(SOCIO-)ECOLOGICAL TOOLS AND INSIGHTS FOR A CHANGING CLIMATE

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Ву

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(SOCIO-)ECOLOGICAL TOOLS AND INSIGHTS IN A CHANGING CLIMATE

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DEDICATION

For Emelyn Piotter,

a dear friend and colleague,

a great scientist, artist,

and champion for the natural world;

you are deeply missed.

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	
LIST OF FIGURES	VI
LIST OF TABLES	VII
ABSTRACT	VIII
CHAPTER 1: UNINTENDED CONSEQUENCES? LETHAL SPECIMEN COLLECTION ACCELERATES CONSERVATION CONCERN	; WITH 1
SPECIMEN COLLECTION AMID INSECT DECLINES	
A CASE STUDY FEATURING BUMBLE BEES	
MATERIALS AND METHODS	9
RESULTS	11
Author Contributions	
DATA AVAILABILITY	13
Acknowledgements	
References	14
SUPPLEMENTARY MATERIALS	
CHAPTER 2: PROGRESS AND POTENTIAL OF ACOUSTIC MONITORING TECHNOLOGIES FOR	25
INTRODUCTION	
ACOUSTICS OF THE BUMBLE BEE COLONY	
BUMBLE BEE ACOUSTICS ON OR NEAR FLOWERS	
POTENTIAL APPLICATION: USING AM I TO STUDY PATHOGENS	
ACKNOWLEDGEMENTS	
KEFERENCES	
CHAPTER 3: FLIGHT ACOUSTICS PROVIDE CUES FOR TRACKING MORPHOLOGICAL TRAITS C	OF BUMBLE
BEES AND PHENOLOGICAL PHASES OF COLONIES	
Abstract	
INTRODUCTION	
Methods	53
RESULTS	57
DISCUSSION	58
Author Contributions	62
Data Availability	62
ACKNOWLEDGEMENTS	62
References	63
CHAPTER 4: SHOW-ME RESILIENCE: ASSESSING AND RECONCILING EXPERT PERCEPTIONS (
RESILIENCE IN RURAL MISSOURI	
Abstract	79
INTRODUCTION	80
METHODS	83
RESULTS	
Discussion	96
AUTHOR CONTRIBUTIONS	
ACKNOWLEDGEMENTS	
KEFERENCES	

SUPPLEMENTARY MATERIALS	
CHAPTER 5: CONCLUSIONS	127
VITA	

v

LIST OF FIGURES

Figure 1.1. Sampling approach and conservation awareness over time	18 19
Supplementary Figure 1.1. Total bumble bee publications over time	20
Supplementary Figure 1.2. Pinned bumble bee specimens over time	21
SUPPLEMENTARY FIGURE 1.3. BUMBLE BEE SAMPLING INTENSITY OVER TIME.	22
SUPPLEMENTARY FIGURE 1.4. GOOGLE SCHOLAR PUBLICATIONS OVER TIME	23
Figure 2.1. Photos of bumble bee, colony, and microphone	43
Figure 2.2. Waveform and spectrogram of bumble bee fanning	44
FIGURE 2.3. WAVEFORM AND SPECTROGRAM OF BUMBLE BEE ARRIVAL BUZZ.	45
FIGURE 2.4. WAVEFORM AND SPECTROGRAM OF BUMBLE BEE DEFENSIVE BUZZING.	46
FIGURE 2.5. SPECTROGRAM AND POWER SPECTRAL PLOT OF BUMBLE BEE FLIGHT AND POLLINATION BUZZES.	47
Figure 3.1. Typical life cycle of a bumble bee colony	70
Figure 3.2. Linear regression between fundamental frequency and body size of bumble bees	71
FIGURE 3.3. DISTRIBUTIONS OF FLIGHT BUZZ FUNDAMENTAL FREQUENCY BY CASTE AND SPECIES.	72
Figure 3.4. Ridge plot of Bombus appositus.	73
Supplementary Figure 3.1. Ridge plots of Bombus nevadensis colonies	76
Supplementary Figure 3.2. Ridge plots of Bombus sylvicola colonies.	77
Supplementary Figure 3.3. Ridge plots of other monitored <i>Bombus spp.</i> colonies	78
Figure 4.1. Conceptual diagram of the steps to resilience	08
FIGURE 4.2. EXPERT CONCEPTUALIZATION OF THE MEANING OF RESILIENCE	09
FIGURE 4.3. EXPERT-IDENTIFIED THREATS FACING RURAL MISSOURI	10
Figure 4.4. Expert-identified concrete steps1	11
Figure 4.5. Vulnerabilities and concrete steps	12
FIGURE 4.6. SANKEY DIAGRAMS OF SYSTEMS THINKING AND CONCRETE STEPS	13

LIST OF TABLES

TABLE 1.1. NON-LETHAL METHODS FOR INVESTIGATION OF BUMBLE BEES	24
TABLE 2.1. APPLICATIONS OF AMT IN INVESTIGATIONS OF BUMBLE BEES.	48
Supplementary Table 3.1. Flight buzz frequency and intertegular distance by species and caste.	74
TABLE 4.1. LIST OF INTERVIEWED POSITIONS AND AGENCIES, INSTITUTIONS, OR ORGANIZATIONS.	114
TABLE 4.2. THREATS TO RURAL MISSOURI IDENTIFIED BY INTERVIEW PARTICIPANTS	115
TABLE 4.3. EXPERT-IDENTIFIED CONCRETE STEPS ALONG WITH THE COMMUNITY CAPITAL TO WHICH THEY MOST CLOSELY	
CORRESPONDS	122

(SOCIO-)ECOLOGICAL TOOLS AND INSIGHTS FOR A CHANGING CLIMATE

ABSTRACT

In one way or another, climate change is impacting all social, economic, and ecological systems on the planet. Scientists worldwide warn of catastrophic and irreversible damage to social and ecological systems in absence of rapid, far-reaching, and unprecedented shifts in energy and land use. Yet, many social systems continue to operate business-as-usual, and decision-making across multiple levels of social organization continues to neglect the use of scientific evidence to minimize long-term risk. Contemporary biodiversity losses are occurring on scales that surpass the major extinction events in geological records, threatening the loss of critical ecosystem services, such as pollination, that underpin myriad facets of human societies as well as ecosystem resilience. In my dissertation, I call into question conventional lethal sampling approaches for bumble bees, an economically and ecologically important pollinator group, and simultaneously advance non-lethal techniques. Additionally, with aims to advance climate action in Missouri, I investigate how state-level decision-makers and land-use experts are thinking about climate resilience in the context of rural Missouri.

More specifically, in chapter one, I explore how the use of lethal sampling, a traditional entomological sampling approach, has changed over time with evidence of numerous declining bumble bee populations. Global declines of bumble bees are welldocumented and have spurred widespread conservation efforts. However, lethal sampling continues to serve as a common entomological practice despite conservation concern. In collaboration with a research team from the Galen lab, I review 411 bumble bee-related publications from 1970–2019 alongside records from over 230,000 pinned bumble bee pinned specimens to discern whether lethal sampling has decreased with heightened conservation awareness and availability of novel non-lethal sampling methods. Our literature review shows that lethal sampling of bumble bees has instead kept pace with publication output. Interestingly, the highest rates of lethal sampling are found in papers demonstrating conservation awareness and persist despite low scholarly impact in comparison to papers based on non-lethal alternatives. Facing numerous pressures, vulnerable bumble bee populations may be less resilient to traditional sampling norms than broadly assumed. We highlight non-lethal sampling alternatives and underscore the need for proactive, empirically informed sampling guidelines that reflect the conservation needs of bumble bee pollinators.

In chapter two, I review advances in acoustic monitoring technologies for bumble bees and discuss potential applications. Acoustics show promise for use in bumble bee investigations, as bumble bees create a range of distinguishable sounds while flying, sonicating (buzzing on flowers to eject pollen) and interacting within the colony, making them amenable for acoustical surveys. Acoustics offer an alternative sampling approach that is affordable, scalable, and non-destructive, with potential to augment conservation and agricultural practices. Application of AMT to investigate bumble bees is still nascent in development, and improvements are needed across all stages of the AMT process, from sensor technologies and data transfer to audio classification and user interfaces. I review the sound-producing activities of bumble bees, highlighting extant research and

ix

underscoring opportunities for further investigation. I conclude by reiterating the importance of cross-disciplinary collaboration between ecologists and computer scientists to monitor and manage species of conservation concern.

In chapter three, I advance acoustic applications in bumble bee research using a combination of field work and literature surveys. Leveraging technological advancements that allow for remote monitoring and automated processing of information, such as acoustics, has been identified as a key next step for pollinator research. I test whether the acoustics of bumble bee flight buzzes can be used to track morphological traits and phenological phases of foragers throughout the season. I used flight cage experiments and a literature survey to extend data on the relationship between the fundamental frequency of flight buzzes and body size across castes and species. I then use these data to test whether acoustics can track caste size dimorphisms across species and variation in intraspecific worker size. Next, I acoustically monitored wild bumble bee colonies in subalpine and alpine ecosystems in Colorado, United States, where I corroborated acoustic data with in-person observations to distinguish phenological phases (queens only vs. queens and workers) of the colonies. I demonstrate that remotely monitoring bumble bee colonies with acoustics can provide large datasets with cues for different morphological and phenological features of the colony and discuss potential applications.

In chapter four, I investigate climate resilience in rural Missouri. Rural areas of the United States – approximately 97% of the total land area – often lag urban areas in the implementation of climate adaptation practices. Understanding how perspectives vary within and among actors in the rural land use decision-making ecosystem can help to identify catalysts and constraints for climate change adaptation planning and action. I conducted semi-structured interviews with 23 experts – policymakers, state/federal agency professionals, non-profit organization leadership, and researchers – at the nexus of rural land use, agriculture, natural resources, and conservation in Missouri to elucidate conceptualizations of climate resilience. I aligned interview questions with NOAA's Steps to Resilience to investigate participants' perceptions of the major vulnerabilities of rural communities and landscapes, threats to rural vitality, and potential concrete steps for making rural Missouri more resilient in the face of climate change. I then discuss examples of climate resilience in Missouri and conclude with suggestions for potential next steps towards climate resilience in the state.

CHAPTER 1: Unintended consequences? Lethal specimen collection

accelerates with conservation concern

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Specimen collection amid insect declines

Global declines of arthropods have garnered widespread attention because their loss threatens critical ecosystem services such as decomposition, pest control and pollination (Sánchez-Bayo et al., 2019 and citations therein). Although the extent of the 'insect apocalypse' is currently under debate (Didham et al., 2020), insect declines are well-documented worldwide, with habitat loss, agricultural intensification and climate change cited as primary drivers of losses in biomass and diversity (Raven and Wagner 2021). These losses have stimulated conservation action and research effort. However, lethal sampling continues as a common entomological practice despite conservation concern and increasing research. Facing myriad extant pressures, vulnerable insect populations may be less resilient to traditional sampling norms than broadly assumed. We raise as an emerging concern the potentially damaging yet unknown impacts of contemporary specimen collection on wild insect populations. Reviewing the literature on temporal sampling trends in bumble bees as a case study, we highlight the value of non-lethal sampling alternatives and underscore the need for proactive, empirically informed sampling guidelines that reflect taxa-specific conservation needs. Conventional entomological practices for surveys and vouchers assume that lethal sampling has little impact on populations in the wild (e.g., Layberry and Jones 2009). This assumption is based on the rationale that specimen collections remove a trivial fraction of individuals from wild populations. However, for insect species that are rare, distributed in few, isolated sites, or demonstrably vulnerable to anthropogenic disruption, this assumption may not hold. Smaller populations in fragmented habitats have limited gene flow (Jha, 2015), greater susceptibility to genetic drift (Lozier et al., 2011) and are less resilient to repeated lethal sampling (Rodríguez-Estrella and Moreno, 2006). When multiple biotic and abiotic processes act to reinforce and accelerate population decline, such vulnerable populations may succumb to 'extinction vortices' (Gilpin and Soulé, 1986). The resilience of insect populations to lethal sampling depends on life history, mobility, phenology and habitat size, attributes that differ among species and populations. It follows that tolerable sampling thresholds could vary among taxa over their geographic distributions. Yet few studies have investigated the biological impact of lethal sampling on wild insect populations.

Conservation awareness can spur funding for research and public interest programs, accelerating the development of technologies and methods to better monitor species of conservation concern. Increasingly, scientists are applying non-destructive techniques to investigate taxa ranging from charismatic megafauna to arthropods. Although non-destructive sampling of insects poses challenges, technological innovations have provided new opportunities to study different facets of insect life histories without killing them. For example, non-lethal techniques such as genetic analyses, videography and acoustic sampling have been applied to a broad scope of investigation including taxonomy, behavior, evolution, and ecology over the last two decades (see Barlow and O'Neill, 2020 for review). However, absent wider adoption of non-lethal methods, the intensity of lethal sampling will be driven by the size and effort of the research community.

Although specimen collection has been the subject of lively debate over several decades (Rocha et al., 2014 and citations therein), it is accepted as standard research practice (Salvador and Cunha, 2020). Voucher specimens have proven value in cross-temporal studies of taxonomy, natural history, global change biology, ecology and evolution (e.g., Vaudo et al., 2018; Meineke et al., 2019). Nonetheless, most would agree that benefits of research practices including lethal sampling must be balanced against their potential costs to biodiversity and ecosystem services (Winker et al., 2010). In other words, an analysis of the costs and benefits associated with lethal sampling should inform its use.

A case study featuring bumble bees

Has use of lethal sampling changed over time in response to growing conservation concern? We consider this question in bumble bees (Bombus), as they are economically and ecologically important pollinators with documented declines worldwide. Population sizes of more than 60% of extant bumble bee species are decreasing and approximately 45% are classified by the International Union for Conservation of Nature as vulnerable, endangered, or critically endangered (IUCN, 2020). Local extinction and range compression are driven by habitat loss, agrochemicals, disease and climate change, threatening pollination services in both agricultural and natural ecosystems (Dicks et al., 2020). Bumble bee declines have stimulated a proliferation of conservation research over the last two decades (Cameron and Sadd, 2020), and while research interest on vulnerable taxa can expedite conservation action, research methods themselves may conflict with conservation goals.

To investigate temporal sampling trends we conducted a literature review of 411 bumble bee-related journal articles published from 1970–2019. Because specimen collection data were lacking in our surveyed publications, we evaluated sampling intensity over the same time period using an open-source database of more than 230,000 pinned bumble bee specimens as a proxy. We asked how the rate of lethal sampling has changed over time and specifically whether it has declined with increasing conservation awareness. We classified conservation awareness binomially (i.e. 'aware' or 'unaware') based on the paper's use of the terms "decline", "biodiversity", or "conservation" (see Materials and Methods).

Our review of more than 400 publications and 230,000 specimens reveals an accelerating increase in bumble bee research over the past fifty years (Supplementary Figure 1.1), regardless of whether studies use lethal or non-lethal sampling methods (Figure 1.1a). The overall rate of lethal collection in North America has accelerated (Supplementary Figure 1.2) despite a decline in bumble bee sampling intensity per publication (Supplementary Figure 1.3). Conservation awareness does not appear to drive the modest decrease in bumble bee sampling intensity over time. To the contrary, the number of papers demonstrating conservation awareness increased sharply in the early 1990s (Figure 1.1b). Interestingly, papers with conservation awareness were associated with the highest rates of lethal sampling (Figure 1.1c). These results indicate that despite a growing volume of bumble bee research, including evidence that some bumble bee species are threatened, researchers are as likely to sample lethally now as in the mid-1900s.

There are a number of reasons to expect impacts of lethal sampling on wild bumble bee populations to be more negative now than a half a century ago. First, research has become more concentrated in a smaller area of suitable bumble bee habitat. Currently, only ~13% of global land area is protected, and it is uncertain how these protections will fare under increasing food and energy demands (Golden Kroner et al., 2019). Future agricultural expansion and intensification of agrochemical application is anticipated (Ray et al., 2013), threatening habitat for pollinators, including bumble bees. Second, climate change is intensifying, with more extreme climate events (Collins et al., 2013) impacting pollinator health, floral communities, and for bumble bees, population persistence (Dicks et al., 2020). Third, global transit of commercial bumble bees for crop pollination is facilitating the spread of diseases and pressures from invasive species, leading to declines in native congeners (Dafni et al., 2010). Last, the synergistic effects of these combined stressors on small populations with low genetic diversity are likely to accelerate and exacerbate species declines (e.g., Gilpin and Soulé, 1986; Goulson et al., 2015). Taken together, current and future projections of anthropogenic pressures imply a rising risk of extinction for many bumble bee species and populations worldwide. As

these pressures escalate even the relatively modest threats associated with lethal sampling may amplify losses for bumble bee populations.

Numerous non-lethal approaches were featured in the papers we investigated, including DNA analyses, photographic and acoustic observations. These research tools offer alternatives that lessen the impact of specimen collection on wild populations. The use of commercial bumble bees for research has also become widespread since the 1990s (n = 63, or approx. 16% of all papers from this study). Although commercial bumble bees can spread pathogens and competitively displace other pollinators (e.g., Dafni et al., 2010), they are valuable for laboratory studies that investigate host-pathogen dynamics, behavior, evolution, and physiology, and for working out methods before field application (e.g., Holehouse et al., 2003). Commercial colonies and non-lethal techniques provide useful data to future scientists and allow us to answer important questions about bumble bee colonies, populations and communities (Table 1; see also review by Barlow and O'Neill, 2020).

Voucher collections alone are unlikely to represent a primary cause of population losses in insects. Only in rare instances have collections been shown to contribute to population loss or species extinction (see Minteer et al., 2014 for review). Furthermore, we do not claim that annual collections of ~6000 bumble bees per se (in line with our results from the SCAN database) from across North America have had marked negative impacts on most wild populations. However, the current impact of specimen collections on wild bumble bee populations is simply unknown. For bumble bees, colony size predicts fitness (e.g., Müller and Schmid-Hempel, 1992), so it follows that lethal sampling before gynes are produced could have negative impacts on colony productivity. Yet, this research question is largely unexplored. More data on fitness impacts of removing individuals from colonies and the extent to which impacts vary among species and populations would help pinpoint taxa with high vulnerability to lethal sampling. Instead, researchers seem to have assumed without evidence that specimen collection is innocuous during a time when the practice of killing bees is increasingly widespread.

While we recognize that journal access by search engines can be prone to temporal biases, an identical Google Scholar search revealed similar trends to those cited here, indicating that our results are not search engine specific (Supplementary Figure 1.4). Our measurement of conservation awareness is coarse-grained but tracks largescale trends in the research community (Cameron and Sadd, 2020). The increased volume of lethal sampling may reflect the community's response to the urgency of knowledge about imperiled species. Unfortunately, harmful impacts of this approach are likely to increase if the number of researchers continues to rise as bumble bee populations decline.

When it comes to reducing lethal sampling in insects of conservation concern, the onus is on the research community, including editorial boards and reviewers for academic journals and granting agencies, to promote responsibility. More care can be taken to ensure that current collection efforts align with taxa resilience. We urge professional societies to require justification for lethal sampling and to mandate deposition of specimens into open access collections upon publication. Additionally, we suggest that basic information of collections, such as number of specimens of each species and caste as well as where they are housed, should be made clear in all publications.

Current and proposed collection efforts already exceed taxonomists' capacity to identify and describe (Portman and Tepedino, 2021). Simultaneously, more aggressive passive sampling methods like bowl traps are scaling up – despite known taxonomic biases and monitoring limitations – producing massive collections of bees that require considerable time, money, expertise, and other resources to process (Portman et al., 2020). A related issue is that existing databases that, like SCAN, provide access to specimen records, are largely under-curated and under-used. SCAN is funded and maintained by the National Science Foundation and currently comprises over 21.8 million freely accessible digital records of more than 238,000 species, but requires more dedicated maintenance and curation to improve data quality. Our point is that greater effort should be made to measure the impact of collections and to standardize access to and usefulness of museum specimen data already available (Figure 2). Protocols that promote the utility of existing specimen collections should be championed and should accompany strides to reduce future collection effort.

We encourage investigators to follow the 'Insect Collectors Code' (Trietsch and Deans, 2018), to cooperate with other researchers in evaluating the resilience of bumble bees and other insects to repeated lethal sampling, and to develop and follow realistic, evidence-based protocols when sampling (Strange and Tripodi ,2019; Woodard et al., 2020; Tepedino and Portman, 2021). Outlining clear and consistent sampling protocols – ones that embrace non-lethal techniques, take advantage of extant museum specimens and, when necessary, use empirically informed lethal sampling more selectively – is imperative for investigation of bumble bees and other vulnerable insects moving forward. These efforts will facilitate a more forward-thinking, innovative, and truly conservation motivated research community.

Materials and methods

Review of journal articles

In March 2020, we used the Web of Science database to find peer-reviewed papers based on bumble bee observations. Using "Bombus" along with one or more of the terms, "abundance", "distribution", "pollination" and "occurrence", the search generated 5256 qualified papers published between 1895–2019. Too few (n = 41) papers were found from 1895–1969 for meaningful comparisons, so we limited our sample to 1970–2019 (n = 5215). We randomly subsampled approximately 8% of papers per decade for in-depth review. To avoid pseudo-replication, when multiple papers had the same first author, one was chosen at random. Fifteen papers were eliminated as they were not suitable for analyses (reviews and data papers) or had unclear sampling methods, resulting in 411 papers total. For each journal article, we assessed whether lethal and/or non-lethal sampling techniques were used and whether the paper was explicitly written to have conservation relevance. Sampling method was treated as a binomial variable -'one' if lethal methods were used and 'zero' if only non-lethal methods were used. We characterized conservation awareness by searching for the terms "conservation", "biodiversity", "decline" or their derivations in the main body of the paper, excluding the literature cited. Conservation awareness was assigned by giving papers containing any of

these terms a score of one and those lacking all of the terms a score of zero. When not stated explicitly, lethality was inferred if the authors mentioned pinning collected specimens, housing collections in museums or storing bees in preservatives. The use of commercial bumble bees for laboratory experiments was considered a non-lethal method, and accordingly, the euthanization of commercial bees was not considered a form of lethal sampling.

Bumble bee sampling intensity

Sampling intensity was not directly investigated in the literature analysis because data on the number of bees killed per paper were not available for most papers. Instead, to ask whether reductions in sampling intensity might offset increases in the number of studies using lethal sampling, we constructed a proxy for annual sampling intensity by dividing the total number of pinned bumble bee specimens in the open-source Symbiota Collection of Arthropods Network (SCAN 2020) database by the number of journal articles from the search engine results for each year of our study. We obtained records for 233,327 unique pinned specimens in North America from 1970-2019 matching the search criteria of genus = Bombus. Because these data were collected in early 2020, the year 2019 was excluded from analyses as investigators likely have not had ample time to submit specimens to databases. Therefore, we used 232,566 specimens from 1970-2018 for our analyses. To ensure that individual specimens were not counted more than once, we used the *distinct()* code from the *dplyr* package to remove duplicate rows. The SCAN database is primarily focused on North American specimens, and so we filtered our Web of Science search engine results for papers specific to North America (n = 1231) to estimate annual sampling intensity.

Statistical analyses

To analyze trends in the volume of journal publications (n = 5215) over time we used a log-linear model for the number of papers as a function of year of publication. To compare how rates of lethal and non-lethal sampling have changed over time, we used analysis of covariance (ANCOVA) with sampling method (i.e., lethal vs. non-lethal) as the categorical variable, year of publication as the continuous variable, and number of publications per year as the outcome variable. Number of papers per year was transformed logarithmically to meet assumptions of normality.

We investigated the change in conservation awareness over time using a logistic regression with conservation awareness as a function of year of publication. We used a Chi-square contingency test to assess whether conservation awareness was associated with sampling method (lethal vs. non-lethal). In addition, a logistic regression was used to test whether temporal changes in the probability of lethal sampling depended on conservation awareness. Here, conservation awareness was the categorical variable, year, the continuous variable, and sampling method the outcome variable. Because both bumble bee sampling intensity and specimen counts over time were parabolic after being log-transformed, we modelled each in separate analyses using a quadratic regression with year as the continuous variable. All analyses were conducted in R (version 3.5.2; R Core Team 2018).

Results

Review of journal articles

Total publications per year based on bumble bee observations have increased loglinearly over the last 50 years (y = -46.64 + 0.02x, adjusted r2 = 0.95, p < 0.0001; Supplementary Figure 1.1). ANCOVA indicated that neither sampling method nor its interaction with publication year explained a significant portion of the variance in publication rate (p > 0.52 for both). Over the 50-year survey, approximately 44% of all papers used lethal sampling despite a nearly tenfold increase in the number of papers published per year during the 2010s compared to the 1970s (Figure 1.1a).

The probability of papers exhibiting conservation awareness increased more than thirtyfold from the 1970s to the 2010s (logistic regression, z-score = 7.969, p < 0.0001; Figure 1.1b), and papers that exhibited conservation awareness were more likely to use lethal sampling than papers that did not (χ 2 = 8.135, df = 1, p = 0.004). While conservation awareness predicts the probability of lethal sampling in a given year (logistic regression, z-score = 2.159, p = 0.0004), the direction of the effect is contrary to our expectation. Papers with conservation awareness showed an increase in the probability of lethal sampling from ~42-54% over time while the probability of lethal sampling declined from ~57-27% in those without conservation awareness (Figure 1.1c). *Bumble bee sampling intensity*

Using an index of specimens killed per year based on SCAN specimens from North America, we found that fewer bees were killed per paper in recent decades compared to the mid-1900s (y = 3257.44 - 3.25x + 0.0008x2, adjusted r2 = 0.49, p < 0.0001; Supplementary Figure 1.3). However, this trend is too weak to offset the increase in publication volume. Instead, the total number of bumble bee specimens in SCAN has risen quadratically since conservation awareness began to increase in the early 1990s (y = 3666.15 - 3.67x + 0.0009x2, adjusted r2 = 0.32, p < 0.0001; Supplementary Figure 1.2), from an annual average of 2577 specimens per year in the 1990s to a peak of 6644 in the 2010s.

Author Contributions

All authors contributed to the development of the project as well as data collection. ZM collated and analyzed data, developed figures, and wrote the manuscript with feedback from all authors.

Data Availability

Data and code are available upon request. Please contact the author at

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Figure 1.1. Sampling approach and conservation awareness over time.

(a) Number of publications using lethal (blue circles, solid line) vs. non-lethal (green triangles, dashed line) sampling methods in bumble bee investigations from surveyed literature (n = 411). Regression line represents model prediction. Note use of log scale on the y-axis. (b) Probability of papers exhibiting conservation awareness as a function of year of publication. (c) Probability of lethal sampling in bumble bee research for conservation aware (blue circles, solid line) and unaware (purple triangles, dashed line).
Best fit lines based on binomial logistic regression are shown with likelihood of lethal

sampling (0 = non-lethal, 1 = lethal) plotted as a function of conservation awareness.

Grey shading indicates 95% confidence intervals.



Figure 1.2. Bumble bee specimens.

(a) Curated bumble bee specimens are underutilized and offer myriad opportunities for non-lethal investigations. (b) Curated museum collections may be especially useful for studying taxa of conservation concern, such as *Bombus pennsylvanicus*, a species with declining populations currently classified as 'vulnerable' by IUCN RedList. Photo credits:

Christian A. Perez-Martinez



Supplementary Figure 1.1. Total bumble bee publications over time.

Total bumble bee publications (n = 5215) from Web of Science search criteria each year from 1970-2019. Regression line represents model prediction and grey shading indicates 95% confidence intervals. Note use of log scale on the y-axes.



Number of pinned North America bumble bee specimens per year from the SCAN database (SCAN 2020). The blue trend line represents the prediction of the quadratic regression and grey shading indicates 95% confidence intervals. Note use of log scale on the y-axis.



Supplementary Figure 1.3. Bumble bee sampling intensity over time.

The number of SCAN specimens divided by the number of Web of Science papers per year from 1970-2018 (SCAN 2020). Grey shading indicates 95% confidence intervals around quadratic regression line. Note use of log scale on the y-axis.



Supplementary Figure 1.4. Google Scholar publications over time.

Number of publications using bumble bee data in each decade from 1970-2019 using Google Scholar instead of Web of Science. Grey shading indicates 95% confidence interval around the regression line. Note use of log scale on the y-axis.
Non-lethal method	Applications		
DNA or Molecular Analyses	Taxonomic identification (Holehouse et al., 2003); conservation genetics/genomics (Lozier & Zayed 2017, Chaline et al., 2004)		
Acoustics	Landscape pollination services (Miller-Struttmann et al., 2017); behavioral ecology (Galen et al., 2019); co-evolution (De Luca & Vallejo-Marin 2013); colony activity (Heise et al., 2020)		
Fecal samples	Pathogens (Graystock et al., 2013); gut microbiome (Zhao 2018); pollen surveys (Lynn et al., 2020)		
Photo/video	Identification to morphospecies (Thompson & Zung 2015); pollination biology (Steen & Orvedal 2011)		
Telemetry/radar	Distribution/dispersal (Hagen et al., 2011); nest site selection (Makinson et al., 2019); see Mola & Williams 2019 for review		
Mark-Recapture	Population dynamics (Boyle et al., 2018); foraging range (Mola & Williams 2019)		
Museum specimens	Pathogens, phylogenetics, population dynamics (Vaudo et al., 2018); biodiversity/conservation (Colla et al., 2012); dietary breadth (Simanonok et al., 2020)		

Table 1.1. Non-lethal methods for investigation of bumble bees

CHAPTER 2: Progress and Potential of Acoustic Monitoring Technologies for Investigating Bumble Bees

Introduction

Pollination is a vital ecosystem service for both natural and agricultural ecosystems. Most flowering plants – including many staples in the human diet such as fruits, vegetables, and nuts – require animals for pollination. The majority is done by over 20,000 species of bees, some of which are managed commercially to provide these services. The global industry of pollination is valued at \$153 billion annually and is increasing in demand to meet the needs of a growing human population (Gallai et al., 2009). However, both managed and wild bees, especially the ecologically and economically important bumble bees (*Bombus spp.*), are suffering alarming declines worldwide, presenting serious implications for food security and biodiversity. Despite numerous pleas by farmers and scientists for improved management and monitoring methods (Graystock et al., 2013, Goka et al., 2001) precision techniques for these essential pollinators are still lacking.

Recent advances in acoustic monitoring technologies (AMT) show promise for bumble bee investigations. Bumble bees create a range of distinguishable sounds while flying, sonicating (buzzing on flowers to eject pollen) and interacting within the colony, making them amenable for acoustical surveys (Figure 2.1). While acoustic-based techniques have been used to study bumble bees, most of these efforts pre-date advancements in computer programming, machine learning and automation, and thus have not been widely adopted. Current standard practices in bumble bee monitoring include netting, trapping, and in-person observations, which are laborious, costly, and often require lethal collection of bumble bees. AMT offer an alternative approach that is affordable, scalable, and non-destructive, with potential to augment conservation and agricultural practices. The sounds produced by bumble bees may be useful to researchers and farmers regardless of their implications for survival and reproduction. The types of questions that can be answered will differ, as some bumble bee sounds produced have roles in communication with other bumble bees or with predators – e.g., 'buzz runs' and defensive 'hisses' – making them amenable for eavesdropping on colony behavior; others are by-products of non-communicative activities – e.g., flight buzzes – providing opportunities to remotely track and monitor bees foraging on flowers. This review focuses on audio signals that are distinguishable rather than biological signals that are communicative; the former includes the latter, but not vice versa.

Application of AMT to investigate bumble bees is still nascent in development, and improvements are needed across all stages of the AMT process, from sensor technologies and data transfer to audio classification and user interfaces. Here, I review the sound-producing activities of bumble bees, highlighting extant research and underscoring opportunities for further investigation. For each sound or soundscape, I emphasize the acoustic features that make it unique to particular behaviors and discuss how AMT could benefit bumble bee research and agriculture. In particular, I examine sounds produced from (1) within bumble bee colonies and from (2) bumble bees on or near flowers; (3) I then discuss the potential application of AMT to study a major threat to bumble bees; and (4) I conclude by reiterating the importance of cross-disciplinary collaboration between ecologists and computer scientists to monitor and manage species of conservation concern.

Acoustics of the Bumble Bee Colony

There are over 250 species of bumble bees, and they are distributed in most temperate and mountainous regions worldwide (Goulson et al., 2010). They are important pollinators for many wildflowers and crops such as tomatoes and berries. Like honey bees and ants, bumble bees are social, exhibiting both cooperation and division of labor within their colonies. Bumble bee colonies vary in size from 20-400 individuals depending on the species and provide shelter for many stages of life history including egg-laying, wax cell construction, rearing workers, resource caching and producing the next season's queen bees. Fertilized queens overwinter underground then begin colonies anew the subsequent spring. Wild bumble bees establish their colonies in old animal burrows or other small cavities; colonies reared for commercial use in crop pollination are housed in small plastic or wooden containers that can be moved among greenhouses during flower blooms. The soundscape of bumble bee colonies is abuzz with a variety of sounds, many of which have distinguishable acoustical characteristics. To date, bumble bee colony bioacoustics research has been concentrated in four areas: (1) thermoregulation, (2) foraging, (3) defense and (4) dominance.

Thermoregulation

Bumble bees thermoregulate their nests to maintain suitable conditions for rearing brood. Colony task allocation between brood maintenance and thermoregulation tracks ambient temperature and is acoustically detectable (Vogt, 1986). In warmer than ideal conditions for rearing brood (greater than ~32 C for *B. terrestris*), bumble bees induce heat loss via convection by fanning their wings inside the colony, creating a sustained broadband acoustic signal with fundamental frequencies between 180-200 Hz (Heidelbach et al., 1998; Figure 2.2). In colder temperatures, bumble bees are able to warm themselves by two mechanisms: (1) 'non-shake shivering', or tetanus (rapid, fine muscle contractions that cause little if any external motion or sound – Heinrich & Esch, 1994); and (2) by decoupling their wings and rapidly contracting thoracic flight muscles (i.e. 'shivering' – Esch et al., 1991). Bumble bees can warm their thoraxes up to 20 degrees C warmer than ambient temperature and use this mechanism to incubate brood and maintain nest temperature (Heinrich, 1975). The amplitude from the sound generated by a shivering bumble bee positively correlates with metabolic heat flux, suggesting that acoustic monitoring serves as a proxy for heat production in bumble bee colonies (Schultze-Motel & Lamprecht, 1994).

The degree to which these sounds are communicative to nestmates is unknown, but they are contextually distinguishable and informative, nonetheless. AMT offers a lowcost, passive solution to monitoring important colony activity such as the behavioral tradeoffs between thermoregulation and brood maintenance or foraging activity. Scientists may learn how behavioral tradeoffs induced by extreme weather events affect colony survival and farmers learn when to intervene if colonies are under thermal stress. *Foraging*

Bumble bees gather pollen and nectar from flowers to feed the developing brood of their colony. As they come and go from the colony and interact with nestmates within the colony, they create distinguishable sounds associated with foraging that can be used to track behavior and inform management decisions. The efficiency with which social bees can relay information about foraging resources has implications for the survival of the colony. Honey bees and some tropical bees perform vibratory 'dances' in which they encode messages that inform nestmates of direction, distance, and height of resources (Von Frisch, 1967, Nieh, 2004). While bumble bee communication of floral resources is regarded as rudimentary and thought to occur primarily through pheromones, several reports describe hurried 'buzz runs' to recruit other workers to forage for novel nectar resources: after arrival to the colony, foragers move rapidly about the colony, bumping into and climbing over other bees, depositing nectar into honeypots, and fanning their wings audibly in rapid, pulse-like buzzes (Dornhaus et al., 2003, Oeynhausen & Kirchner, 2001; Figure 2.3).

Other reports of foraging related sounds include the 'humming' or 'buzzing' sounds between the queen and workers and the larvae while feeding (Duchateau, 1989, Katayama, 1998) and 'leaving sounds' (Heidelbach et al., 1998, Dornhaus et al., 2003). There is also note of 'honking' in workers and 'barking' in queens, but these are not described quantitatively, and their biological significance is unknown (Heidelbach et al., 1998). Upon return to the nest, B. impatiens foragers use bursts of vibrations at ~600 Hz to prompt other workers to begin foraging (Su, 2009). Playback experiments of these vibro-acoustics prompted more colony recruitment events than a similar playback experiment with white noise, suggesting that bumble bees may use vibro-acoustics as

29

communicative signals. However, the extent to which bumble bees use other vibroacoustics for communication of foraging resources is still poorly understood.

More recently, Heise et al., automated detection (Heise et al., 2020) and classification of arrival and departure buzzes (Heise et al., 2019) in audio from microphones housed within bumble bee colonies. Arrival buzzes are characterized by a gradual crescendo and an abrupt offset (Figure 2.3) as the bumble bee approaches and lands at the colony entrance. Departure buzzes are characterized by an abrupt onset and a brief decrescendo as the bumble bee initiates flight and departs from the colony entrance. Heise et al., developed a model that differentiates the buzz types by computing smooth amplitude envelopes and calculating the distance from signal start and stop to the maximum peak amplitude in the segment (Heise et al., 2020). Buzzes are classified as arrivals when distance from signal start to peak amplitude is greater than the distance from peak amplitude to signal stop, and vice versa with departure buzzes. Heise et al., automatically isolate buzz events from other noise using spectral features of the audio (Heise et al., 2019). Because bumble bee buzzes have high harmonicity, frame-by-frame searches for events with harmonic ratios > 0.5 yields high accuracy for automatic detection. This is further enhanced by parameterizing thresholds of fundamental frequencies that correspond to experimentally derived ranges of bumble bee buzzes.

Colony arrival and departure data allow for the remote monitoring of foraging activity, while simultaneously providing proxies for colony size and growth rate, timing of foraging activity and alignment of foraging with floral resources. Next steps include automatically classifying queens and workers by their differences in fundamental frequency due to body size differences: queens are typically larger and have lower fundamental frequencies in their flight buzzes compared to the smaller workers. Automatic classification of caste could highlight how early season queen foraging affects colony success and could also provide a proxy for reproductive output at the end of the season by quantifying the queens that leave the colony. Further downstream developments that connect these software to the Internet of Things (IoT) are still needed to make them more user-friendly for biologists and farmers.

Defense

Bumble bees also exhibit sound-producing behavior relating to the defense of the colony. For example, B. terrestris reacts to mammalian breath and CO2-enriched air by 'hissing', a type of buzz with closed wings that occurs at a higher amplitude than buzzes and the vibrational pulses described by Su (2009) (Kirchner & Roschard, 1999). Hissing response increased with CO2 concentration in the air: ambient air blown on the colony elicited no response, while human breath (3.5% CO2), and enriched compressed air at 5% and 10% correlated positively with colony hissing.

Likewise, Kirchner & Roschard (1999) showed that if a mouse (a common colony predator) touches a bee or any part of the comb, or if the colony undergoes physical disturbance, it prompts hissing from nestmates. The intensity of hissing in the ultrasonic frequency range is much higher than in other types of buzzing, suggesting that it is amenable for automated detection and classification (Figure 2.4). Whether these behaviors are consistent across stimuli (i.e., predators and disturbance) in natural ecosystems or if they vary among species appears to be unexplored. It may nonetheless benefit the commercial bumble bee industry and farmers to remotely monitor predation of colonies to rapidly intervene.

Dominance

In-colony acoustics are also found in displays of dominance by parasitic cuckoo bumble bees (*Psythyrus spp.*) that invade and usurp nests of bumble bees. Cuckoo bees perform high-pitched, folded-wing buzzes after bouts of "mauling" and "pushing" other workers and the queen, which prompt workers to disperse within the colony (Fisher & Weary, 1988). These 'dominance' buzzes have fundamental frequencies between 300-400 Hz but a mean dominant frequency of ~820 Hz. In the same study, Fisher and Weary (1988) showed that bumble bees respond to playback pure-tone frequencies between 200-6000 Hz (with the majority of workers responding to tones between 700-2000 Hz) by briefly pausing or dispersing off the comb. This further suggests that bumble bees perceive and react to vibro-acoustic stimuli. However, this study had only two replicates, and has since not been repeated.

Bumble Bee Acoustics On or Near Flowers

Flight Buzzes

Beyond the colony, bumble bees generate sounds as they fly from flower to flower (Figure 2.5). Flight buzzes have historically received little notice from researchers but have recently garnered attention for remotely monitoring foraging bumble bees. Computational auditory scene analyses (CASA) was used to detect bumble bee buzzes in environments with low signal to noise ratios (Heise et al., 2017). In particular, spectral clustering and novel 'focal templates' – dynamic T-F filters corresponding to known parameters of event of interest – were employed to detect and characterize faint bumble bee buzzes at floral resources. Importantly, this algorithm showed high levels of detection accuracy – on par with or exceeding human performance – from audio collected in noisy natural environments.

Galen et al., (2019) used this software to monitor bumble bee behavior during a total solar eclipse and Miller-Struttman et al., (2017) built upon this work to show that flight buzz acoustics can be used to identify different functional groups (based on body size, tongue length and fundamental frequency) and to estimate overall bumble bee activity. Miller-Struttman (2017) also showed that buzzes can predict pollination services of two different alpine clovers. If these results translate to other bumble bee-pollinated plants, such as orchards and food crops, AMT may have applications for real-time monitoring and assessment of crop pollination. In this vein, Van Goethem (2019) demonstrated an integrated IoT system that uses machine learning and sensor arrays to monitor insect movement across large agricultural fields and Silva et al., (2013) used machine learning and audio analyses to distinguish insect types in the field.

Additionally, Gradišek et al., (2017) showed that flight buzzes may be used to identify bumble bees to the species level. They used machine learning and rule-based identification to differentiate queens and workers of 12 species in eastern Europe based on fundamental frequencies and audio spectra. Flight buzzes can be detected in noisy environments and are replete with useful information, demonstrating promise for further application. Major next steps for bumble bee flight buzz research include: continue to refine software to identify species and functional groups in other geographical areas; develop semi-permanent or permanent microphone arrays that use long-life batteries or solar power and transfer data via Bluetooth technology; connect acoustic analyses from microphone arrays near flowers and within bumble bee colonies to a user-friendly interface.

Buzz-pollination

Buzz-pollination, or sonication, is the act of vibrating anthers of flowers to release pollen and has been studied extensively in bumble bees. Approximately 20,000 species of plants have their pollen 'locked' in poricidal anthers and require sonication to undergo pollination and thus reproduction. Bees use a unique buzz that is different than their flight and defensive buzzes, and from pollination buzzes of other bumble bee species (De Luca et al., 2014, Pritchard & Vallejo-Marín (2020; Figure 2.5). The fundamental frequency of pollination buzzes can be predicted in part by body size (De Luca et al., 2019) and has harmonics that extend above 2000 Hz (De Luca et al., 2013).

The amount of pollen released by buzz-pollination depends on several factors. In one study, amplitude and duration of pollination buzzes were positively correlated with pollen release in anthers of Solanum flowers, but with no relationship between pollen release and buzz frequency (De Luca et al., 2013). Harder and Barclay (1994) showed that variability in sonication frequency affects pollen release: frequencies of less than 400 Hz (typical of bumble bees' fundamental frequencies) released ~10% of available pollen, whereas 450-1000 Hz (typical of low-amplitude buzz-pollination harmonics) released ~23%, although both had similar amplitude. Morgan et al., (2016) found that naïve *B. terrestris* decreased both amplitude and buzz frequency with increasing experience with *Solanum rostratum* flowers, suggesting that bumble bees can 'fine-tune' frequency and amplitude with floral familiarity. AMT could be used to monitor pollination and predict seed set for the 20,000 plant species – including economically important crops like blueberries, kiwis, and eggplants – that require buzz-pollination to reproduce.

Potential Application: Using AMT to Study Pathogens

One of the gravest modern threats facing bumble bees is pathogen spread. Commercial bumble bees are shipped internationally to meet agricultural pollination demands. Although quality standards require bumble bee colonies to be verified as pathogen-free before shipping, one study found that over 75% of 'verified' commercial colonies were still infected with pathogens (Graystock et al., 2013). Ineffective monitoring methods are contributing to worldwide movement of pathogens Goka et al., 2001), resulting in more rampant disease spillover from managed to wild bumble bee populations. Disease agents including the trypanosome *Crithidia bombi* (a unicellular parasitic protozoan) and the fungus *Nosema bombi* are implicated in the declines of several bumble bee species worldwide, including the federally endangered Patagonian bumble bee (*Bombus dahlbomii*) of South America.

However, pathogens vary in their behavioral and physiological costs to bumble bees. For example, the trypanosome affects colony growth rate and survival by altering foraging behavior and pollen input (Brown et al., 2003). Conversely, the fungal pathogen affects worker behavior in the colony (making them more lethargic) and reduces sperm production in males and survival of new queens to sexual maturity (Otti & Schmid-Hempel, 2007). Both pathogens also uniquely affect the gut microbiome which plays a vital role in colony immunity (Koch & Schmid-Hempel, 2012). These unique changes in bumble bee behavior and physiology within the colony environment suggest that acoustic monitoring technologies (AMT) may have promise for monitoring the pathogen status of commercial and wild bumble bee colonies.

Qandour et al., (2014) used AMT to detect varroa infection in honey bee hives, but similar approaches have yet to be applied to bumble bees. Commercial colonies can be readily purchased, outfitted with sensors, and infected with different pathogens to test soundscape differences. If behavioral changes are distinct under different pathogens and pathogen loads, then AMT and machine learning could be used to detect and identify pathogens. Acoustic screening prior to colony transit could provide the commercial bumble bee industry with an additional safeguard to lessen the global spread of pathogens. Given the numerous extant negative pressures on bumble bee health, such as climate change, habitat loss and agrochemicals, alleviating the impact of pathogens on bumble bees is necessary. Reduced transit of pathogens confers resilience to pollination services in agricultural and natural ecosystems, benefitting food security and the preservation of global biodiversity.

Conclusion

All the sounds produced by bumble bees in the colony and in the field could contain information that aids our understanding and ability to monitor these important pollinators (Table 2.1). Investigations that attempt to decipher acoustic communication (e.g., foraging 'buzz runs') and use non-communicative sounds (e.g., flight buzzes) as indicators of information are both worthwhile avenues of study. Although acoustics have received growing attention across many sectors, they have scarcely been applied to bumble bees. Of the bumble bee studies that have used acoustics, few embrace key technological advancements such as CASA, machine learning and automation that enhance the utility of audio data.

Given global declines of bumble bee populations and future demands for pollination, the preservation of key pollinator groups is a priority for maintaining global health and biodiversity. Bumble bee investigations that use AMT are financially and logistically feasible, non-destructive to wild bee populations and have potential to be standardized and scaled across sectors and continents. Cross-disciplinary collaboration between ecologists and computer scientists is critical to advance this research area. Ecologists can provide a deeper understanding of the biological context and implications of bumble bee sound-producing activities, while computer scientists can automate audio processing and develop user-friendly interfaces. The principal aim of highlighting the progress and potential of AMT in investigations of bumble bees is to spur discourse and collaboration between ecologists and computer scientists to help preserve an important and vulnerable pollinator group.

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37

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Figure 2.1. Photos of bumble bee, colony, and microphone.

(a) Microphones, such as this USB microphone with windsock, can be installed near flowers to capture the audio of flight buzzes from (b) foraging bumble bees. Microphones can also be housed within (c) artificial domiciles or commercial colonies to record acoustic behavior from (d) within bumble bee colonies. Photo credits: Figure 1a, 1b, and 1c are courtesy of the author; figure 1d is courtesy of Dr. Anton Gradišek (Jožef Stefan Institute, Slovenia).



Example of (a) waveform and (b) spectrogram of fanning in bumble bee colony. Fanning creates a sustained broadband sound with equivalent fundamental and dominant

frequencies. Little acoustical energy is produced above the second harmonic.



Figure 2.3. Waveform and spectrogram of bumble bee arrival buzz.

Example of (a) waveform and (b) spectrogram of arrival buzz and subsequent 'pulse' buzzes (demarcated by red brackets) from alpine forest bumble bee (*Bombus sylvicola*) colony. Pulse buzzes have roles in dispersing pheromones to recruit other bumble bees to forage for resources.



Figure 2.4. Waveform and spectrogram of bumble bee defensive buzzing.

Example of (a) waveform and (b) spectrogram of defensive buzzing in *Bombus impatiens* colony. Black arrow denotes the onset of physical disturbance to the colony. Note that acoustical energy extends to ultrasonic regions.



Figure 2.5. Spectrogram and power spectral plot of bumble bee flight and pollination buzzes.

Example of (a) spectrogram of pollination and flight buzzes (demarcated by red brackets) in the alpine forest bumble bee, *Bombus sylvicola*. As bumble bees fly from flower to flower to buzz-pollinate for pollen, they generate distinct audio signals. (b) Flight buzzes are typically characterized by clear harmonic stacking and equivalent dominant and fundamental frequencies, shown here with power spectral density plot; (c) pollination buzzes are characterized with dominant frequencies at higher harmonic levels.

Table 2.1. Applications of AMT in investigations of bumble bees.

	Bumble Bee		
	Sound-Producing	Microphone	
CHAPTER 3	Behavior	Placement	Applications
CHAPTER 5.			temperature fluctuations via fanning to cool
			down
Flight			colony (Vogt, 1986) and incubating to warm up
			colony (Esch et al., 1991);
acoustics			behavioral tradeoffs (Vogt, 1986); colony heat
			production and
provide cues	thermoregulation	in colony	metabolism (Schultze-Motel & Lamprecht, 1994)
			automated colony entrance traffic monitoring
for tracking	foraging and		(Heise et al., 2019);
	recruitment	in colony	forager recruitment (Su, 2009)
			defense against intrusion (Kirchner & Roschard,
	defense	in colony	1999)
			usurpation of nest by parasitic bees (Fisher &
	dominance	in colony	Weary, 1988)
			automated buzz detection (Heise et al., 2017);
			functional traits,
			pollination services and landscape-scale bee
			activity (Miller-Struttman et al., 2017);
			bee behavior during environmental change
			(Galen et al., 2019);
			bee pollination efficiency (Van Goethem et al.,
		in field near	2019); species identification Gradišek et al.,
	flight	flowers	2017)
			plant-pollinator co-evolution (De Luca et al.,
			2013); variation among species (Gradišek et al.,
		in field near	2017);
	buzz-pollination	flowers	pollen release (Harder & Barclay, 1994)

morphological traits of bumble bees and phenological phases of colonies

Zachary Miller, David Heise, Erica Sarro, Lauren Sullivan & Candace Galen

Abstract

Leveraging technological advancements that allow for remote monitoring and automated processing of information has been identified as a key next step for pollinator research. However, the utility of these 'e-ecology' datasets depends on the ease of collection and the quality of information they confer. Acoustics offer low cost, non-invasive methods for studying various aspects of bee behavior and life history. Here, we test whether the acoustics of bumble bee flight buzzes can track morphological traits and phenological phases of foragers throughout the season. First, we used flight cage experiments and a literature survey to extend data on the relationship between the fundamental frequency of flight buzzes and body size across castes and species. Next, we acoustically monitored 14 wild bumble bee colonies of eight different species in subalpine and alpine ecosystems in Colorado, United States, where we corroborated acoustic data with inperson observations to distinguish phenological phases (queens only vs. queens + workers) of the colonies. Bumble bee size is inversely related to the fundamental frequency of flight buzzes for the 28 bumble bee species for which data were available. And because bumble bees have pronounced caste size dimorphism and workers exhibit considerable size variability within the colony, the fundamental frequency of flight buzzes can be used to recognize the timing of life history events, such as the onset of worker foraging. We conclude with a discussion of potential research applications as well as limitations of acoustic approaches for studying bumble bees.

Introduction

There is a growing need for low cost, automatable, remote monitoring methods for pollinators of conservation concern, as increased surveillance across life history stages could help address knowledge gaps to inform conservation efforts and environmental policy. Bumble bees, important pollinators for most temperate plant communities and food crops, face declines globally that are driven by complex interactions of climate change, disease, agricultural chemicals, competition with invasive congeners, and habitat degradation (Goulson et al., 2008, Goulson, 2010). Unraveling the complex interacting drivers of pollinator declines requires large spatiotemporal datasets that are difficult to obtain using conventional sampling methods (e.g., in-person observations). Several 'e-ecology' approaches for studying pollinators have emerged over the last two decades, including radio frequency identification (RFID), radar/lidar, and automated acoustic monitoring (Barlow & O'Neill, 2020). The suitability of applying these methods for investigating bumble bees varies by research question, as each approach offers different types of information and has unique sets of limitations and challenges (see Barlow & O'Neill, 2020 for review).

Acoustic monitoring shows promise as a viable sampling approach for investigating bumble bees. Advantages of acoustic monitoring systems include affordability of sensors, ease of use, non-lethal sampling, and passive data collection. Passive acoustic monitoring is a rapidly growing monitoring approach that has been applied to numerous taxa including birds, bats, and marine life (Perez-Granados & Traba, 2021, Revilla-Martín et al., 2021, Sousa-Lima, 2013). Passive acoustic monitoring allows researchers to eavesdrop on species that use acoustic communication or emit noise as byproducts of behavior, providing information about animal presence, behavior, interactions, functional traits, and/or phenology (Browning et al., 2017, Gibb et al., 2018, Sugai et al., 2019).

Bumble bees produce many noises as byproducts of activities such as thermoregulation and flight (Miller, 2021). Attributes of these acoustic signals such as fundamental frequency, harmonicity, amplitude, and signal patterns can provide important information about the behavior and identity of the signaler (regardless of whether the noises are biological signals *strico sensu*), allowing for numerous research applications both in the field and in the colony (Abdollahi et al., 2022). For example, acoustically monitoring bees in flight or at floral resources can provide information about bee behavior, functional traits, species identity, and pollination services (Galen et al., 2019, Miller-Struttman et al., 2017, Gradišek et al., 2017). At the colony level, acoustic monitoring can be used to eavesdrop and distinguish behaviors such as defensive buzzing and thermoregulation and to track foraging activity at the colony entrance (Kirchner & Roschard, 1999, Schultze-Motel & Lamprecht, 1994, Heise et al., 2020).

The negative relationship between body size and the fundamental frequency of animal calls, songs, or other vocal cues is well known across taxa (e.g., Dunn et al., 2015, Thiagavel et al., 2017) including some bumble bee species (Miller-Struttman et al., 2017, De Luca et al., 2019, Gradišek et al., 2017) but has not been leveraged for remotely monitoring bumble bee colonies. If differences in body size cause a detectable difference in flight buzz acoustics across castes and species, then remotely monitoring the soundscape of colony foraging activity may confer morphological trait information that is amenable for a suite of research questions. Unlike worker castes in honey bees and stingless bees, bumble bee workers have marked size variation, and workers within a single colony can have up to 10-fold differences in size (Couvillon et al., 2010). Bumble bee worker body size influences foraging ability, pollination services, task allocation within the colony, and fitness across species (Kelemen et al., 2022, Austin & Dunlap, 2019, Kelemen & Dornhaus, 2018, Spaethe & Weidenmüller, 2002), suggesting that eavesdropping on colony activity could provide insight into how these behaviors and services are distributed according to caste or body size.

Additionally, if caste size dimorphism is acoustically detectable across species, then acoustics may be useful for remotely monitoring phenological phases of the colony. Bumble bees exhibit pronounced caste size dimorphisms with queens being on average 42% larger than the workers (Cueva del Castillo & Fairbairn, 2012) and in some cases more than twice the size (Shpigler et al., 2013). Bumble bee colonies undergo distinct developmental stages in their annual lifecycle (Goulson, 2010; Figure 3.1). Colonies are founded and occupied by a single queen who forages for pollen and nectar to rear workers. After emergence, workers assume foraging roles, freeing the queen to shift to egg-laying to maximize colony size. Finally, the colony senesces after the production of gynes (unfertilized queens) and males at the end of the flowering season. Improving our capacity to remotely track the phenological phases of bumble bee colonies at individual, species, or community scales could be important for understanding how these transitions align with or respond to ecological factors such as the phenology of floral resources (Forrest, 2015), the abundance of competitors or nest parasites (Morales et al., 2022, Figueroa et al., 2021), or changes in temperature or precipitation (Guiraud et al., 2021). Here, we extend data on the relationship between body size and fundamental frequency of flight buzzes for bumble bees and ask whether acoustics can track phenological phases of the colony. We monitored wild bumble bee colonies in domiciles and collected morphological and acoustic data from wild-caught bumble bees and literature surveys to investigate (1) whether fundamental frequency of flight buzzes from foraging trips can inform body size differences among foragers and (2) thus discern the onset of worker foraging.

Methods

Data Collection

Body Size & Fundamental Frequency

We collected data on bumble bee body size at Pennsylvania Mountain (PM), Park County, CO, USA in 2020 and, for two additional species (*Bombus dahlbomii* and *B. ruderatus*; C. Galen, unpublished data), in Puerto Blest, Argentina in 2019. At PM, 2-3 researchers walked the krummholz and tree line (elevation: 3552-3664m) on sunny days between 0900-1200hrs to collect foraging bumble bees once per week from July 3 to August 5, 2020. We opportunistically netted foraging bumble bees, chilled them to torpor in vials on ice, identified to species and caste, and measured intertegular distance (ITD – the span between the base of the wings on the thoraxes of bees), a proxy for body size (Cane, 1987).

After bees returned to ambient temperature, we conducted audio recordings of flight buzzes inside a small, domed mesh tent (approximately 1.5x1.5x1.5m). We recorded each bumble bee for 1-2 minutes with a Zoom H4N Pro handheld audio

recorder (sampling rate: 48kHz) held approximately 15-45cm from the bee in flight. All bees received a small dot of red paint on the thorax prior to being released to prevent recapture. The same protocol was used in Puerto Blest, Argentina in 2019 for ITD and fundamental frequency measurements of *B. dahlbomii* and *B. ruderatus* queens.

We estimated fundamental frequency of flight buzzes using the Plot Spectrum tool (Hann Window, FFT size 8192) from the audio software Audacity v2.4.1 following methods described in Heise et al. (2019). Flight buzz fundamental frequency was averaged by individual, caste, and species.

Literature Survey

We conducted a literature survey to find flight buzz fundamental frequencies and ITD measurements for additional castes and species of bumble bees. We searched Google Scholar using the term "Bombus" with "fundamental frequency" and "flight" to find papers with fundamental frequency measurements of flight buzzes, and with "ITD", "ITS", "intertegular distance" or "intertegular span" to find papers with measurements of ITD. Papers that did not identify bees to caste were not included, and only species with both ITD and fundamental frequency measurements were retained for analyses. *Phenological Phase*

Acoustics data to assess phenological phases came from bumble bee colonies monitored at two sites in Park County, Colorado, USA – Pennsylvania Mountain (PM) and Spivak Ranch (SR) – in 2019 and at the Rocky Mountain Biological Laboratory (RMBL; E. Sarro, unpublished data), Gunnison County, Colorado, USA in 2021 using methods described in Heise et al. (2019). In brief, we placed wooden domiciles (15x15x15cm) across the landscape in subalpine and alpine ecosystems in late May or early June to attract nest-hunting queens. For the subset of boxes that were occupied, we monitored colonies regularly from June-August using in-person observations and acoustics at PM and SR and acoustics at RMBL.

At PM and SR, we collected audio recordings of 3.5-8 hours between 0700-1700hrs 1-2 times per week using USB microphones (DB9PRO VR1.0, Arcos Global Ltd, UK – sampling frequency: 48kHz) placed within the domiciles. We conducted in-person observations of colony activity concurrently with acoustic sampling for 10 minutes every hour from 0900-1500hrs once per week for each of the occupied boxes to record foraging activity and caste. We annotated the onset of worker foraging to demarcate the shift between the queen only phase and the queen + workers phase of the colony for each box at PM and SR. At RMBL, we conducted audio recordings 5-6 times per week using USB microphones placed near the colony entrance. We were unable to monitor colonies through the production of gynes and males at the end of the season, so we report here only on the transition from queen to worker foraging for each colony.

Audio processing

We processed audio recordings from the colonies using the automated buzz detection system described in Heise et al. (2020). In this system, harmonic ratio and spectral features (e.g., spectral centroid and spectral spread) are used to distinguish buzzes from other noise. Then, buzzes are classified as arrivals or departures based on amplitude envelopes (Heise et al., 2020). After processing colony-level data with the buzz detection system, we noticed several detected buzz events occurring outside of the expected range of fundamental frequency (e.g., queen buzzes more than double the known fundamental frequency, but still within the parameterized frequency range of >125 and <260Hz of the software). Upon visual inspection in Audacity following methods from Heise et al. (2019), we identified these events as false positives. To eliminate outliers, we imposed caste- and species-specific thresholds of fundamental frequency from known buzzes. Specifically, we used three standard deviations above and below the mean of both queen and worker fundamental frequency for each species from the literature survey or cage experiments, and data points above or below these values were eliminated.

Statistical analyses

Body Size & Fundamental Frequency

To test the relationship between acoustics and bee body size, we ran a linear model (*Im*) with average flight buzz fundamental frequency as the dependent variable and average ITD as the independent variable. Because the ITD data were right skewed, we log-transformed ITD measurements which normalized the data for testing.

Phenological Phase

To test whether acoustics of foraging activity provides cues for demarcating the transition from queen to worker foraging, we assessed the standard deviation of flight buzz fundamental frequency from foraging trips before and after the onset of worker foraging using a mixed effects model (*Imer* from the *Ime4* package) with standard deviation of fundamental frequency as the dependent variable, phenological phase (i.e., queens only or queens + workers) as the independent variable, and colony and day of

year as random effects. We calculated test statistics using type II sums of squares in the function *anova*. We report marginal (for fixed effects) and conditional (for fixed and random effects) r² values using the function *rsquaredGLMM*. All analyses were conducted in R (version 3.5.2; R Core Team 2018).

Results

Body Size & Fundamental Frequency

In total, we collected 71 bumble bees of 11 species at PM for ITD and flight buzz fundamental frequency measurements, as well as five *B. dahlbomii* and five *B. ruderatus* queens from Puerto Blest, Argentina (see Supplementary Table 1). From our literature survey we found an additional 15 species for which both fundamental frequency and ITD data were available, resulting in 28 species in total. We used all 28 species in our analysis of average flight buzz fundamental frequency and average ITD, and we found a significant inverse relationship (adjusted r² = 0.51, p < 0.0001; Figure 3.2). Larger bumble bees produce flight buzzes with lower fundamental frequencies than smaller bumble bees for the 28 species for which data were available. In general, queens are larger than workers, but there is considerable interspecific size variation, and queens of one species may be smaller than the workers of another.

Phenological phase

In 2019, six bumble bee queens founded colonies in domiciles at PM (*B. sylvicola*, n = 3; *B. flavifrons*, n = 1; *B. frigidus*, n = 1; *B. mixtus*, n = 1) and four at SR (*B. nevadensis*, n = 4). In 2021, three bumble bee queens (*B. appositus*, n = 1; *B. centralis*, n = 1; *B. rufocinctus*, n = 1) founded colonies at RMBL. All thirteen colonies survived to produce

workers. At PM and SR, we acoustically sampled boxes an average of eight times over the course of the season, but the total number of days sampled varied by box (range: 5-12 times) depending on when colonies were founded. At RMBL, boxes were sampled an average of 15 times (range: 14-16).

Using known buzzes of queens (from the queen only phase) and workers (from in-person observations), we compiled foraging activity from across the season to show the interspecific variation in flight buzz fundamental frequency by caste for all species monitored (Figure 3.3). In our analysis of the flight buzz fundamental frequency and phenological phase, we found that the standard deviation of flight buzz fundamental frequency can be used to discern whether a colony is in the queen only phase or the queen + workers phase (F = 43.48, p < 0.0001; marginal r² = 0.29, conditional r² = 0.51). Because foraging workers have more size variability than the individual queen of the colony, the standard deviation of flight buzz fundamental frequency for any given day when workers are foraging is significantly higher compared to days of queen only foraging, allowing for the remote recognition of the onset of worker foraging using acoustic cues. We use a ridge plot to visualize the shift between phases (Figure 3.4) for one exemplar, *B. appositus* (for ridge plots of all species, see Supplementary Figures).

Discussion

Our results demonstrate that remotely monitoring the soundscape of bumble bee colonies can provide information about both morphological traits of foragers and phenological phases of the colony. Specifically, flight buzz fundamental frequency can be used to approximate bumble bee size across species and castes, with lower fundamental frequencies being associated with larger bees (Figure 3.2). Similarly, because of the pronounced caste size dimorphisms of bumble bees, workers and queens are acoustically discernable for many of the colonies monitored in this study (Figure 3.3). Lastly, flight buzz fundamental frequency distributions of foraging bumble bees can be used to recognize the timing of foraging onset by workers in the colony (Figure 3.5).

The use of passive acoustic monitoring for a variety of terrestrial and aquatic wildlife has burgeoned over the last two decades (Sugai et al., 2018). Importantly, passive acoustic monitoring is not limited to species that use acoustic communication (e.g., birds, singing insects, anurans, etc.) but can be used for noises that are byproducts of behavior or locomotion. For example, Revilla-Martín et al. (2021) eavesdrop on bat activity near cave entrances and use bat passes as a proxy for estimating roost size. Most of the research using acoustics has focused on mammals (especially bats and cetaceans), birds, and anurans, with less than 5% of all investigations focusing on invertebrates (Sugai et al., 2018). For insects, acoustic monitoring has been used to investigate acoustic communication (e.g., cicadas, katydids, and crickets), to detect the swarming sounds of mosquitoes or chewing sounds of insect pests (Mankin et al., 2011), and, more recently, to investigate various facets of beehives (Abdollahi et al., 2022).

Our results contribute to our understanding for bumble bee colony soundscapes and suggest numerous potential research applications. First, monitoring bumble bee foraging behavior by body size may provide insights into energy budgets of the colony, as metabolic rates and resources (i.e., pollen and nectar) returned to the colony scale with body size, with larger bees having higher metabolic rates but also returning
proportionally more resources to the colony (Heinrich, 1975, Minahan & Brunet, 2018, Billardon & Darveau, 2019, Goulson et al., 2002). Understanding the distribution of foraging activity by worker size variability could also help pinpoint the role body size plays in mediating colony fitness. While wide variation in worker size is associated with access to more floral resources and lower susceptibility of population declines (Peat et al., 2005, Austin & Dunlap, 2019), mean worker body size is more important for determining colony performance (Hermann et al., 2018).

Additionally, acoustic monitoring may be useful for estimating colony fitness across species. Gynes (unfertilized queens) are typically much larger than workers (Cueva del Castillo, 2012), so the production and foraging activity of gynes at the end of the season should be associated with a surge of low fundamental frequency flight events in the colony soundscape that are discernable from worker foraging activity. Similarly, for many species, queens stop foraging once the workforce emerges, except in alpine ecosystems where the flowering season is abbreviated, queens continue to forage throughout the season (Macior, 1974, Miller-Struttman & Galen, 2014). Eavesdropping on colonies could help identify the circumstances that dictate whether queens continue to forage later in the season, and the impact this has on colony size and fitness.

In combination with vegetation data and/or environmental data, the acoustic monitoring of foraging behavior by body size can provide cues for understanding pollination services, phenological match-mismatch, and drivers of colony success across life history stages. Pollination effectiveness is mediated in part by body size (Wilmer & Finlayson, 2014, Jauker et al, 2016), with larger individuals more effectively delivering pollen than smaller individuals. At population and community scales, tracking the onset of worker foraging could inform the extent to which phenological phases of bumble bee colonies are driven by or respond to changes in floral resources and abiotic conditions, potentially shedding light climate impacts and vulnerabilities by region.

One of the primary challenges in automated acoustic monitoring systems for wildlife is classification accuracy, which can compromise the utility of the data (Balantic & Donovan, 2019). By constraining outputs with caste- and species-specific upper and lower fundamental frequency thresholds, we reduced the number of false positives in this project. However, this step requires having prior knowledge of fundamental frequency by caste and species. Identifying the acoustic characteristics of the false positive events or incorporating more stringent parameters (e.g., imposing stage-specific and/or species-specific fundamental frequency thresholds) are next steps for improving detection and classification accuracy. Other limitations and challenges to passive acoustic monitoring for bumble bees are difficulties finding wild bumble bee colonies (Liczner & Colla, 2019), lack of standardized and open-sourced audio processing tools (Gibb et al., 2019), and a limited scope of questions that can be answered.

Our findings showcase information that can be gleaned from acoustic cues within bumble bee colonies. Although acoustic monitoring is not amenable for all research questions, it does provide useful information about bumble bee foragers and phases of the colony, unlike other e-ecology approaches such as lidar/radar or RFID tracking. Acoustic monitoring also offers benefits such as being scalable, non-invasive, passive, and easy to use. Passive acoustic monitoring is a viable monitoring approach that may complement other methods to help disentangle drivers of bumble bee declines and improve conservation efforts for important pollinators.

Author Contributions

ZM designed the project with input and guidance from CG & LLS. DH provided software and expertise for processing audio data. CG provided unpublished data from Argentina (*B. dahlbomii* and *B. ruderatus*) and ES provided unpublished data from RMBL (*B. centralis, B. appositus, B. rufocinctus*). ZM collected all other data (either from the field or literature surveys), conducted analysis, developed the figures, and wrote the manuscript. Both DH and ES contributed valuable feedback that improved the project. All authors contributed to manuscript editing.

Data Availability

Data and code are available upon request. Please contact the author at zjmiller14@gmail.com.

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Figure 3.1. Typical life cycle of a bumble bee colony.

(A) Gynes (young queens) from the prior season are (B) inseminated by conspecific males before (C) overwintering. Upon (D) emergence in the spring, the queen forages on floral resources, (E) founds a new colony, and (F) rears a workforce to build up reserves for making new gynes and males for reproduction later in the season. The transition from the queen as the only forager to the workforce foraging, or steps E to F, is the phenological phase that we are demarcating acoustically. Illustration from Sarro et al. (2022).



Figure 3.2. Linear regression between fundamental frequency and body size of bumble bees.

Linear regression between fundamental frequency and body size (intertegular distance) of bumble bees, distinguished by caste (queens in blue and workers in orange). The black trend line represents the prediction of the linear regression and grey shading indicates 95% confidence intervals (adjusted r2 = 0.51, p < 0.0001). Note the log scale on the y-axis.



Figure 3.3. Distributions of flight buzz fundamental frequency by caste and species.

Distributions of the flight buzz fundamental frequency of foraging trips by bumble bee species and caste. Each panel represents a wild bumble bee colony (occupying a small wooden domicile) that was monitored acoustically at least once per week from shortly after occupying the domicile throughout the production of workers. Each plot therefore represents repeated sampling of foraging trips throughout the season. Density curves are scaled to 1 to better visualize the distinct distributions of both queens (blue) and workers

(orange).



Figure 3.4. Ridge plot of Bombus appositus.

Ridge plot of the fundamental frequencies of flight buzzes from one colony (B. appositus; E. Sarro, unpublished data) across the season (see Supplementary Materials for additional ridge plots for each bumble bee colony monitored). Foraging trips from DOY (day of year) 161-167 are from only the queen and the asterisk at DOY 182 marks the onset of worker foraging. Because workers have more variation in size, the fundamental frequency of their

foraging trips has wider variation compared to the queens. Note the gap in time between

DOY 167 and 182.

Supplementary Table 3.1. Flight buzz fundamental frequency and intertegular distance by species and caste.

Species	Caste	Mean Flight Buzz Frequency (Hz)	SD of Flight Buzz Frequency (Hz)	Mean ITD (mm)	SD of ITD (mm)	n
Bombus appositus	queen	123.330	8.485	6.030	0.071	2
Bombus appositus	worker	166.670	NA	4.450	NA	1
Bombus balteatus	queen	134.577	11.053	5.486	0.347	15
Bombus balteatus	worker	158.968	21.872	4.415	0.858	10
Bombus bifarius	queen	152.750	7.077	4.793	0.234	4
Bombus fervidus	queen	131.330	NA	5.480	NA	1
Bombus fervidus	worker	142.000	NA	4.640	NA	1
Bombus flavifrons	queen	151.443	13.879	4.763	0.146	3
Bombus flavifrons	worker	187.963	16.371	3.228	0.305	9
Bombus frigidus	queen	151.665	8.959	5.020	0.764	2
Bombus frigidus	worker	190.136	16.216	3.184	0.239	5
Bombus insularis	queen	124.000	NA	5.260	NA	1
Bombus melanopygus	worker	180.670	NA	3.950	NA	1
Bombus mixtus	worker	178.670	NA	3.170	NA	1
Bombus rufocinctus	worker	135.165	7.304	4.555	0.177	2
Bombus sylvicola	queen	166.500	0.240	4.650	0.311	2
Bombus sylvicola	worker	189.788	20.086	3.446	0.214	11
Bombus dahlbomii	queen	119.111	3.444	9.838	0.605	5



Supplementary Figure 3.1. Ridge plots of *Bombus nevadensis* colonies.

Ridge plots of the flight buzz fundamental frequency of foraging activity (monitored from flight activity at the entrance of the colony) over the season for four *B. nevadensis* colonies at Spivak Ranch, Colorado. DOY is day of year, and the asterisks mark the onset of worker foraging.



Supplementary Figure 3.2. Ridge plots of *Bombus sylvicola* colonies.

Ridge plots of the flight buzz fundamental frequency of foraging activity (monitored from flight activity at the entrance of the colony) over the season for three *B. sylvicola* colonies at Pennsylvania Mountain, Colorado. DOY is day of year, and the asterisks mark the onset of worker foraging.



Supplementary Figure 3.3. Ridge plots of other monitored *Bombus spp.* colonies.

Ridge plots of the flight buzz fundamental frequency of foraging activity (monitored from flight activity at the entrance of the colony) over the season for colonies of *B. flavifrons, B. frigidus, B. centralis, B. mixtus* colony at Pennsylvania Mountain or Rocky Mountain Biological Laboratory in Colorado. DOY is day of year, and the asterisks mark the onset of worker foraging.

CHAPTER 4: Show-Me resilience: Assessing and reconciling expert

perceptions of climate resilience in rural Missouri

Zachary J. Miller, Caleb O'Brien, Casey Canfield & Lauren Sullivan

Abstract

Climate change poses serious risks to natural ecosystems and human communities across the globe, presenting novel challenges to decision-makers at all scales. Rapid and widespread adaptation measures are necessary to establish more resilient social and ecological communities. Yet, rural areas of the United States - approximately 97% of the total land area – often lag urban areas in the implementation of climate adaptation practices. Understanding how perspectives vary within and among actors in rural landuse decision-making can help to identify catalysts and constraints for climate change adaptation planning and action. We conducted semi-structured interviews with 23 experts - policymakers, state/federal agency professionals, non-profit organization leadership, and researchers - at the nexus of rural land use, agriculture, natural resources, and conservation in Missouri to elucidate conceptualizations of climate resilience. We aligned our interview questions with NOAA's Steps to Resilience to investigate participants' perceptions of the major vulnerabilities of rural communities and landscapes, threats to rural vitality, and potential concrete steps for making rural Missouri more resilient in the face of climate change. Overall, we found that most experts conceptualized climate resilience as responding to hazardous events rather than anticipating or planning for hazardous trends. The predominant threats identified by

participants were flooding and drought which aligns with climate projections for the Midwest. Participants proposed a wide variety of concrete steps across community capitals but had the highest agreement on expanding existing programs, especially through the Missouri Department of Natural Resources and the Natural Resources Conservation Service. We found that the most comprehensive suite of solutions was offered by participants thinking across social, ecological, and economic systems, highlighting the need for collaboration across domains to develop more holistic solutions to climate-associated threats.

Introduction

Across the globe, climate change is impacting social, economic, and ecological systems at all scales (IPCC, 2022). Climate change is characterized by unpredictable, spatially heterogeneous, and erratic shifting weather patterns and events, which poses challenges that are often unique by region (IPCC, 2022). For example, in the US, western states face increasing frequency and severity of droughts and wildfires (Westerling et al. 2006), coastal states confront sea level rise and increasing storm surges (Sweet et al. 2017, Garner et al. 2017), whereas the Midwest contends with increased precipitation, more extreme rainfall events, and more frequent and intense heat waves (Villarini et al. 2011, Ebi & Meehl 2007). Thus, there are no 'one size fits all' adaptation responses and understanding how decision-makers across multiple scales perceive climate-related threats is necessary to minimize risk to local communities, ecosystems, and economies.

A recurring challenge in climate adaptation is the coordination of decision-makers and stakeholders with different levels of scientific background, diverse ideological perspectives, varying incentive structures that motivate planning, and contrasting perceptions of climate change. This is especially true of the rural-urban divide in the US, where climate change perception varies according to ideology, beliefs, or political affiliation, with urban areas typically leaning liberal and rural areas leaning conservative (Howe et al. 2015). For example, rural midwestern farmers tend to remain skeptical about the cause, certainty, and severity of climate change, while urban areas tend to have more targeted climate plans in place (Chatrchyan et al. 2017, Mase et al. 2017, Aderonmu et al. 2021, Broto & Burkeley, Lamb et al. 2019). Urban areas are often the centers of financial and human capital and can more quickly respond to extreme climate events (Javadinejad et al., 2019), whereas rural areas control land-use and natural resources but are often lacking in financial resources and tend to depend on the government to aid in disaster recovery (Javadinejad et al., 2019). Coordination of both rural and urban actors is needed to help develop and implement more effective adaptation efforts.

Despite having only 19% of the population, rural areas comprise approximately 97% of land in the United States (US Census Bureau, 2016). Therefore, most of the maintenance of ecosystem services, management of natural resources for goods and services, as well as the implementation of large-scale adaptation and mitigation efforts falls under rural purview. Rural decision-makers – from leaders in state and federal agencies to advocacy groups and lawmakers – are often responsible for championing, promulgating, and overseeing the programs and policies related to agriculture, conservation, and natural resources (Daniell, 2011, Lyle, 2015). Yet, the decision-making process for rural areas is highly complex and hierarchical, varying not only by region but also by scale (i.e., from the individual or household to farm or community level), where climate change adaptation is mediated by interactions and feedbacks among and across scales (Lyle, 2015). Pinpointing how rural experts and decision-makers perceive climate threats or conceptualize climate resilience remains a challenging, but critical step for climate adaptation, as their perceptions influence feedbacks for decision-making at larger scales (Daniell, 2011, Lyle, 2015).

Resilience is an important for concept for climate adaptation, as it provides a framework for communities to assess threats, vulnerabilities, and risks and plan for uncertain climate futures (Nelson et al. 2007). Resilient communities or landscapes can absorb perturbations or disturbances without losing functions (Willis et al., 2018, Longstaff et al., 2010) The term "resilience" is widely used in academic and policy spaces, but it remains a complex and multidimensional concept that is defined differently within and across disciplines (Payne et al., 2021, Sharifi, 2016). Here we use the term according to the 2022 IPCC Report, where it is defined as "the capacity of interconnected social, economic, and ecological systems to cope with a hazardous event, trend or disturbance, responding or reorganizing in ways that maintain their essential function, identity and structure" (IPCC 2022).

We use rural Missouri as a case study to explore how experts in agriculture, conservation, and natural resources conceptualize resilience in the context of climate change. Both temperature and precipitation patterns in Missouri are changing, with the most marked changes being warmer minimum temperatures, extended growing seasons, increased annual precipitation, and more extreme rainfall events (Kunkel et al. 2013, Pryor et al. 2014). Missouri has seen an increase in major flood events over the last two decades, causing extensive crop loss and damage to infrastructure, and climate projections suggest that Midwestern floods are likely to increase in frequency and intensity (Hershon 2020, Neri et al. 2020, Kunkel et al. 2013). Climate-associated impacts in Missouri are therefore likely to worsen in absence of widespread climate adaptation measures. We used semi-structured interviews guided by NOAA's Steps to Resilience (NOAA, 2014, Gardiner et al. 2018; Figure 4.1) to explore the following research questions:

RQ1: How do rural experts conceptualize resilience in the context of climate change? RQ2: What are the major threats to rural Missouri's communities and landscapes identified by rural experts (Steps to Resilience #1)? RQ3: What vulnerabilities of rural Missouri's communities and landscapes are identified by experts (Steps to Resilience #2) RQ4: What concrete steps do rural experts identify to make rural Missouri more resilient in the face of climate change (Steps to Resilience #3)? Finally, we highlight examples of climate resilience in Missouri and propose potential next steps for climate resilience measures in the state based on our results (Steps to

Methods

Sample population

Resilience #4).

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We focused our sampling on experts who operate at the nexus of land use, agriculture, natural resources, and conservation in rural Missouri. The term 'expert' describes individuals with extensive background knowledge, access to privileged information, and/or that are responsible for informing, prioritizing, developing, and/or implementing programs, policies, or decision-making (Otto-Banaszak et al., 2011). To identify potential interviewees, we first conducted preliminary interviews with four key informants, from whom we also sought insights about pertinent topics and resources associated with our research questions.

Drawing on those preliminary interviews and targeted internet searches, we identified an initial pool of 40 potential participants using purposive sampling (Patton, 2002). We sought experts with a range of vantages on rural Missouri, including legislators, academics, state and federal agency employees, and representatives from nongovernmental organizations. We sent recruitment emails to all potential participants inviting them to participate. If they did not respond, we sent a follow-up email approximately one week later. We also sought additional interview subjects during interviews through snowball sampling (Bernard, 2006). We asked each interviewee to identify additional relevant candidates. If the candidate represented a yet underrepresented perspective in our sample, we requested an interview with the subject. Three participants were added via snowball sampling.

In total, we conducted 23 interviews from March to May 2022. All interview candidates belonged to one of four sectors – non-profit organization (n=10), state/federal agency (n=4), state-level general assembly (n=6), and university (n=3) – and

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Commented [CC3]: How many were ultimately recommended?

Commented [CC4]: How many additional people did you reach out to?

were engaged in the rural policymaking ecosystem. All participants from agencies and non-profits held leadership roles (Table 4.1). Four of the six legislators were appointed to rural districts, and two were appointed to urban districts but served on committees related to agriculture, conservation, natural resources, and/or rural economic development.

All participants held a bachelors-level degree or higher. Seven participants held terminal degrees (i.e., JD and/or PhD), and five held masters' levels degrees. Eighteen participants had academic backgrounds in STEM or agriculture, thirteen had personal backgrounds in farming, and participants had an average of 17 years of experience in their field. Seven participants were females and 16 were males.

Interview protocol and coding approach

We conducted Interviews either in-person or via Zoom video-call. The interviews lasted an average of 43 minutes (range: 20-66 minutes). Our primary interview themes were guided by the first three steps from NOAA's 'Steps to Resilience' (NOAA, 2014): (1) explore hazards, (2) assess vulnerability and risk, and (3) investigate options (Figure 4.1). Thus, during the semi-structured interviews, we asked participants about their understanding of resilience and their perceptions of vulnerabilities, major threats, and potential solutions within the context of climate resilience in rural Missouri (see supplementary materials for interview protocol). For all climate related questions, we used an 'adaptive framing' approach, and did not attribute climate change to anthropogenic causes (Coleman et al. 2022). We recorded each interview and transcribed the audio using Otter AI software. We spot checked the transcriptions for accuracy and used these as the basis of all data analysis. Two authors coded each interview using a consensus coding approach to arrive at agreement about each code. In instances of impasse or confusion, we consulted the other authors to achieve resolution. We used QDA Miner Lite for coding interview transcriptions, and we produced all figures using RStudio v1.4.1106 (Rstudio Team, 2020). This project and all associated materials were approved by the University of Missouri Institutional Review Board in March 2022 (Project #2090263). All participants provided informed consent.

Here, we describe in more detail our coding and analytic approaches for each research question:

RQ1: How do rural experts conceptualize resilience?

To address this question, we deductively coded participants' responses to "What does resilience mean to you (in the context of rural Missourians and rural landscapes?)" and other relevant interview segments identified via keyword searches. We coded responses according to the 2022 IPCC definition of resilience:

"The capacity of interconnected social, economic and ecological systems to cope with a hazardous event, trend or disturbance, responding or reorganizing in ways that maintain their essential function, identity and structure" (IPCC 2022).

In addition to the components of resilience described above, we coded for an additional term, 'anticipate,' which is part of the IPCC's 2012 definition of resilience,

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because we felt this constituted an important distinction for understanding resilience in Missouri (IPCC 2012).

RQ2: What are the major threats to rural Missouri's communities and landscapes identified by rural experts?

We first used an open coding approach (i.e., breaking the textual data into its discrete, salient components) for organizing participants responses to the threats to rural Missouri, as this approach is useful for identifying key concepts from a broad range of responses (Williams & Moser, 2019). We then used axial coding (i.e., identifying, organizing, and linking connections between groups) to further clarify, categorize, and refine participants' responses.

RQ3: What vulnerabilities of rural Missouri's communities and landscapes are identified by experts?

Participants' responses to questions relating to vulnerabilities were deductively coded according to the community capitals framework. This framework, developed by Emery, Fey & Flora (2006), posits that communities possess and can mobilize varying levels and ratios of seven types of capital. These seven capitals are natural, human, cultural, social, political, built and financial. Although scholars often use the community capitals framework to explore communities' assets, the model can also be used to better understand constraining factors within systems (Sketch, Dayer & Metcalf 2019). Thus, vulnerabilities were coded as a lack of the community capital to which they most closely associated.

87

We also coded participants' responses for emergent themes related to vulnerability. Through an iterative process of coding and consulting literature, we included 'institutional capital' in addition to the seven traditional capitals. Institutional capital relates to the systems of rules and governance, as well as the coordination and performance of both public and private institutions (Farmer & Taylor, 2012). *RQ4: What concrete steps do rural experts identify to make rural Missouri more resilient?*

We coded participants' perspectives on concrete steps using open and axial coding methods. We proceeded through iterative rounds of inductive and deductive coding to address the breadth of steps identified and to categorize them loosely within the Community Capitals framework. Lastly, we compared the proportion of responses in each community capital between vulnerabilities and concrete steps to elucidate whether participants thought of concrete steps within the same domains as the vulnerabilities.

Results

RQ1: How do rural experts conceptualize resilience?

All participants identified at least two of the 12 aspects of the IPCC definition(s) of resilience but varied considerably in the complexity of their responses. The average number of aspects met by each participant was 5.47 (standard deviation = 1.5, range: 2-8). Participants thought of resilience in the context of economic, ecological, and social systems nearly equally. The most identified aspects of resilience were 'hazardous event' (n=16) and 'capacity to cope' (n=16), and the least identified aspect was 'interconnected' (n=2). Overall, most participants conceptualized resilience as coping with or responding

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to a hazardous event and fewer conceptualized it as anticipating or reorganizing for hazardous trends (Figure 4.2).

Several participants thought of resilience as the ability to 'bounce back' after perturbations to the system, or to maintain identity or function:

"Immediately what comes to mind is the ability to weather a challenge or to bounce back from said challenge."

"Resilience me, to me means being able to adapt to sustain functionality." "Yeah, resilience is about identity. It's about maintaining identity in the face of changes in the face of disturbance."

Many participants thought of resilience as being able to remain economically viable through ups and downs:

"...when I think of resilience, I think, can we help a producer or farmer, ranch owner, forest landowner, be able to long term handle the ups and downs and the climate instability? Are there ways that we can build a systems approach to help them ride out those ups and downs?"

"To me, it's about making sure that you can continue to operate year in and year out."

Some participants conceptualized resilience primarily as a human attribute relating to positivity and determination:

"I think of resilience, in many ways, I think of people being resilient and not giving up and not being discouraged. I think of farmers as resilient when it comes

to being optimistic and planning the crops raising their cattle year after year. I think that resilience is something that has helped our country be strong..." RQ2: What are the major threats to rural Missouri's communities and landscapes identified by rural experts?

In general, the predominant threats identified by participants related to changing precipitation patterns. Participants identified both changing trends (increasing precipitation and increasing temperatures) as well as more frequent extreme events (heavy rainfall, flooding, and drought; Figure 4.3; Table 4.4). Additional major threats included industrial agriculture's reliance on external inputs, demographic changes related to rural exodus, and both regulation and deregulation of agriculture (Figure 4.3; Table 4.4).

"You know, the old timers would say that the rains would come more gentle than they than they do now. You wouldn't get like five, six-inch rains as a common occurrence."

"On the flooding piece, that's a more immediate threat and I feel like that's ramping up. And I think everybody's recognizing the more intense more frequent weather patterns we're having."

"You know, what is the average age of the farmer now? It's like 57? That's a problem."

"A lot of farmers have a system that's very dependent on using a lot of fertilizer. Well, this year, fertilizer product prices almost doubled." Overall, participants perspectives on the threats facing rural Missouri aligned with projections of climate change for the Midwest, citing changing precipitation patterns, flooding, and drought as the primary concerns. However, they were also keen to point out that they are simultaneously facing other major internal (e.g., rural exodus) and external (e.g., market forces of commodity crops) pressures that threaten rural vitality, and multiple participants highlighted a need for more creative solutions and problem solving.

"I think, again, we need to, we need to start coming up with more creative solutions, and not banking on that business as usual."

"You've got to be creative to engage in problem solving but being creative is extremely difficult and extremely difficult when you're scared to death of losing what you love."

Lastly, some threats mentioned by participants were at odds with others. For example, several participants mentioned deregulation (i.e., loosening regulations on agriculture) as a threat for rural Missouri, especially in the context of confined animal feeding operations. Conversely, other participants thought that regulations (i.e., tightening regulations) were the threat because they constrict Missourians' ability to earn an income.

RQ3: What vulnerabilities of rural Missouri's communities and landscapes are identified by experts?

Seven of the eight community capitals were cited as having vulnerabilities, but the most often mentioned vulnerabilities were associated with human capital (n=18),

natural capital (n=17), and built capital (n=15). Only one participant identified vulnerabilities associated with institutional capital, and none identified vulnerabilities in political capital.

A recurring vulnerability was the lack of systems thinking when facing problems and trying to develop solutions. Participants also identified lack of education, inability to access resources, and incapability to see the bigger picture as the vulnerable components of human capital in rural Missouri.

"I think it's a challenge for our rural communities to see the bigger connectedness of our system, whether we're talking about the food system or overall biosphere."

"The lack of education and lack of educated people makes things very vulnerable. I think it just leads to people not knowing what to do or how to do it...If you don't have a good education, you're toast."

"The human capital brain-drain from rural communities [is what makes rural Missouri vulnerable]."

The vulnerable aspects of natural capital in rural Missouri that participants identified were often related to proximity to river systems, soil health and the heterogeneity of fertile soils, and fragmented habitats.

"I think the smaller the community, the more vulnerable it is, the more you know, the more niche-specialized it is, the more vulnerable it is. And I think that, to me, that means like, Ozark streams and things like that those truly unique ecosystems that only exist in a few places, I think, just by the nature of how

specialized they are and how small they are they they're inherently more vulnerable."

"River systems [are vulnerable]. ...hardscaping and controlling the river has to change in my opinion, especially with these more intense and more frequent storms. We need to be able to revert river systems back to more of their systematic functions, like maybe let a floodplain be a floodplain instead of you know, channelizing and not allowing the river to expand and, and shrink based on flows."

"Marginal soils [make parts of Missouri vulnerable]. Like parts of southwest Missouri or the Missouri Ozarks, you know, the soils are very thin, and what little soil was there has often been eroded away."

Despite being asked about vulnerabilities in the context of climate change, participants were keen to point out general vulnerabilities facing rural Missouri. For example, for built capital, participants identified deteriorating infrastructure – especially bridges, roads, and wastewater treatment facilities – and a lack of broadband access in rural parts of the state as vulnerable capitals. Other important vulnerabilities included the idea of 'rural exodus' and associated cascading effects (e.g., aging rural population, fewer people returning to farming careers, dead and dying small towns, inability for families to earn a viable income in rural areas), the lack of social cohesion (such as distrust in the government and failure of leadership), as well as lacking cultural capital (including ingrained traditions that are reluctant to change and a weak sense of identity across the state). Lastly, multiple participants mentioned the lack of cohesion and vision between and across institutions, and that there was an absence of big picture dialogue, planning, and action in the state. Although some agencies had climate agendas in place or in progress, contention on the veracity and gravity of climate change within the agency made the policies little more than perfunctory.

RQ4: What concrete steps do rural experts identify to make rural Missouri more resilient?

Participants cited a wide variety of concrete steps to help make Missouri more resilient. Overall, there was low agreement on concrete steps, with 28 distinct steps that were mentioned only once. Steps that were mentioned more than once are shown in Figure 4.4. Concrete steps were cited across all eight community capitals (Table 4.3). The community capitals with the highest amount of cited concrete steps were institutional (n=8), built (n=6), and financial (n=6), and the fewest belonged to cultural (n=3) and political (n=2). The most recurring themes of concrete steps (n=5) included expanding the reach and effectiveness of existing programs, landscape scale conservation (n=3), improvements to and diversification of energy grid (n=3), and developing systems thinking across institutions and decision-makers (n=3). Other important steps (identified by at least two different participants) included were expanding broadband access, institutionalizing the monitoring of waterways and water quality, improving profitability of agriculture with value-added products and agritourism, and developing a shared language and vision for the state. Participants' responses illustrate that proposed solutions do not necessarily align with the community capitals cited as vulnerable (Figure 4.5).

94

"We need more integrated landscape practices. So, putting in pollinator habitat, putting in biologically diverse conservation buffers, having tree planting where appropriate, appropriate use of grazing strategies, fitting all those things together, kind of from a landscape perspective is something we don't tend to look at too much. But it's something I've been encouraging people to think about..."

"I think the programs we just talked about are concrete steps, right? I think many of those are already in place. Now, they may not be perfectly implemented, there may be a lot of room in the margin for improvement."

"I think we have to continue to figure out ways to get urban and suburban people to experience, respect, and appreciate rural Missouri and vice versa. Because we're all we're all in this together, you know. We have to stop putting ourselves in our little camps and silos."

"Another thing that we're really starting to break out into [to expand the reach of our programs] is female landowners. We're doing a lot of stuff with getting women outdoors and further developing their skill set outdoors."

Because numerous participants mentioned vulnerabilities associated with siloed thought and action as well as the need for systems thinking as a concrete step, we were curious how a *lack* of systems thinking might be associated with the breadth of concrete steps mentioned by the participants. That is, do participants that identify resilience as belonging to a particular system – social, ecological, or economic – propose concrete steps across the same suite of community capitals? We explored this emergent trend using Sankey diagrams, and we found that only the participants that think of resilience
across integrated social, ecological, and economic systems identify concrete steps in each of the community capitals (Figure 4.6). Participants that associated resilience with only one system had concrete steps in fewer of the community capitals.

Discussion

Through semi-structured interviews with 23 experts – policymakers, state/federal agency professionals, non-profit organization leadership, and researchers – at the nexus of rural land use, agriculture, natural resources, and conservation (Table 4.1), we sought to elucidate expert conceptualizations of climate resilience in rural Missouri. We used NOAA's Steps to Resilience framework (Figure 4.1) to guide interviews and overall, we found that:

- Interview participants had diverse conceptualizations of resilience ranging from primarily attributes of optimism and determination to a focus on disaster recovery and maintenance of functionality. In general, more participants understood resilience as an act of responding to hazardous events rather than anticipating hazardous trends (Figure 4.2).
- Participants perspectives on the threats facing rural Missouri largely aligned with projections of climate change for the Midwest, with floods and droughts cited as the most prominent threats (Figure 4.3; Table 4.2). However, numerous non-climate stressors, such as farm consolidation and demographic changes, also factor into participants' understanding of the threats facing rural Missouri.

- Participants offered a wide range of potential concrete steps to bolster rural resilience, but we found little agreement on specific steps. The possible steps identified most frequently were associated with expanding or adapting existing programs, building a more resilient energy grid, promoting landscape-scale conservation, and encouraging systems thinking, (Figure 4.4; Table 4.3)
- Participants identified human, natural, and built capitals as rural Missouri's most vulnerable assets. As a group, most concrete steps primarily addressed institutional, financial, and built capitals (Figure 4.5).
- Participants who thought of resilience as taking place across interconnected social, ecological, and economic systems identified concrete steps that addressed a broader range of capitals compared to participants that primarily described resilience within a system (Figure 4.6).

We found experts' primary conceptualizations of resilience as 'bouncing back' are consistent with related findings in the literature, where the objective is to return to a former state after a disturbance (e.g., Nelson, 2011, Kais & Islam, 2016). Scholars argue that aspects of this conceptualization may be problematic and that it is the most basic form of resilience, often associated with denial of any problem and avoidance of any systemic changes (Kais & Islam, 2016, Handmer & Dovers, 1996). Conceptualizations of resilience that are more open, flexible, and adaptive, or that consider 'bouncing forward' to a reorganized future state, tend to be associated with addressing the fundamental cause of the problem and often seek transformational political and cultural shifts (Handmer & Dovers, 1996). A more adaptive conceptualization of resilience may be needed for robust resilience measures to be implemented across rural Missouri.

Our interview participants identifed lacking human capital as the primary vulnerability in rural Missouri. Human capital – the skills, knowledge, and capacities of individuals in a community – is cited as being an important and necessary catalyst for transformational change in communities (Emery & Flora, 2006). Indeed, one study found that investment into human capital led to investments made into other capitals (i.e., political, natural, built, and social), leading to a 'spiraling up' of communities in Missouri are cited as having limited human capital, focusing development efforts on building local capacity and leadership may be a promising next step. Several participants pointed out Missouri's unique conservation and soil, water, and park taxes, which provide funding for county conservation offices, each of which has an associated university extension agent. Further investment into and coordination of the personnel and leadership of these programs may help bolster human capital through means such as landowner workshops, farm tours, or strategic listening sessions.

Interview participants were keen to point out measures of resilience that are in place or in progress as a response to changing precipitation trends. For example, Governor Mike Parsons created the Flood Resilience Advisory Working Group (FRAWG) to assess flood risk and identify priority areas for funding after the 2019 flood of the Missouri River. In response to FRAWG's recommendation for enhanced water monitoring capabilities of Missouri's waterways, Governor Parsons proposed slating \$10.4 million of the 2023 state budget to form the Missouri Hydrology Information Center (MOHIC). While it is argued that reactionary efforts like this are drafted quickly and tend to lack public input and consideration of populations that are disproportionately impacted (Burnstein & Rogin, 2022), its aim to improve monitoring, mapping, and predictive capacity of precipitation and flood levels across the state will likely benefit planning and response measures in subsequent floods.

In another example cited by multiple participants, state and federal public and private sectors partnered to setback a levee in Atchinson County, MO after damages incurred from the 2019 flood. The project was led by the Atchinson County Levee District with help from the US Army Corps of Engineers, The Nature Conservancy, and several state agencies. This project showcased attributes of effective resilience-building efforts. First, the effort required and benefitted from collaboration by disparate organizations, that, in total, cover social, ecological, and economic domains. Second, by reorganizing systems in anticipation of future floods, future risk to communities and economies is lessened. Deeper investigation into this project may shed light on how to coordinate diverse actors for further collaborative resilience measures in other parts of the state.

Because participants had the highest level of agreement on expanding existing programs as a concrete step, future research could investigate extant programs and policies for rural communities and landowners to develop resilience. Several state and federal level programs and policies – e.g., landowner assistance programs through USDA, the Department of Conservation, or the Department of Natural Resources – were identified by participants as being useful for developing resilience, but it is unclear the

extent to which those initiatives are robust to climate projections. Other potentially fruitful areas of research include efforts seeking to understand the challenges and barriers involved in implementing concrete steps and fostering resilience-enhancing communities of practice.

Although some threats and solutions mentioned by participants were at odds, disagreement on the best path forward was not universal. Several trends emerged from interviews that seemed to have robust support across sectorial and ideological lines. In a highly politically charged atmosphere, pinpointing overlapping priorities is vital for maintaining progress towards community resilience (Swyngedouw, 2013, Pepermans & Maeseele, 2016). Individuals and groups hoping to advance rural resilience in Missouri should avoid "reinventing the wheel" and instead seek existing programs and policies that could be adapted or expanded to accommodate the projected impacts of climate change.

Ideas and conceptualizations elicited through semi-structured interviews are necessarily provisional, partial, and spur-of-the-moment, these results offer a preliminary glimpse into how rural experts in a Midwestern state are thinking of climate threats, vulnerabilities, and concrete steps towards more resilient communities and landscapes. Nonetheless, our results underscore the need for inter-agency collaboration and coordination to identify and implement creative solutions. Many of the challenges facing rural Missouri are broad and multifaceted—involving multiple systems and community capitals. Meaningful solutions to these challenges will likely require similarly broad and multifaceted efforts. Therefore, enhancing rural resilience requires laying the

groundwork for large-scale collaborative efforts by entities operating from a range of positions and levels within rural systems. One way to proactively prepare for changing trends is by fostering mutual understanding and trust among relevant actors. Trust, for example, is among the most powerful predictors of outcomes in many situations related to natural-resource management (Coleman & Stern, 2018; Stern & Baird 2015). A group of rural actors equipped with strong trust and deep understanding of one another's perspectives and interests may be better positioned to not only respond to hazardous events, but to act in uncertainty and proactively prepare for hazardous trends.

Author Contributions

ZM & COB conceptualized the project with input and guidance from CC & LLS. ZM conducted all the interviews, ZM & COB coded participants' responses, COB crafted the tables, and ZM developed the figures and wrote the manuscript with contributions from COB. All authors contributed to editing.

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Figure 4.1. Conceptual diagram of the steps to resilience.

This approach is designed to be an iterative process and is useful for multiple scales of organizations from neighborhoods and communities to regions or states. Steps 1-3 (outlined with maroon circles) are the focus of this project. Figure adapted from NOAA's Climate Resilience Toolkit (NOAA, 2014).



Figure 4.2. Expert conceptualization of the meaning of resilience.

Expert conceptualization of the meaning of resilience in the context of rural Missouri. Reponses were coded according to the IPCC definition of resilience. Each term on the yaxis represents one of the key components of the definition, and the plot is ranked in descending order of the number of times each key component was addressed during the interviews.



Figure 4.3. Expert-identified threats facing rural Missouri.

Each term on the y-axis represents threats to rural Missouri, and the plot is ranked in descending order of the number of times each threat was addressed during the interviews after filtering for threats that were mentioned >1. For the full list of the threats identified, see Table 4.3.



Figure 4.4. Expert-identified concrete steps.

Expert-identified concrete steps to make rural communities and landscapes in Missouri more resilient. Each term on the y-axis represents a concrete step, and the plot is ranked in descending order of the number of times each was addressed during the interviews after filtering for concrete steps that were mentioned >1. For the full list of the proposed concrete steps identified, see Table 4.4.





Proportions of participants' responses associated with each community capital for both vulnerabilities (yellow bars) of rural Missouri and concrete steps (green bars) towards resilience.





Sankey diagrams depicting the connections between systems identified in participants' conceptualizations of resilience and the community capitals associated with proposed concrete steps to make rural Missouri more resilient. (a) Participants thinking of resilience primarily in economic systems did not identify concrete steps to build natural or human capitals; those thinking of resilience primarily within social (b) or ecological (c) systems did not identify concrete steps associated with political capital; and (d) participants that thought of resilience in interconnected social, ecological, and economic systems identified concrete steps associated with all community capitals. Node size represents the total number of connections between systems and capital associated with of concrete steps.

Positions (# individuals)	Total	Agency, Institution, or Organization	Total
Executive Director (3), Deputy	23	Missouri Department of Agriculture,	16
Director (2), Legislative Liaison (1),		Missouri Department of Conservation,	
Policy Coordinator (2), State		Missouri Department of Natural	
Coordinator (1), State		Resources, USDA Natural Resources,	
Conservationist (1), State Director		Environment Missouri, Missouri Coalition	
(1), Director of Regulatory Affairs		for the Environment, Missouri Farm	
(1), Executive Vice President (1),		Bureau, Missouri Pork Association,	
Director of Research (1), Faculty		Missouri Soybean Association, The Nature	
(2), Extension (1), State		Conservancy, Pheasants/Quail Forever,	
Representative (6)		Missouri Farmers Care, Missouri Energy	
		Initiative, Renew Missouri, University of	
		Missouri, Missouri State Capitol	

Table 4.1. List of interviewed positions and agencies, institutions, or organizations.

Threat	Detail	Emblematic quote	n
	Flooding	We've got two big river systems, the Mississippi and the	1
		Missouri, and I always think of those as vulnerable in in	1
		terms of the potentials for a for flood. We've had, within	
		my career, several floods, and so I think bottom land can	
		be quite vulnerable.	
	Drought	They just can't get out of the grips of the drought out	9
		West that has liquidated the cow herd If we were to	
ters		get into the grip of something like that, it would be a	
al disas		huge threat to rural resiliency.	
latura	Changing	Changes in precipitation patterns and kind of flashiness	6
e and r	precipitation	of streams.	
Climat	patterns		
	Heavy	rainfall events are coming harder, right? Rainfall has	3
	precipitation	changed. And you can see it across our farms: It's hard	
	events	to manage erosion, when you get 10 inches in one	
		rainfall event.	
	Increased	Increasing temps at nighttime, increasing water temps.	3
	temperatures		
	(air and water)		

Table 4.2. Threats to rural Missouri identified by interview participants.

Climate change	In the long term, it's definitely climate change.	2
Diseases and	Another big hazard right now that everybody faces is	2
pests	foreign animal disease possibilities.	
Earthquakes	I've lived here since 1989. I still sort of can't believe we	1
	haven't had another giant earthquake along the Madrid	
	fault line	
Extreme	More extreme weather has been a challenge	1
weather		
Extreme wind	extreme wind wiped out not only fields, but also grain	1
	storage systems, damaged equipment the farmers had	
	and buildings.	
Heatwave	we had temperatures over 100 all summer long. It did	1
	not matter how much you water corn, or how much you	
	watered soybeans, or rice. Bees would not pollinateit	
	was too hot during the day and the night for everything	
	to pollinate. We did not make a crop.	
Less predictable	Seasons are changing; they are shorter. They're getting	1
weather	shorter. I'm not sure what people are supposed to think	
patterns	when it's 75 degrees one day, and it's going to be	
	snowing the next. How is that supposed to be	
	sustainable for a farming operation?	
		1

	Consolidation of	We've got more and more efficient And so, for	8
	farms	communities are dependent on there being lots of	
		people in the neighborhood it gets harder and harder	
		as we learn how to produce more with less and fewer	
		people.	
	Rising input	Right now, it's gas prices, you know, the gas prices are	5
se	costs	going all the way up, clipping four dollars So that is an	
ket for		immediate, real concern that is happening right now.	
d mar	Market forces	I stress out a lot about our existing forested areas with	4
ure an		timber pricing.	
gricult	Overreliance on	The minute that you can't get energy from Russia, the	4
trial ag	imports	minute that you can't get wheat from the Ukraine, you	
Indus		start to see how badly that just screws up our entire	
		global economy.	
	CAFOs	I think that these CAFOs are a huge threat to rural	2
		Missouri. I think short term, it's good to have jobs, and I	
		am very appreciative of the food that is produced in	
		these places, but these corporate farms they're	
		putting profit before what's right for the environment.	

	E: : 1		4
	Financial	How do young people get into farming? It takes a lot of	1
	barriers to	capital there are really few opportunities for people	
	workforce entry	to engage in that industry without capital	
	Foreign	The foreign ownership, at least in Missouri [of] land is a	2
	ownership	big one.	
	Monoculture	monocultures	1
	Novel product	Plant-based meats and things like that. I think that even	1
	classes	lab-based meats, I guess is even more of a concern. At	
		least plant-based come from agriculture.	
	Reliance on	The vulnerability of reliance on fossil fuels.	1
	non-renewable		
	inputs		
	Rural exodus	The depopulation of some parts of rural Missouri just	6
		makes any basic infrastructurekeeping school systems	
ų		viable, keeping healthcare systems viableinto a real	
1 facto		challenge.	
lation	Demographic	The farming community, ranching community, are just	5
Popu	changes	getting older, and older, and older.	
	Urbanization	Increase population growth is going to do even more	2
		encroachment on current existing forested areas.	

			1
	Regulation	Regulations can harm agriculture, too much regulation.	3
		I always say that farmers and ranchers are the best	
		protectors of our animals. You know, we raised calves in	
		our house by the stove, we take care of our animals	
		we gave them best care and thought about them as a	
		valuable asset, not just something we're going to	
		butcher or whatever We care for them.	
	Deregulation	40 to 45 years of deregulating the agriculture market to	2
		make sure there are no safeguards, and no safety net	
ctors		and no backup for farmers to make a living It's ruined	
ocial fa		agriculture in this country, which is in turn rural and	
and Sc		rural communities.	
litical	NIMBYism/lack	Agriculture has to be smart about the way it grows. I'm	2
Pc	of community	not saying that we should just be able to throw a chicken	
	buy-in	barn or a hog barn up in anybody's backyard, but there	
		has to be fair balance and all that. And I do worry about	
		that balance long term as we get further and further	
		removed from where our food comes from.	
	Tariffs	And if we lose that ability to export through lack of	2
		trade deals or something in the mix, it doesn't allow our	
		pigs to move and flow For example, right now Canada	
		is in the market selling more pork to Japan, because they	
1	1		1

		have a lesser tariff than the United States does. We can	
		produce the pigs better and less expensively, but the	
		tariffs make our pork more expensive than Canadians at	
		the moment.	
	Geopolitics	China's a rising global superpower that does not share	1
		our values. And they continue to rise in part because we	
		weren't able to come up with the deal on the ground.	
	Domestic	I'm tempted to say politics.	1
	politics		
	Tax credits	And that government should not get in the way of that	1
		with tax credits by picking winners and losers. That's the	
		legislative aspect is to stay on the way.	
	Disconnection	Just the disconnect of people with nature that	1
	from nature	diminishes quality of life, whether we recognize it or not,	
		it is happening. Everything from, you know, air quality	
		and to mental health.	
tem	Fragmentation	more fragmentation and more ecological damage.	2
cosyst	Invasive species	Invasive species that could come up like kudzu, and it's	1
ded e		already been seen in the Boot Hill, but those kinds of	
Degra		invasive plants that are typically southern if they move	

	into those rural landscapes that could have a huge	
	impact	
Contaminated	Anybody who relies on surface waters for drinking water	1
water	is going to is vulnerable when we have overuse of	
	pesticides and fertilizer [which can] run off and pollute	
	our waterways, which some people rely on for drinking	
	water, [and] can leach through the soil and get into our	
	groundwater. And many rural communities, especially	
	in southern Missouri, rely on their private wells for the	
	drinking water.	
Degradation of	If we continue to diminish our natural landscapes	1
natural	that's just kind of all encompassing.	
resources		
Erosion	Just increased erosion and the nutrients that introduces	1
	to waterways.	

Table 4.3. Expert-identified concrete steps along with the community capital to which they

correspond.

Primary Community Capital	
Addressed	Concrete Step
	Enable rural broadband
	Advance energy storage tech
0. 14	Advance precision agriculture
Built	Establish a renewable, diverse, and resilient grid
	Repair infrastructure
	Stop development in floodplains
	Combat invasive plant species
	Diversify crops
	Advance landscape-scale conservation efforts
Natural	Promote native plants
	Support on-farm biodiversity
	Establish/expand riparian corridors
	Build shared language and priorities
6	Generate urban buy-in for rural priorities
500101	Conduct more research on rural needs
	Promote social diffusion of innovation
	Establish consistent regulation across
	jurisdictions
Institutional	Generate revenue through taxation
Institutional	Institutionalize monitoring efforts
	Enshrine the right to repair
	Adjust zoning regulations
	Promote agritourism
	Establish hemp/medical marijuana market
Financial	Streamline approval of new technologies
	Support value-added agriculture
	Expand tax credits for farmers
Human	Dismantle silos; encourage systems thinking
	Support education
Cultural	Depoliticize discourse
Cultural	Prioritize long-term planning
Political	Advance specific legislation
	Expand existing programs
Crosscutting ideas	Hold strategic listening sessions
	Host landowner workshops

Supplementary Materials

Interview Protocol

Instructions

The interviewer will print out the protocol and take notes on the protocol sheet during the interview. Once the interview is complete, the interviewer will upload a scanned copy of the annotated protocol to the Microsoft OneDrive folder shared by the research team. *Thank you again for agreeing to participate in this research project. I really appreciate you taking the time to talk with me. The purpose of the study is to gauge how decision-makers are thinking about climate resilience in the rural parts of Missouri and to put together a toolkit of the programs and policies that are in place to support rural communities and ecosystems. I will be conducting interviews with policymakers and decision makers in agriculture, conservation, and natural resources. I expect the interviews to last 30-60 minutes.*

Before we begin the interview, do you have any questions about the process? If any other questions arise at any point in this study, you can ask them at any time. Is it okay if I record our conversation? This will help me to remember everything we talked about.

(Start recording)

- Did you get a chance to look over the informed consent document that I sent?
- If yes,

o Great, do you have any questions about it?

o So just to confirm, you consent to participating in this research?

- · If no,
- o Review the informed consent document
- o So just to confirm, you consent to participating in this research?

Interview questions:

Background information

- 1. What is your role in your organization, and how did you come to work in that position?
- 2. How long have you been working in this sector?
- 3. To what extent does your work focus on rural areas of the state?

Project questions

Resilience & vulnerability

- 1. What does resilience mean to you? (in the context of rural Missourians/landscapes)
- 2. How does your work involve resilience?
- 3. What makes a community/region particularly vulnerable?

4. Are there natural communities/ecosystem services that are particularly vulnerable? Why or why not?

Threats

- 1. What are the major threats to rural Missouri?
- 2. Do you see these threats changing in 5 years? 25 years?
- 3. What planning cycles do you operate on/how far out in time are you planning?

Programs, policies, concrete steps, and stakeholder engagement

- What are some examples of programs/policies that might aid with climate impacts on human and natural communities?
- 2. From your perspective, which programs/policies are effective? Why?
- 3. Are there gaps that could be filled?
- 4. What concrete steps do you think could make a difference for building more resilient rural landscapes and communities?
- 5. What are the barriers to make these changes?
- 6. Who is responsible for funding/organizing/implementing?

- 7. What key individuals/organizations/stakeholders should be involved in this discussion and/or part of the problem-solving team?
- 8. Do you have suggestions for how to connect these groups to move forward on improving/augmenting programs and policies for greater climate resilience in rural Missouri?

As part of this project, I plan to share anonymized and aggregated results with project participants. Would you be interested in participating in a focus group to discuss results and paths forward?

Is there anything important that you would like to add that we didn't touch on?

(stop recording)

Thank you so much for sharing your time and insights with me. I will be in touch with you once I am ready to share my findings from the project. Please do not hesitate to reach out to me if you have any questions or concerns or anything else to add.

CHAPTER 5: Conclusions

The findings presented here advance our understanding of sampling methods for bumble bees, which are important pollinators for many food crops and temperate plant communities. By highlighting sampling techniques that are potentially at odds with conservation efforts, I aim to help facilitate a more forward-thinking, innovative, and truly conservation motivated research community. In an increasingly fragmented landscape with dwindling stocks of biodiversity, the onus is on the research community to ensure that our approaches do not negatively impact the organisms and ecosystems that we set out to understand. Simultaneously, this dissertation advances non-lethal acoustic approaches for studying bumble bee colonies and underscores the potential for acoustic monitoring techniques as a viable, affordable, non-invasive, and scalable sampling technique. Lastly, by investigating the conceptualizations of resilience of landuse experts and decision-makers in rural Missouri, I pinpointed overlapping challenges and priorities, which is a vital step for the state to develop more resilient communities and landscapes in the face of climate change. These tools and insights advance more conservation-oriented research techniques and lay the groundwork for expanding climate adaptation efforts throughout rural Missouri.

VITA

Zachary J. Miller was born in April of 1988, and he grew up south of St. Louis in Missouri, United States of America. Miller earned a Bachelor of Arts degree in Environmental Studies with an emphasis on sustainable food systems from Truman State University in Kirksville, Missouri. Subsequently, he served in the United States Peace Corps in Paraguay as an Agricultural Extensionist from 2013-2015. Miller began his PhD work with Candace Galen in the fall of 2017 and transitioned to Lauren Sullivan's lab in the summer of 2021. For part of his PhD research, Miller helped developed acoustic tools for investigating bumble bees, demonstrating the viability of alternative, non-lethal methods for studying important pollinators. He contributed to long-term data collection at Pennsylvania Mountain in Fairplay, CO, and helped use these climate and floral data to understand how shifts in climate affect plant-pollinator relationships. He also investigated how rural experts and decision-makers in Missouri perceive climate resilience. Miller is passionate about science communication, cross-sector collaboration, and evidence-based public policymaking. He has accepted a position as Program Coordinator with MOST Policy Initiative in Jefferson City, Missouri.