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Characterizing the Range Shifts of Two Peromyscus Species in Maine

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CHARACTERIZING THE RANGE SHIFTS OF TWO *PEROMYSCUS* SPECIES IN MAINE

by

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ABSTRACT

In a changing climate, two species of mice in Maine (*Peromyscus maniculatus* and *Peromyscus leucopus*) are currently undergoing range shifts. The objective of my thesis is to determine the historical and current range of each species within the state of Maine. I used two approaches. I assembled ear biopsies collected this summer in Acadia National Park and throughout the state by the Gardner and Levesque labs to genotype the mice as either *P. maniculatus* or *P. leucopus*. Additionally, I summarized research that denotes where the two species were historically present around the state. These species are functionally impossible to tell apart in the field, and projects that use small mammal trapping often simply choose one of the two species to identify all uncertain mice. A lack of genotyping and data from a current time frame hindered our understanding of the ranges of the species. However, knowledge of the ranges of the deer mouse and the white-footed mouse could yield information as to how the two species might differ as reservoirs for tick-borne disease, catalysts for forest community development, and models for mammalian range shifts.

DEDICATION

This thesis is dedicated to the wildlife that has been disturbed for the sake of research projects involved in this thesis, and in others that have furthered the author's education. The author acknowledges the sacrifice that other livings things must give in order for humans to learn about and begin to protect the natural world.

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INTRODUCTION

As the climate continues to change, many species are undergoing unprecedented range shifts (Chen et al. 2011). Ecologists are becoming intimately familiar with the new pressures introduced by climate change that force species to adapt or go extinct. These pressures can manifest in a myriad of ways: a dwindling food source, habitat fragmentation, or ecological mismatch (Tyson and Lutscher 2016). We are still discovering the extent of the damage climate change is affecting on the earth's ecosystems. One of the biggest pressures for mammals is to shift their range to retain the environmental gradients of the habitat they have adapted to.

A well-documented example of this phenomenon takes place in northern Alaska. There, subsistence hunters relied on marine mammals like fur seals until recently, as sea ice dwindled and the ecosystem began to change, removing this source of food. A longer growing season allowed woody shrubs like alder (*Alnus incana*) and willow (*Salix* spp.) to prosper, growing taller and more numerous than before (Tape et al. 2006). Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) arrived in the area to browse on this new growth (Tape et al. 2016), providing a new food source for the indigenous population and untold ecological consequences for other organisms.

Range shifts are not usually this simple. Often, they are entangled with other differences like habitat and land use change, as humans alter their landscape to suit their needs. Ecological complexity makes it difficult to identify which specific mechanisms and variables facilitate range shift and which do not (Oliver and Morecroft 2014). Documenting changes in range will help ecologists understand when and why a species moves, which would have huge implications for our struggle to predict how landscapes

will change, how we manage wildlife, and how to maintain ecosystem services that humans rely on (Pecl et al. 2017). Every organism serves a different role in its environment and therefore is important in characterizing the massive ecological changes that are already making themselves known.

As we study how mammals use their space differently with a changing climate, model species are useful as a baseline to gain insight into how other species might operate. Mice and other small mammals are popular study organisms because they are relatively easy to trap, they reproduce quickly, and are small. Additionally, from a trophic perspective, mice in the northeast are a common food source for predators from birds to other mammals and fluctuations in their range would affect their predators as well (Tyson and Lutscher 2016). Thus there are several reasons any dispersal is important to notice.

Here in Maine, two mice with a similar life history and survival strategy have been on the move (Choate 1973). The deer mouse and the white-footed mouse, *Peromyscus maniculatus* and *Peromyscus leucopus* respectively, are very difficult, if not impossible, to reliably tell apart in the field (Parren and Capen 1985). This makes characterizing their range a challenge because genotyping (using DNA to identify species) is required to obtain a certain identification, establishing the importance of genetic analysis like multiplex PCR. Genotyping also reveals the extent to which the species have hybridized.

The mice are fairly elusive and do not have any direct connections to the daily lives of most people, so it is not immediately obvious why understanding their range is important. However, there are three main reasons why this phenomenon is important not only to ecologists but to the general public as well. First, mice play an important role in

the development of forest communities with their seed predation behaviors and can shape habitat quality for other species (Boone and Mortelliti 2019), including those of interest to wildlife managers like the white-tailed deer, moose, and lynx. Also, the mice act as hosts for disease vectors and reservoirs for the disease they transmit, namely the black-legged tick (*Ixodes scapularis*) (Fiset et al. 2015). The two species may have different competence as hosts for this vector and therefore pose separate risks for humans. As the range of the hosts of a vector expand, its range may expand as well (Ogden et al. 2006, Roy-Dufresne et al. 2013). Finally, the range shifts of species such as deer mice could act as a predictive model for other mammalian range shifts. Small mammals are easier to obtain a large quantity of data on than megafauna like bear and moose. The study of these species could reveal patterns in climate migration that are unique to mammals, which would provide information useful in predicting the movements of other species.

Small mammal distributions have been studied more extensively in bordering states and provinces (Fiset et al. 2015, Leo and Millien 2017), but Maine remains a missing puzzle piece that could help us complete the picture of how these two species are moving in the Northeast. I conducted a literature review and used genotyped samples to build a picture of potential range shifts in *Peromyscus maniculatus* and *Peromyscus leucopus* within Maine. These species, generally considered to be slightly more cold-tolerant and more warm-tolerant respectively, could reflect how temperatures are affecting local mammalian populations. With this information, in the future we can gain insight as to whether they will adapt to a changing environment or move to follow the environmental gradients they are adapted to.

METHODS

To determine where the two species historically and currently occur in Maine, I performed a systematic review of the existing literature. This review started with a basic search on engines including Web of Science, Google Scholar, and in digital libraries such as JSTOR, Ebsco and Wiley. Keywords used to search for relevant articles included: *Peromyscus*, range shift, Maine, *maniculatus*, *leucopus*, New Hampshire, Quebec, migration, distribution, presence, climate change. I also searched the references in the most relevant studies I found to lead me to other useful information. Many of these articles describe Maine, but others include relevant information about surrounding states and provinces for better context.

I used two parameters to evaluate the relevance of an article to my work: if it was relevant to Maine and included information one or both of *Peromyscus maniculatus* and *Peromyscus leucopus*. Some very old chapters or articles fulfilled these criteria but did not contain enough information to be of use, so these were excluded. I kept track of articles in a Microsoft Excel spreadsheet and gathered the following information from them: date, author(s), location by town, *P. maniculatus* presence, *P. leucopus* presence, and whether samples had been genotyped.

To supplement the literature review, genotyping was completed by Dr. Ek Han Tan's lab to genotype *Peromyscus* samples. I obtained the samples from the Levesque, Mortelliti, Gardner, and Gill labs, some historical samples and others live-trapped the previous summer. Ear biopsies were taken from the mice to use in genotyping. In this case, PCR is used to identify and amplify a small segment of DNA from a tissue sample, in this case segments that are characteristic of either *Peromyscus maniculatus* or

Peromyscus leucopus (Tessier et al. 2004). The lab followed the protocol found in the article discussing *Peromyscus* species identification from Tessier et al (2004), which involved mixing reaction buffer, primers, DNA polymerase, template DNA, MgCl2, and dNTP. Temperature was adjusted to denature the DNA strands, and PCR products were then run on 3% agarose gel. The only departure from this protocol was the use of GoTaq G2 Master Mix for bioassays, and information from genotyping was added to the Excel spreadsheet for input into GIS to create a map.

These data made it possible for me to create a map in GIS showing where specimens were collected and identified by others over the years. The map was created as part of the coursework for GIS200 with the help of Dr. Tora Johnson through the University of Machias. My own data was supplemented by that of the Maine Office of GIS to provide map inputs such as rivers, which act as natural barriers, and state borders.

RESULTS

The literature review yielded 19 relevant articles (Table 1), some in Maine detailing the distribution of *Peromyscus maniculatus* or *Peromyscus leucopus*, and others in Quebec or elsewhere in the United States documenting either the range shift of these mice or climate information pertinent to their distribution, to provide context to the Maine samples. Genotyping of 25 samples yielded 9 distinct locations with 16 of the samples identified as *P. leucopus*, 8 identified as *P. maniculatus*, one without any amplification of DNA and one potential hybrid (a result of reproduction between one of each species) showing amplification of both species-specific primers (Table 2). The hybrid was found on Mount Desert Island in the summer of 2019. These data were added to the map for a total of 65 points. Only 14 of these were in the "current" category (Figure 2), with a majority of 51 points in the "historical" category (Figure 1).

On the historical map (Figure 1), near the Bangor area there are two points on either side of the Penobscot River that represent *P. maniculatus* in Argyle and *P. leucopus* in Greenbush. Later in time, in the current map, *P. leucopus* was found in Bradley and both species are present on the other side of the river in Orono.

Table 1. Results of literature review, including authors, date, location, species present in study, and whether the identification was confirmed with genotyping

	Authors	Date	Location	*maniculatus*	*leucopus*	confirmed?
1	Garman *et al*	1994	MDI	y	y	n
2	Aquadro *et al*	1980	Massachusetts	y	y	y
3	Elias *et al*	2004	Holt Research Forest	n	y	n
4	Rich *et al*	1996	several	y	y	y
5	Choate	1973	several	y	y	y
6	Tessier	2004	Quebec	y	y	y
7	McCracken *et al*	1999	Holt Research Forest	n	y	n
8	Kilpatrick *et al*	1989-1993	several	y	y	y
9	Cole	1993	Isle Au Haut	y	n	n
10	Leo *et al*	2017	Quebec	y	y	y
11	Fiset *et al*	2015	Quebec	y	y	y
12	Dragoo *et al*	2006	several	y	n	y
13	Millien *et al*	2015	Quebec	y	y	y
14	Yang	2011	Yosemite	y	n	y
15	Moscarella	2019	Great Lakes	n	y	y
16	Ledevin	2013	Quebec	y	y	y
17	Glazier	1980	New England	y	y	n
18	Hoymack *et al*	2005	Northern Maine	y	n	n
19	Wood *et al*	2015	Eustis	y	n	n

Table 2. Species ID of mice in Maine. X denotes presence of identifying segments of DNA. O denotes absence.

Sample	Original Name	Additional Info	*P. maniculatus*	*P. leucopus*	Notes
--	Han's House	Orono, Maine	O	X	
A	010-PEI	MDI	O	X	
B	UMPI Pero 9 Nov 19	Presque Isle	X	O	
C	1233	MDI 2019	X	X	Hybrid? Equal amplification of both bands
D	1230	MDI 2019	O	X	
E	1234	MDI 2019	--	--	No amplification
F	1	Stillwater 1973	X	O	
G	2	East Corinth 1990	O	X	
H	3	East Corinth 1990	O	X	
I	4	East Corinth 1990	X	O	
J	5	No location, 1992	O	X	
K	6	No location, 1974	X	O	
L	7	East Corinth 1990	X	O	
M	8	Argyle 1989	X	O	
N	9	Argyle 1989	X	O	
O	10	Greenbush 1989	O	X	
P	11	Greenbush 1989	O	X	
Q	PE6	MDI 2019	O	X	
R	003-PE2	MDI 2019	O	X	
S	PE4-001	MDI 2019	O	X	
T	PE7	MDI 2019	O	X	
U	PE5	MDI 2019	O	X	
V	C4	Penobscot Experimental Forest	O	X	
W	10/12/17	Penobscot Experimental Forest	O	X	
X	9/14/17	Penobscot Experimental Forest	O	X	

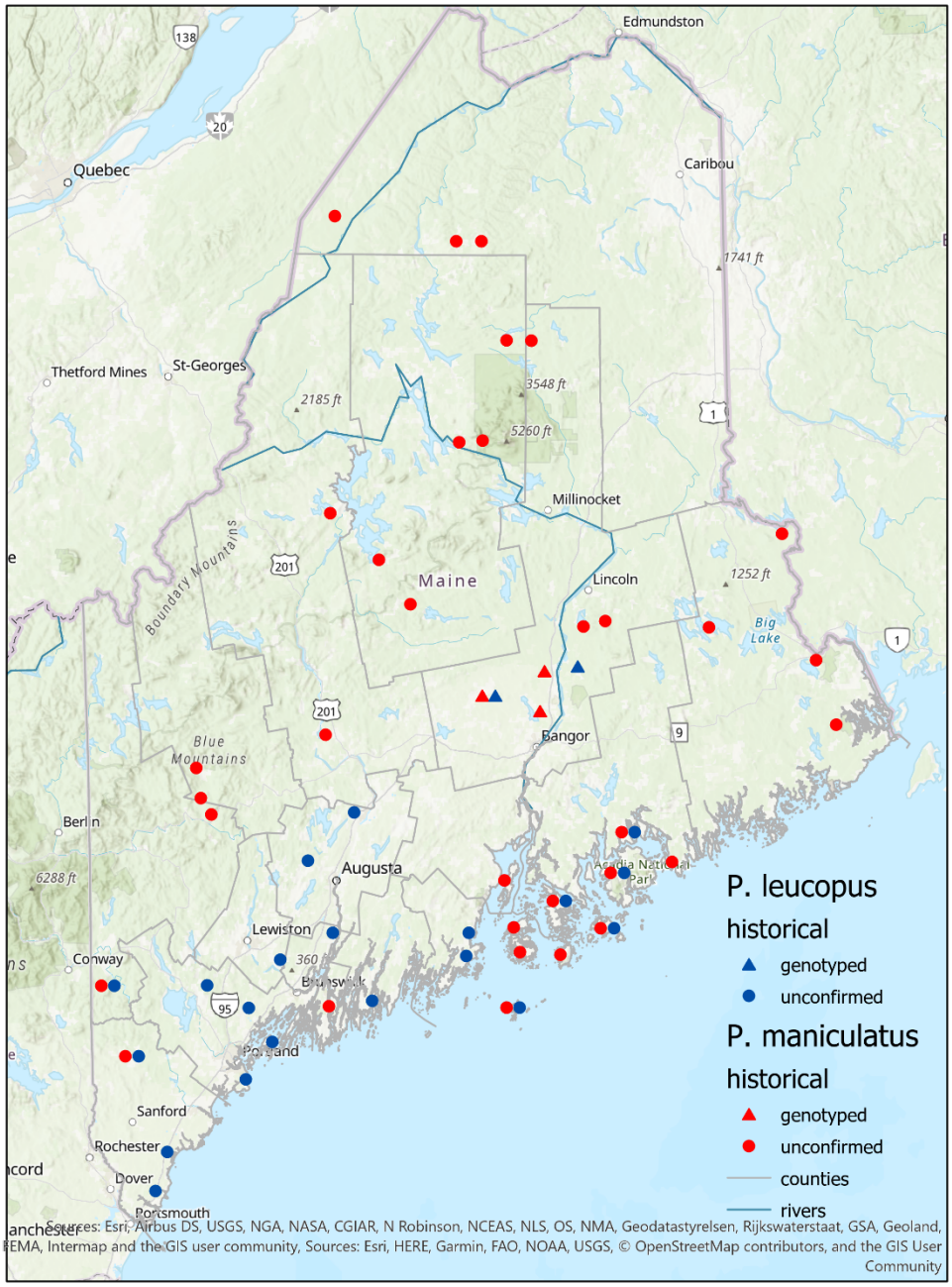

Figure 1. Map of historical (before 2000) confirmed locations of *Peromyscus maniculatus* and *Peromyscus leucopus* in the state of Maine, United States. Maine Office of GIS data was used for county borders and rivers.

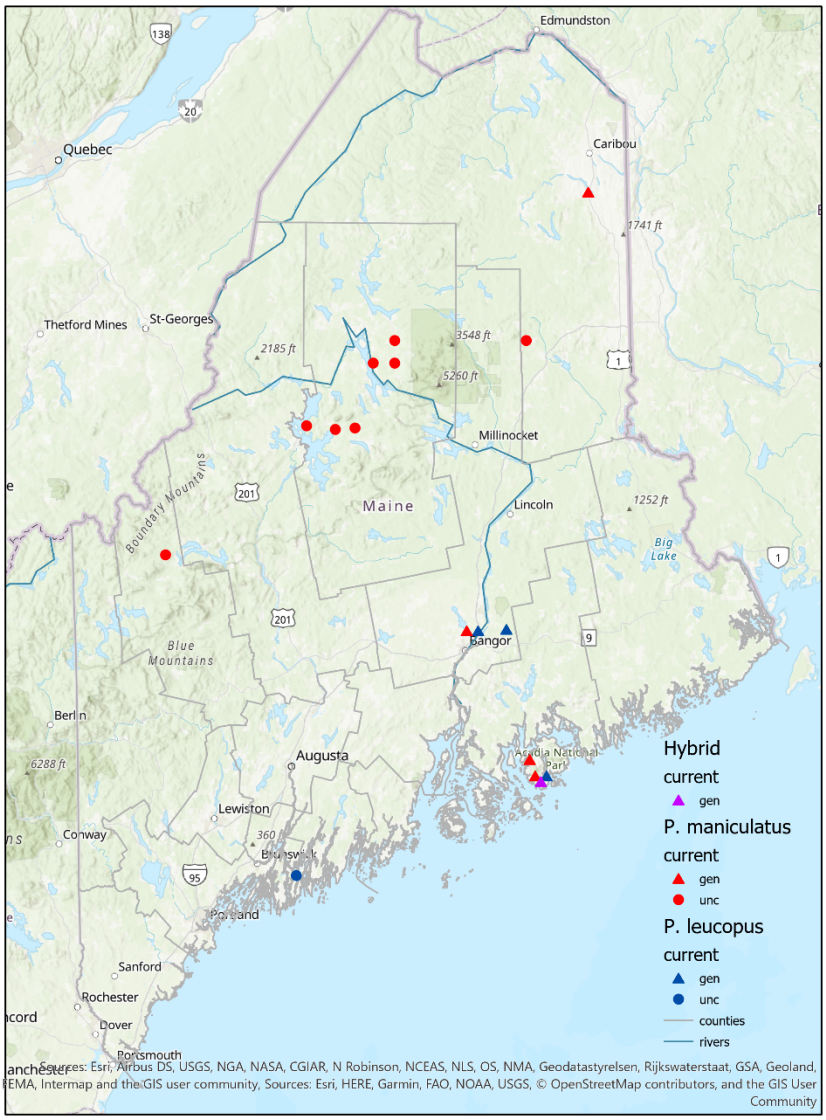

Figure 2. Map of current (after 2000) confirmed locations of *Peromyscus maniculatus* and *Peromyscus leucopus* in the state of Maine, United States. Maine Office of GIS data was used for county borders and rivers.

DISCUSSION

I found that *Peromyscus maniculatus* and *Peromyscus leucopus* have been present in Maine's landscape differently in the last 20 years than they were before the year 2000. The southern part of the state appears to dominated by *P. leucopus* in both time frames, and the northern part of the state remains a stronghold for *P. maniculatus*. However, in the current map there appears to be some more mixing, or both species inhabiting the same area, in the southern, central, and coastal parts of the state. Also, *P. leucopus* is now present on both sides of the Penobscot River, and there is a potential hybrid that was found on Mount Desert Island.

Hybridization is a potential consequence of range shift of similar species. The two species were found to have a low frequency of hybridization in Quebec where their ranges overlap (Leo and Millien 2017). Northern and southern flying squirrels have experienced a degree of hybridization as warm temperatures facilitated a move north by the southern species (Garroway et al. 2010). Loss of habitat for the southern flying squirrel also could have contributed to this shift (Garroway et al. 2010), which could be true also of *Peromyscus leucopus* in increasingly developed areas as its behavior around humans changes. These mice are not a conservation concern at this time, but hybridization from anthropomorphic influences is generally seen as incompatible with conservation goals (Allendorf et al. 2001). A topic for further study could be comparing distribution of the two species to human impact in Maine or elsewhere.

A challenge in this project was that many observations of the two species were not confirmed with genotyping, rendering them much less credible. For example, older notes rely on pelage or tail length differences, which vary within species and cannot

reliably distinguish between species (Feldhamer et al. 1983). However, to only focus on genotyped samples would be to omit a large amount of the literature, especially that of the historical data. Also, hybridization may have taken place in low frequencies in recent years (Leo and Millien 2017), creating the possibility that these mice really did look different from each other several decades ago. Presence of hybrid *Peromyscus* individuals found could also imply that *P. maniculatus*, the more cold-associated species, can tolerate warmer temperatures and will stay in the southern part of its range. Although the two species presumably have different adaptations, their life histories and morphologies are similar, which could explain the continued presence of *P. maniculatus* in the southern and coastal parts of the state. Since the mice are difficult to tell apart in the field, genotyping would be necessary for more study into this topic. Interestingly, one of the mice collected on Mount Desert Island showed amplification for both identifying strands of DNA (Table 2), so it could be a hybrid. Genotyping offers a definite identification and can give us insight into the potential movements of both species and their genetic interactions (Tessier et al. 2004).

The oldest sources I have found take more of a natural history approach than an experimental one, with coarse surveys of every mammal in an area. For example, Cole (1993) focused on Isle Au Haut, and simply wrote down every mammal observed, naming the deer mouse among them (Cole 1993). For those who are familiar with the ambiguity between the two species in the field, it is very common to simply make an educated guess about the identity of all the mice and refer to all specimens that way. This makes sense for scientists who do not have the resources or study focus to genotype every sample they come across. Others have attempted to identify the mice based on

other features, like pelage color, relative size, and especially skull measurements (O'Connell and Connery 1993, Rich et al. 1996). They have had some success, but the older papers are generally more successful in the morphological method of identification since the two species are now being found in the same areas and are more difficult to tell apart.

Some newer studies followed the same approach as the older ones, but many supplemented their work with genotyping to link the mice with a habitat type. The general rule of thumb has been that *Peromyscus maniculatus*, being more cold-tolerant selects colder boreal forests while *Peromyscus leucopus* prefers southern hardwood forests (Fiset et al. 2015). In Maine, these two forest types are not always discrete – often, they are mixed or at least close together (Chokkalingam and White 2001) . The state (and to a lesser degree, the rest of New England) represents a border between two biomes and therefore the wildlife that specialize in each forest type. There is a gap in the literature as far as recent studies on the movements of these species. More work on this topic can be found by our neighbors in New Hampshire and especially Quebec (Tessier et al. 2004, Fiset et al. 2015, Leo and Millien 2017), which provides some context to what may be happening in Maine. These studies have found that *P. maniculatus* tends to be found in colder boreal forests while *P. leucopus* appears to be colonizing from the south, but also that the two species have a low degree of hybridizations where their ranges meet. Maine is still a missing puzzle piece within the broader context of mammalian migration and climate change - we do not know yet how these findings manifest (or not) in the state. This lack of information is evident in the number of observations from before 2000 versus after 2000.

Land use change is another factor that could explain the differences in distribution for these species. Other recent studies move away from the general survey type of study and toward more applied problems (McCracken et al. 1999, Wood and McKinney 2015), often related to forestry practices, as logging remains a major industry in Maine and foresters are concerned what impacts the growth of forests (Boone and Mortelliti 2019) . These studies tend to be more relevant to the question this study addresses, as they touch on the direct foraging behavior of the mice. If the mice strongly prefer the seeds of certain species, they may migrate to follow the range shifts of those species, especially as forest composition in the state differs due to climate change (Gasperini et al. 2016). Logging practices like clear-cutting and selective harvest drastically change the habitat quality of forests (Fuller et al. 2004). However, no matter the cause, range shifts are not usually a uniform and simple phenomenon that is easy to detect.

A complicating factor visible in many studies involves rivers or other waterways (Fiset et al. 2015). Small mammals cannot easily cross large bodies of water (what we consider large is likely different than what they consider large) and so their migrations may cease or change near rivers or lakes. This is relevant in Maine and especially in Orono because we are right next to the Penobscot River, the largest inland water system in the state. As seen in the historical map, the waterway represents one type of natural barrier to the mice and interrupts the interactions the two species may have with each other, like any potential hybridization or pursuit of certain trees. This information could be used to learn about more significant barriers, such as mountain ranges or presence of humans to larger species, as well as predict the changes in forest communities if mice immigrate or emigrate to different stands. There is not yet data on a large enough scale in

Maine to really see how closely these mice follow their preferred tree species (or definitively what those species are), but we know that habitat conservation plays an important role in protecting species. The relationship the mice have with their habitat could yield detailed information about how Maine's climate is changing on a finer scale.

CONCLUSION

My findings show that there is movement from *P. maniculatus* and *P. leucopus* in Maine, evident in multiple factors: *P. leucopus* seems to have crossed the Penobscot River at some point, there has been a potential hybrid found on Mount Desert Island, and the distinct boundaries between the northern and southern/coastal parts of the state have been less clear due to municipalities that report the presence of both species. These differences would be clearer with more studies on the distribution of each species, but there is enough to suggest that the mice occupy different areas than they did historically.

Range shifts of these species are visible elsewhere, such as Michigan (Martin 2012) and Quebec (Leo and Millien 2017), so it is likely that one is occurring in Maine as well. However, it may not be just from climate change (although the effects of climate change can hardly be overstated). Habitat and land use changes affect species from insects to small mammals to megafauna like moose and bear (Ross et al. 1999). To better understand what exactly is making these two species move, a multifaceted approach should be taken to assess different aspects of their habitat throughout the state, one that explores multiple potential causes of the change in order to find out the specific mechanisms that are facilitating the shift.

My findings are significant because they lend insight as to how Maine's climate is changing now and how it will change in the future, and how land use and habitat shifts are helping or hurting Maine's native wildlife populations. A more complete understanding of range shifts and climate change within the state is relevant to wildlife managers, other ecologists, and all who benefit from ecosystem services (Chen et al. 2011). My work could

be a starting point to address these questions and others regarding species on the move in the Northeast.

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Molly Rose Bennett was born on March 7th, 1998, in Portland, Maine. She grew up in Falmouth, Maine and graduated from Falmouth High School in 2016. During her time as an undergraduate at the University of Maine, Molly enjoyed gaining an ecological knowledge of a wide variety of species and topics, although she never could choose quite what her favorite taxa are. She plans to continue her formal education with a master's degree and to be a lifelong student of the natural world. In her spare time, Molly likes trail running, spending time with friends human, canine, or otherwise, playing roller derby, trying to change the world a little bit at a time, and taking naps.