and the relative importance of different vertebrate groups in maintaining the structure and resistance of the animal community. Conservation efforts often prioritize endangered or vulnerable species, and understanding their roles within the food web can be useful for effective management. My findings that the loss of bird species has relatively low impacts on the overall food web compared to mammals or lizards highlights the importance of considering the functional roles of different vertebrate groups in ecosystem dynamics. This information can help prioritize conservation efforts and allocate resources more effectively to safeguard critical components of the ecosystem.

Trial and Error

As well as my research ultimately integrated, I ran into several dead ends. Applying community ecology to conservation problems was a learning experience. In this vein, I describe here several aspects of my research that either resulted in dead ends or were superseded by better methods.

Climate Space Diagrams

I initially envisioned using ‘climate space diagrams’ in my research. Measuring species capacity to survive various environmental conditions has been an objective of research for decades. Porter and Gates (1969) invented the “climate space diagram” as a method of visually depicting this relationship, which was refined in subsequent decades (Gates 1980). These diagrams map a parallelogram in an x-y coordinate system, where the x axis is absorbed radiation in Watts/m^2 and the y axis is air temperature in degrees Celsius. The lines of the parallelogram outline the thermal environment and the physiological limits of a given species. With the parallelogram in place, we could then plot specific environmental conditions as points; if those points fall outside the parallelogram for a given species, we know that those specific conditions are lethal. Since their creation, climate space diagrams have been used successfully to show how animals might respond to climate change over their spatial distributions (e.g., Johnston and Schmitz 1997).

I planned to use climate space diagrams at the beginning of my mechanistic modeling project. Through readings of the primary literature, however, I learned that climate space diagrams had become outdated. While climate space diagrams were in use in the 1980s and 1990s, biophysical scientists were simultaneously developing more complex heat budget calculations for endotherms using metabolic and water loss rates (Porter et al. 1994, Porter et al. 2000). Where climate space diagrams estimated potential boundaries for species from a limited set of parameters, heat budgets calculated how a given species would actively respond metabolically given certain environmental conditions. Advancements in this field continued through the 21st century, including developments in using explicit spatial components in biophysical models (Kearney and Porter 2009). The culmination of this progress so far is the NicheMapR package, a suite of programs for the R environment that compute fundamental physical and chemical constraints on living things (Kearney and Porter 2017, Kearney et al. 2020, Kearney and Porter 2020). NicheMapR allowed me to calculate a much broader assortment of variables at a high resolution of environmental data, and its endotherm modeling function was released right as I was deciding on whether to shift away from climate space diagrams (Kearney et al. 2021). I held onto climate space diagrams as a backup method as I worked through the process of obtaining all the necessary parameters for NicheMapR in case I was not able to obtain the results that I needed. Once I knew NicheMapR would work, I decided not to continue using climate space diagrams.

Photogrammetry

Originally, my chapter on calculating bird density focused on the use of photogrammetry. Photogrammetry refers to a collection of different techniques intended to obtain real-world measurements of objects in 3D space from 2D images (Linder 2009). Techniques used in photogrammetry include creating 3D topographic maps, reconstructing objects from 3D point clouds, and measuring coordinates, quantification of distances, heights, areas, and volumes (Aber et al. 2019). It has been used in topographic mapping, architecture, archaeology, engineering, and even entertainment, and its widespread usefulness has resulted in many open-source programs that facilitate photogrammetric analysis and computation. Although high-cost equipment can be and is used, all that is truly required for basic photogrammetry is a digital camera (Medina et al. 2020).

At first, I tested using photogrammetry to calculate the density of each of the bird species found in the Mojave Desert. This was during the Covid 19 pandemic, and so the Harvard Museum of Comparative Zoology was unavailable. The closest museum was at the University of Connecticut, which did not have specimens of all the birds I needed to measure. Instead, I tested the method itself along with a group of assisting masters students. I found that this method was overly time-consuming: collecting data required almost 15 minutes per specimen, while combining the photos into a photogrammetry model required between 1-6 hours per specimen. Furthermore, the final photogrammetry models were not “watertight,” meaning there were small, imperceptible gaps that made it impossible to calculate the volume of a specimens. Although it is possible to repair the “watertight” issue, doing so would have required a further unknown quantity of time. This was a large amount of effort for only a single parameter in the mechanistic model; therefore, after examining my options, I decided to instead focus on estimations of body density that were less time consuming.

Camera and Acoustic Traps

My field surveys initially were to incorporate both camera traps and acoustic recorders. I thought that I would be able to obtain a more comprehensive assessment of the avian community with motion and noise-triggered recording devices that were operating 24/7, as a complement to the 10 minute transect surveys I did. The low population density of vertebrates in the desert, however, resulted almost exclusively in days of acoustic recordings of wind and images of moving bushes. I attempted to improve my sighting rate by baiting these traps as well, testing various mixes of seed, grass, dried insects, and even a water dispenser. Although baiting the traps lured many mammals, birds rarely appeared regardless of the bait used. I knew that this result was not because there were no birds at these sites, as I had conducted transects that revealed birds were indeed present. I determined that the traps were not going to provide me with actionable data and relied on my own surveys instead.

Drone Flights and LiDAR

I was originally unaware of the availability of high-resolution satellite imagery for my study region. The most-used remote sensing data has a maximum resolution of 30 meters, which is incapable of tracking small-scale variables such as shrub density or percent plant cover. I knew that I needed to obtain high-resolution data on vegetation for at least my field survey sites to account for the effect of habitat. Therefore, to obtain remote sensing data at a high resolution I obtained a drone pilot's license from the FAA and flew a Phantom 4 Pro v 2.0 drone over all my sites and used associated software to construct a 3-D image of the flown areas. Using data from the drone was problematic for several reasons:

1. The drone's camera did not have access to the infrared spectrum, instead relying only on red, green, and blue. Cameras that can utilize infrared are much more expensive and were therefore unaffordable. Unfortunately, vegetation-based remote sensing metrics such as EVI and NDVI rely on infrared bands (CITATIONS). This removed the possibility of using vegetation metrics with drone imagery.
2. Flying drones and processing the images took time, reducing the number of total sites from which I could collect data. Flights for high resolution imagery took at least 15-30 minutes per site and had to be performed after a transect was completed to avoid capturing a researcher in the data. This added an extra half an hour to a site visit. As I was following methods from Iknayan and Beissinger (2018) so I could compare our results with them if needed, I could only collect data in the 4 hours post-dawn. Drone flights also had to be done during this time; after this 4-hour period, temperatures were so high that the drone and its controls would overheat. Therefore, I had a choice between drone flights or greater amounts of data from more field surveys.
3. On some days, weather conditions (high wind) made it unsafe to fly. Therefore, days where it was safe to fly were often spent returning to old sites to remotely sense them rather than collecting data from new sites.
4. Large areas of the desert were governed by the National Park Service, and flying drones above Park land is illegal.
5. Data collected from drone flights could only be used in analysis of field survey data and could not be extrapolated to eBird data covering a greater land area. Furthermore, it was impossible for me to travel to all sites where eBird users collected data to remotely sense

the ground with a drone – partly due to the large number of sites and partly due to the illegality of flying over some sites.

I investigated the possibility of using LiDAR instead, which is a remote sensing method that uses light in the form of a pulsed laser to measure distances to the Earth. LiDAR is high resolution data, sufficient to allow researchers to outline the shape of buildings and the structure of vegetation on the ground. However, collection of LiDAR by professionals can be between \$2500-\$30,000 per day, which meant I had to rely on pre-collected data. The USGS had collected LiDAR data of a large portion of my study area, but not all of it. Furthermore, this dataset did not include coverage for large portions of the available eBird dataset, reducing its suitability for my purposes. As I searched for other options, I planned to reduce the scale of eBird data to only the area covered by LiDAR data (in the event I failed). I downloaded these data from the USGS and began analyzing them with LiDAR vegetation tools developed for ENVI (L3Harris Geospatial) by the Boise Center Aerospace Laboratory. These tools allowed for calculation of variables such as percent vegetation cover and height. However, they were developed for more structurally developed ecosystems such as shrublands and forests, and they struggled with creating accurate rasters of desert regions. Both LiDAR and drone flights were rendered unnecessary by my discovery of freely available recent high-resolution satellite imagery for the entire Mojave Desert.

Bayesian Hierarchical Species Distribution Models

I investigated the possibility of using joint species distribution models in my field research chapter. These methods model variation in the number, abundance, identities, and traits of species over space and time by assuming that the species respond jointly to the environment and to each other (Tikhonov et al. 2020). A new joint species distribution modeling R package called HMSC, which uses multivariate hierarchical generalized linear mixed models fitted with Bayesian inference, was released in 2020 (Ovaskainen and Abrego 2020, Tikhonov et al. 2020). I considered using this package to model the effect of environmental variables on the bird community.

HMSC, however, is a complicated program, to the point where the developers published an entire book detailing its use (Ovaskainen and Abrego 2020). It took me several months of working through the chapters before I felt comfortable using the package. However, when I tried using the method with eBird survey results, there was so much data that even a model parallelized to run across multiple computer cores on Tufts' supercomputing cluster could take up to a month to finish. At this point, I asked myself whether using the program was necessary to accomplish the analyses needed for my project or whether I could achieve the same objective with classical GLMs. I realized I was interested in avian richness and abundance and not necessarily individual species responses, which is what I would gain from using HMSC. In contrast, by using classical GLMs I would be able to run multiple models in a relatively shorter time frame and perform model selection. I decided to replace HMSC analyses with classical GLMs in my chapter.

Alternate Research System, with Co-Occurrence Modeling

Although my thesis focuses on the Mojave Desert as a study system, this was not the first system I considered. I originally planned on investigating the potential drivers behind the decline of the American kestrel (*Falco sparverius*), which some ornithologists have suggested is due to increasing predation from Cooper's hawks (*Accipiter cooperii*) or increased competition with European starlings (*Sturnus vulgaris*) (Smallwood et al. 2009). My idea was to use a combination of eBird and BBS data in co-occurrence models to uncover spatial interactions between kestrels, starlings, and hawks. This project would include other, peripherally related species (kestrel predators and potential competitors) in the event a different, unknown relationship acted as a driver. Co-occurrence data is often used to infer strengths of interactions between species (e.g. Harris 2016, Tikhonov et al. 2017, Delalandre and Montesinos-Navarro 2018). Co-occurrence falls into three categories: positive, where species are found together in space; negative, where species are separated in space; and random, or independent, where there is no spatial relationship between species (Popovic et al. 2019). It is generally assumed that positive species interactions such as mutualism or commensalism will result in positive co-occurrence, while negative species interactions such as predation or competition will result in negative co-occurrence (Cazelles et al. 2016).

As I worked on this idea, I realized something important that had been either overlooked or rarely mentioned in the literature: spatial co-occurrence is *not* a reliable indicator of species interactions, even though researchers had used it as such. A single negative interaction could result in positive, negative, or random co-occurrence depending on the ecological context (*Figures 2 and 3*). This meant that my idea of using co-occurrence to investigate drivers of kestrel decline was not valid.

So, I shifted my focus to the Mojave Desert, but also began work on a short review paper documenting the flaws in co-occurrence analysis. In fact, I wrote a complete draft of a paper titled “Negative species interactions can result in either negative or positive co-occurrence in survey data” and proposed it to *Oikos*, who declined to consider it. Unfortunately, as I was editing my draft a paper was published in *Ecology Letters* titled “Co-occurrence is not evidence of ecological interactions” (Blanchet et al. 2020), making the same point with added arguments on conditional probability. I decided that my co-occurrence paper would not make any further contributions to the scientific record and abandoned it.

Future Directions

There is never enough time or funding to successfully complete, or even start, all projects or potential projects over the course of a single PhD thesis. Here I list a few possible future directions that could follow from my research.

Translocation study

The research I conducted focuses on modeling and correlations with survey data. However, I do not do any experimental manipulations (deliberate alteration or modification of one or more factors within a natural environment to observe the resulting effects on ecological processes or organisms), which are the gold standard for testing for the presence and drivers of interactions in community ecology (Brown et al. 2001). The lack of a traditional experiment is the weakest area of my research. Therefore, if this project were to continue, the next step I might consider would be a long-term experimental manipulation that tests my conclusion that birds rely on underground burrows in the Mojave Desert as thermal refugia.

The primary manipulation of this future experiment would revolve around translocation of desert tortoises to set up the following treatments: 1) high numbers of mammal burrows, high number of desert tortoises, 2) low numbers of mammal burrows, high numbers of desert tortoises, 3) high numbers of mammal burrows, low numbers of desert tortoises. Information about vegetation at each plot should be measured as well to incorporate in a final hierarchical model that will be used for the analysis of the data (we know that vegetation should be incorporated as a random variable, since it influences bird distributions in the Mojave Desert). In areas where tortoises were removed, their burrows could be filled or blocked as part of the treatment. The bird field transects that I performed in my research should be done at each of these sites, followed by translocations of desert tortoises. These translocations would then allow one to create the following survey plots: 1) high numbers of mammal burrows, high number of desert tortoises, no translocation, 2) low numbers of mammal burrows, high number of desert tortoises, no translocation, 4) high numbers of mammal burrows, low number of desert tortoises due to a translocation, 5) low numbers of mammal burrows, low number of desert tortoises due to translocation, 6) high numbers of mammal burrows, high number of desert tortoises due to a translocation, and 7) low numbers of mammal burrows, high number of desert tortoises due to translocation. At this point, bird field surveys should be repeated.

There are several reasons why I did not incorporate this proposed project as a part of my thesis:

1. Desert tortoises are categorized as threatened under the Endangered Species Act. The permitting process for translocating these species would go through the USFWS Ecological Services Program, and there are three potential categories for permits. My proposal does not fall under the enhancement of survival nor the recovery permit categories, as translocation of tortoises is an experimental manipulation for birds and is not intended to assist tortoise survival. Instead, the category that best fits the proposal is “incidental take”, which covers activities that may result in the loss of a protected species. Under the law, I would be required to submit and execute a habitat conservation plan in addition to the permit, which is beyond my capabilities as a PhD student [I do note, however, that opportunities can arise that might be taken advantage of, such as the forced relocation of many Desert Tortoises when the military expanded its training area in Ft. Irwin National Training Center, California (Esque et al. 2010).]

2. Translocated tortoises may not survive in the new environment. From a purely research-focused approach, a collapse of the translocated population would mean that the manipulation did not work, either prolonging the length of the experiment or undermining it entirely. Ethically, I also preferred to avoid developing a project that might cause the deaths of threatened species as a byproduct.
3. This project would take at least 5 years. It would require at least 2 years of bird survey data prior to a translocation, followed by a year for the translocations themselves (along with a simultaneous study tracking tortoise survival), followed by 2-3 years for post-translocation bird surveys. Research from Puffer et al. (2022) shows that birds do not find tortoise burrows until at least a year after their creation, and it would take a few years for burrows made in areas formerly occupied by tortoises to collapse. I would have needed to begin this experiment at the very moment I began my PhD at Tufts to obtain satisfactory data.

Creating artificial burrows rather than performing translocations could solve problems 1 and 2. However, it would not decrease the amount of time required to perform this experiment enough to be feasible for me. Again, we know that birds need *at least* one year to find new burrows before they begin using them (Puffer et al. 2022). Therefore, we would need at minimum 4 years, where the first year is without burrows with an installation of artificial ones at the end of the year, followed by 3 years of surveys to allow birds time to locate and use the new refugia.

There was one alternative way of performing this experiment: prior translocations of desert tortoises have been performed to help conserve the species (Field et al. 2007, Nussear et al. 2012, Hinderle et al. 2015). I considered using eBird survey data in these areas before and after translocations occurred, which would allow me to take advantage of this prior manipulation for my own work. However, numbers of eBird surveys in the Mojave Desert are already relatively lower in comparison to more trafficked parts of the country, and there were not enough surveys in translocation areas to obtain data for this project (particularly since most translocations I discovered appeared to have been performed either before or around the time eBird was established).

Evaluating the Efficacy of Artificial Burrows

If underground thermal refugia do in fact support the persistence of Mojave birds, and if desert tortoise loss is a key factor in avian declines, one potential conservation suggestion would be to install artificial burrows across the desert. Logically, this would supplement the burrows lost during the decline of desert tortoises, minimizing the impact of climate change and providing collapsing avian populations a chance to recover. However, some types of artificial refugia can be hotter than those that are naturally occurring (Rowland et al. 2017); there is a recorded instance of hotter temperatures turning a bat box into an oven and cooking the resident bats to death (Flaquer et al. 2014). Therefore, stringent evaluation must be done before any large-scale management using artificial burrows could be implemented – which is another potential future project.

I would set up an experiment where we compare the efficacy of multiple types of artificial burrow. I would set up plots in multiple types of soil and vegetative conditions across the desert so we can get a representative sample of environmental conditions. In each plot, I would install all burrow types we are testing (such as those used for burrowing owls (e.g., Nadeau et al. 2015)). I would block these refugia with mesh so they could not be used by vertebrates (to avoid creating an ecological trap), and I would measure the internal and external conditions at each artificial burrow using devices such as iButtons or Hobos. I would also conduct these same experiments with naturally occurring burrows (without mesh covers), so I could compare to see which artificial refugia most closely replicates burrows dug by vertebrates. This project should be feasible to conduct in a single summer season. I did not include it in my thesis because this is a purely conservation-based question (essentially, which management method is the most likely to work?) and I wanted my thesis to instead focus on combining community and conservation ecology. Although I do have a chapter that is focused on biophysical ecology, that work was a prerequisite to my data chapters.

Creating a Dynamic Food Web

The food web I created of the Mojave Desert is a topological (or static) network, where each link represents the presence of a feeding interaction between predators and prey. However, using a dynamic network in my analysis would provide a greater ability to accurately predict how the food web would respond to realistic extinction cascades. Dynamic networks include models of population dynamics in their links, such as with Lotka-Volterra equations (Ebenman et al. 2004). This is a task possible to achieve in a reasonable time frame for researchers working with microbial communities, as they can control and directly measure the responses of the entire community to population perturbations (Xiao et al. 2017). However, creating a dynamic network that includes larger animals is difficult due to the large amount of data required, and would likely require many years of work. For example, each predator-prey interaction would require data on the amount of biomass or individuals that specific predator removes from the prey population, in addition to the total populations of both species (such as what is used in Lotka-Volterra equations).,Such a massive undertaking would likely be the result of a full research program, or at the least an entire PhD thesis (if the student incorporated methods of allometrically estimating dynamics) (Berlow et al. 2004, Ebenman et al. 2004, Ebenman and Jonsson 2005).

Final Thoughts

I developed community viability analysis to help advance the study of species interactions in conservation ecology. Although there is a myriad of factors that go into investigations of this nature, I feel there is one lesson to take away from this thesis that can provide guidance to conservationists attempting to utilize community ecology. We must have an idea of what we are looking for if we are to unravel the mechanisms that drive communities. My initial method of approaching community-related problems was to choose a system and look for important interactions to study. This was a poor approach due to the overwhelming complexity of ecosystems. Although I was familiar with the ecological theory behind interactive effects, such as apparent competition and trophic cascades, the likelihood of identifying conservation-influencing relationships between species is low when essentially conducting random interaction selection. This lesson should hold significance for environmental managers responsible for preserving specific ecosystems: adopting a focal point within the community, be it a species or a group of species, and then examining the interactions that influence that point, may be a more effective approach than attempting to look for keystone interactions that impact the entire system.

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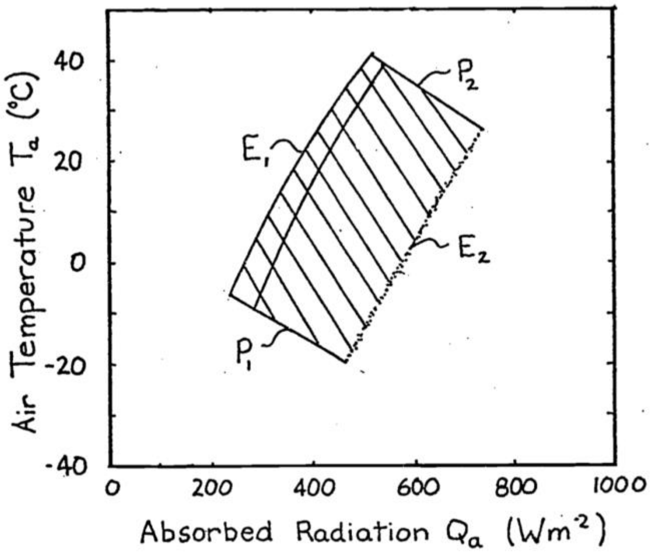

Figure 7-1 An example of a climate space diagram. The northwest (E_1) hatched region and southeast (E_2) boundaries are due to the physical environment. The southwest (P_1) and northeast (P_2) boundaries are due to the physiology of the organism. Figure from Stevenson and Kearney (2020).

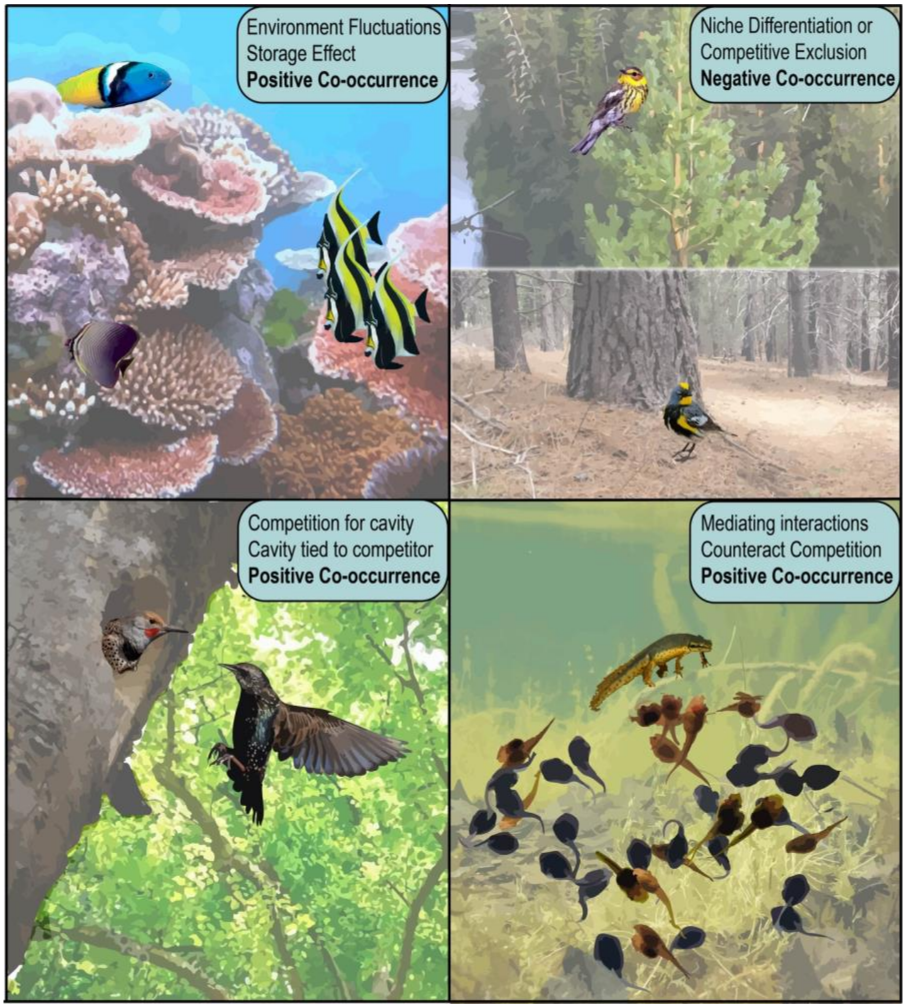

Figure 7-2 Four possible examples of co-occurrence in interspecific competition. No species can be a superior competitor all the time in areas where the environment fluctuates dramatically, "storing" their gains in good years to buffer against bad years and resulting in positive co-occurrence (top left). Dominant competitors can also exclude their competition from foraging habitats, resulting in negative co-occurrence (top right). A resource may also be tied to the presence of one of the competitors – such as how nest cavities are created by woodpeckers – resulting in positive co-occurrence (bottom left). Finally, the effect of a competitively dominant species can be negated by the presence of a predator, resulting in positive co-occurrence (bottom right). I created this figure for my review paper on co-occurrence.

Figure 7-3 Four possible examples of co-occurrence in predator/prey interactions. Predator hunting can deplete prey numbers in the area, resulting in negative co-occurrence (top left). However, predators can then shift their foraging to areas with more prey, resulting in positive co-occurrence (top right). Prey are also capable of avoiding areas where their predators hunt, creating a landscape of fear that results in negative co-occurrence (bottom left). Finally, prey that are hunted opportunistically can randomly co-occur with their predator, so long as the predator hunts equally across all habitats where said prey are found (bottom right). I created this figure for my review paper on co-occurrence.