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Mind the Gap: Effects of Habitat and Climate on Northern Water Snake (Nerodia Sipedon Sipedon) Distribution in Maine

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MIND THE GAP: EFFECTS OF HABITAT AND CLIMATE ON NORTHERN WATER SNAKE (*NERODIA SIPEDON SIPEDON*) DISTRIBUTION IN MAINE

by

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ABSTRACT

Northern water snakes (*Nerodia sipedon sipedon*) have a disjunct geographic range in the northeastern part of their distribution, specifically in Maine with one occupied region about 125 kilometers from any other known population. This gap could be due to a number of factors with some currently affecting the species including dispersal and habitat characteristics, while some factors may have historically affected their distribution, such as retreating glaciers and climate change. We assessed the effects of lake characteristics and bioclimatic variables on the range of *N. s. sipedon* within Maine using a logistic regression built from a generalized liner model. Lake characteristics (e.g. pH, surface temperature, and area) did not affect snake presence within their range, but bioclimatic variables did show statistical significance. In particular, lakes where the snakes were present were warmer than lakes where they were absent. When the bioclimate of the eastern range of *N. s. sipedon* was compared to the range gap the best model based on AIC scores showed that mean temperature of the warmest quarter, annual precipitation, and annual mean temperature were different between the areas. Bioclimatic variables also explained the restriction on *N. s. sipedon* expanding their range northwards. We conclude that bioclimatic variables have a large effect on the current distribution of *N. s. sipedon* within Maine and can help explain why the range gap persists.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

A taxon has a disjunct range when multiple populations are geographically and genetically separated from one another, and these isolated populations usually occur at a taxon's range margin (Bengtsson 1993). Disjunct ranges can result in speciation (Rocha 2003, Craw 2015), but this process takes tens of thousands to millions of years. Disjunct ranges have been seldom studied, and most studies are on plant and fungi species (Schneeweiss and Schonswetter 2010, Salvador-Montoya et al. 2015). Some studies have examined the disjunct ranges of animals, often trying to determine why the populations are disjunct (Baker et al. 2000, Lavers et al. 2006). Disjunct ranges can be driven by tectonic movement (Craw et al. 2015), natural barriers (Rocha 2003), reduction of habitat (Kozak et al. 2006), and climate changes. Many of these range gaps date back to the Holocene or Pleistocene during warm periods when animals were extending their ranges and then reduced to refugia by ensuing cool periods. This is usually the case for reptiles and amphibians as they are ectothermic poikilotherms. This can be seen in the Nova Scotia population of Blanding's turtles (*Emydoidea blandingii*) which are a relic of the mid-Holocene and were restricted to their current refugia during a later cool period (Spooner et al. 2014). The northern water snake (*Nerodia sipedon sipedon*) occurs in the same area and may have undergone a similar process.

N. s. sipedon occurs throughout much of the eastern United States ranging from Maine and Ontario to Alabama and out west to Nebraska and Colorado. They have been the subject of numerous studies, such as foraging methods (Balent and Andreadis 1998) and thermal constraints on swimming (Weatherhead and Robertson 1992). Some studies have looked at habitat selection (Johnson 1980), particularly basking site selection (Robertson and Weatherhead 1992, Burger et al. 2004). Roth II and Greene (2006) looked at third-order selection, and found that within their home range *N. s. sipedon* selected for areas with aquatic vegetation. Other studies have looked at second-order selection; for example Cecala et al. (2010) found that juvenile water snakes selected lower order streams for their home ranges due to the available cover and lack of predators. These finer scale studies can help to inform questions about geographic ranges, i.e., first-order selection. Rose and Todd (2014) looked at the invasion risk of introduced populations of *N. s. sipedon* and southern watersnakes (*Nerodia fasciata*) in California. They developed a species distribution model and found that presence of wetlands and temperature during the warmest and coolest quarters drove the model for presence of *N. s. sipedon*. This model greatly overestimated the current range of *N. s. sipedon* in Maine, most likely due to the presence of wetland habitat. An incorporation of finer scale variables may help to reduce the projected range.

N. s. sipedon in Maine is at the northern range limit of the species but has not been systematically studied. In Maine there are two populations: one which is connected to the main range of *N. s. sipedon* and a second isolated population along the border with New Brunswick in eastern Maine, near Calais (Figure 1). The two populations are separated by about 125 kilometers even though there are many aquatic ecosystems between the two populations that would seem to be good habitat for *N. s. sipedon*. The goals of this study were: (1) to understand the range of *N. s. sipedon* in Maine and (2) to determine what factors affect *N. s. sipedon* presence in Maine, specifically lakes.

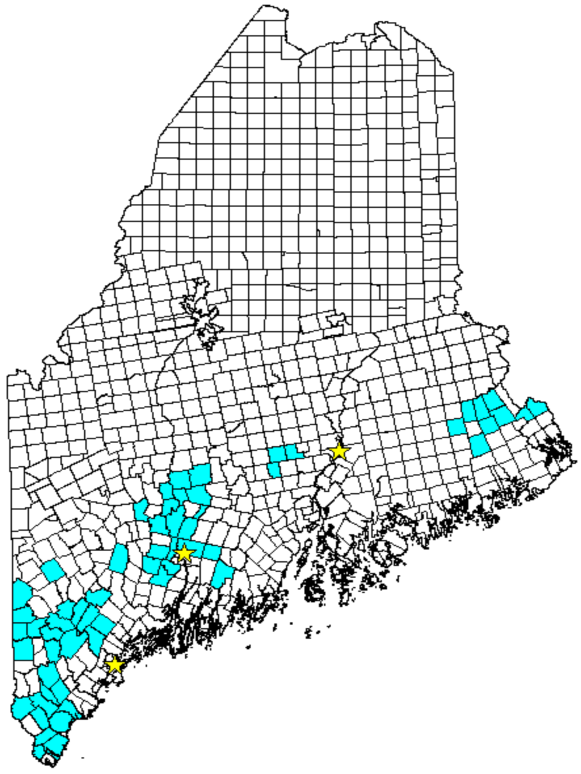

Figure 1. Map of northern water snake (*Nerodia sipedon sipedon*) records in Maine, USA; stars are Portland, Augusta, and Orono.

METHODS

N. s. sipedon records were obtained from the Maine Amphibian and Reptile Atlas Project (MARAP). These records date back to 1906, but a majority are after 1984. We only used records backed with photographs or specimens, or where the snake was handled by a professional biologist. These records were from locations in or close to ponds or lakes (hereafter referred to as lakes). MARAP records were also used to identify comparison lakes where MARAP volunteers had submitted multiple records of species other than *N. s. sipedon*, but no *N. s. sipedon* records. Specifically, comparison lakes for which *N. s. sipedon* was considered absent (henceforth Absence lakes) had four other species recorded or three species observed, and at least one of the three species having multiple records. This indicates that herpetofauna surveyors have probably been to these lakes multiple times.

Multiple lake characteristics were obtained from the Maine Department of Environmental Protection's publicly accessible databases including pH, surface temperature (top meter), mean depth, lake area, and shoreline length. All characteristics were averaged over measurements from the last 20 years. Lake area and shoreline length were used to calculate shoreline development per:

$$D_L = \frac{L}{2\sqrt{\pi A}}$$

In which (L) us shoreline length and A is area.

Two additional lake characteristics were measured using the GIS platform MapInfo and GIS layers from the National Wetlands Inventory (NWI). Because streams provide refuge and hunting sites for juvenile water snakes (Cecala et al. 2010) the number of streams for each lake was recorded and expressed relative to the length of lake shoreline for each lake. Similarly the total area of wetlands greater than 1 ha (Roe et al. 2003) within a 200 m buffer around each lake was measured. Only lentic aquatic ecosystems that were non-adjacent to the lake were counted. The total area of wetlands within the buffer was expressed relative to the total area within the buffer, not including the lake. Bioclimatic variables were obtained from the WorldClim database (http://worldclim.org) and all nineteen were used (Appendix 1). Bioclimatic variables are values of temperature and precipitation which are computed as means, extremes, and ranges. They are measured yearly, seasonally, quarterly, and monthly. Version 1.4 was used at the highest resolution (30 arc-seconds (~1 km)) and tile 13 was used.

Statistical Analysis

The statistical program R version 3.3.2 was used to evaluate relationships between presence, absence, and habitat parameters (both lake and bioclimatic). Lake characteristics were modeled using a logistic regression, because presence and absence data are binomial. Models were compared to one another using p-values. P-values were compared to the alpha value ($\alpha = 0.05$) and were considered significant if they were less than the alpha value. Akaike information criterion (AIC) was not used as not all lakes had available data for every characteristic and therefore the number of parameters within each model differed.

Bioclimatic variables were assessed for their influence in distinguishing Presence and Absence lakes within the potential range of *N. s. sipedon* in Maine; that is comparing locations in their known current range and the range gap. These variables were tested for collinearity between each other, with any relationship having an $r \geq 0.7$ considered as collinear (Dormann et al. 2013) and not tested together in the same model. Variables were assessed using a generalized linear model and compared to a null model. AIC was used to rank the models and determine which model was the best. Models were tested by using a single bioclimatic variable and then variables whose models had ΔAIC values $\geq$ 2.00 compared to the null or previous best model were added to the top model to see if a better model was produced. Bioclimatic variables were also used to compare the climate between the range gap and the disjunct eastern range of *N. s. sipedon*. Specifically, the bioclimate variables of the eight Presence lakes in eastern Maine were compared to the bioclimate variables of 25 background points randomly generated in the gap (Figure 2). Bioclimatic variables were also tested for their effects on the northern range limit of *N. s. sipedon*. Instead of comparing the values between Presence and Absence lake locations we used background points, which are random locations. One hundred background points were created randomly between latitudes 43° and 48° and longitudes -67° and -71.5° and, compared to the Presence lakes (Figure 3).

McFadden's r-squared was calculated for the top models based on AIC scores. These pseudo r-squared values give an estimation of the goodness-of-fit of the model to the data as r-squared values are not reported for linear regressions. McFadden's r-squared values are based off of the log likelihood of the top model and the null model (McFadden 1974), with a value of zero showing very little power, while a value of one showing that the predictors are very strong.

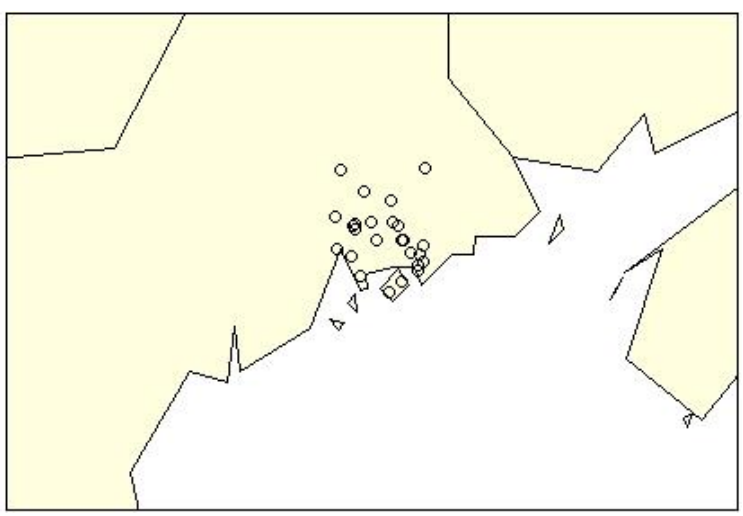

Figure 2. Map of background points used in evaluating the bioclimatic variables driving the difference between the range gap and the eastern range of *N. s. sipedon* in Maine, USA.

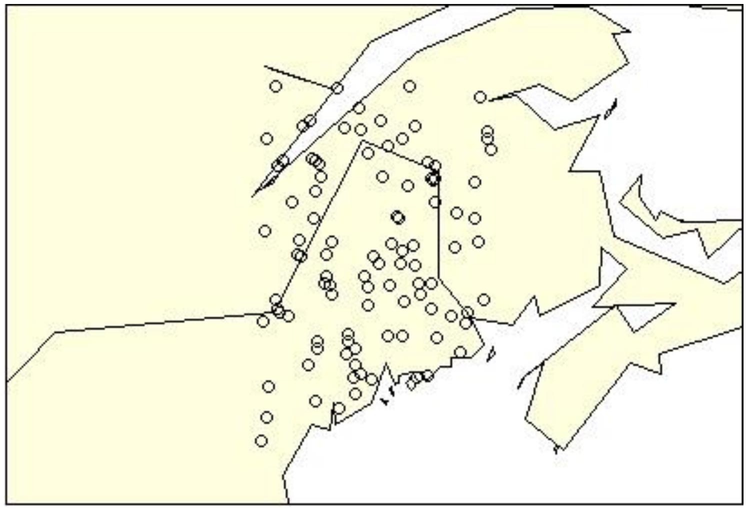

Figure 3. Map of background points used in evaluating the bioclimatic variables driving the northern range limit of *N. s. sipedon* in Maine, USA.

RESULTS

N. s. sipedon were found in 32 lakes and was considered absent from 32 lakes for which MARAP records of other species suggested that *N. s. sipedon* would have been detected if present (Figure 4). Among the 32 Absence lakes, 17 were in the gap between the two Maine populations and 15 were in the known range. 28 species were detected in Absence lakes. Two species were found in more than half of the Absence lakes, the American bullfrog (*Lithobates catesbeianus*), 22 lakes, and the eastern painted turtle (*Chrysemys picta picta*), 18 lakes.

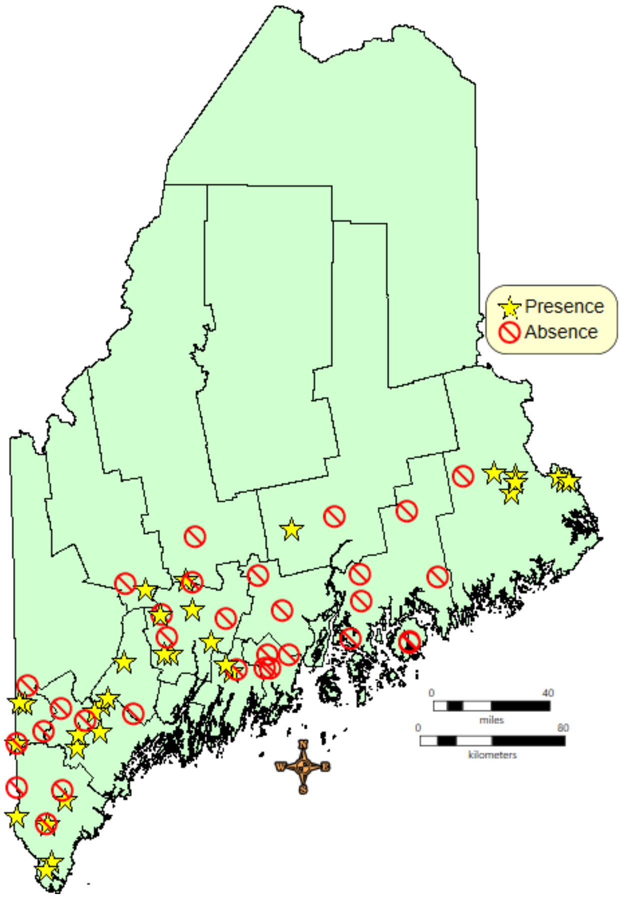

Figure 4. Map of northern water snake (*Nerodia sipedon sipedon*) presence and absence in Maine, USA.

Bioclimatic variables influenced the presence of *N. s. sipedon* in their potential range and helped to explain their range gap. The top model predicting presence within the potential range of *N. s. sipedon* was based on mean temperature of the wettest quarter (Table 1) (Bio 8) with an AIC value of 94.694 and a slope estimate of 0.00913 ± 0.00448. This model produced a McFadden's r-squared value of 0.045. When mean temperature of the wettest quarter was paired with precipitation seasonality (Bio 15) or with precipitation of the wettest quarter (Bio 16) the model also produced a significant result, with ΔAIC values of 1.401 and 1.493 respectively (Table 1). In these models precipitation seasonality had a slope estimate of -0.0023 ± 0.0032. Precipitation of the wettest quarter had a slope estimate of -0.0267 ± 0.0353. Three models could not be produced as the bioclimatic variables were collinear.

Table 1. AIC table of the top 3 models showing the relationship between bioclimatic variables and snake presence within *N. s. sipedon* range.

Model	AIC	ΔAIC
Mean temp. of wettest quarter	94.694	0.000
Mean temp. of wettest quarter + mean temp. of the warmest quarter	94.985	0.291
Mean temp. of wettest quarter + max temp. of the warmest month	95.706	1.012

The top model comparing the eastern population to background points in the gap was based on mean temperature of the warmest quarter (Bio 10), annual precipitation (Bio 12), and annual mean temperature (Bio 1). This model had an AIC value of 18.89; all other models had ΔAIC values ≥ 2.00. This model produced a McFadden's r-squared value of 0.741. Sixteen models could not be produced as the bioclimatic variables were collinear.

Bioclimatic variables also influenced the northern range limit of *N. s. sipedon*. The top model was based on annual mean temperature (Bio 1), mean temperature of the driest quarter (Bio 9), precipitation of the warmest quarter (Bio 18), precipitation of wettest quarter (Bio 16), and precipitation of the driest quarter (Bio 17). This model produced an AIC value of 70.174 (Table 2) and had a McFadden's r-squared value of 0.628. Thirteen models could not be produced as the bioclimatic variables were collinear. The slope estimates of the top model showed a positive relationship between presence and annual mean temperature, mean temperature and precipitation of the driest quarter, and precipitation of the warmest quarter. An inverse relationship was seen between presence and precipitation of the wettest quarter. The top model with isothermality (the mean of the difference of the extreme temperatures of each month divided by the difference of the annual extreme temperatures) (Bio 3) produced a significant model with an AIC value of 71.075 (Table 2). The slope estimates for the parameters in each of these models was greater than the standard errors.

Table 2. AIC table of the best models predicting the influence of bioclimatic variables on the northern range limit of *N. s. sipedon*.

Model [a]	AIC	ΔAIC
Annual mean temp. + mean temp. of driest quarter + precipitation of warmest quarter + precipitation of wettest quarter + precipitation of driest quarter	70.174	0.000
Annual mean temp. + mean temp. of driest quarter + precipitation of warmest quarter + precipitation of wettest quarter + precipitation of driest quarter + Isothermality	71.075	0.901

[a] 13 models not created due to collinearity between variables

Both *N. s. sipedon* Presence and Absence lakes had widely varying characteristics (Table 3). Lakes area ranged from 1.62-12137 hectares, while the average mean depth ranged from 0.6 - 32.6 meters. Surface temperature ranged from 18.96 – 25.25 °C, while pH ranged from 5.98 – 7.65. Shoreline development values ranged from 1.07 – 7.52. Shoreline distance between streams was ranged from 0.24 - 8.58 km, while the proportion of non-adjacent lentic wetlands within a 200 meter buffer ranged from 0 – 0.23.

Shoreline development, streams, and area had the lowest p-values out of the variables tested, but when fitted to a logistic regression were not significant (p-value > 0.05) (Table 4). These variables also had higher standard errors than their estimates (Table 4), showing that the models are unstable and unreliable.

Table 3. Means, medians, and ranges of measured lake characteristics, Maine, USA.

Characteristic	Snakes Present	Mean	Range	Median
Area (hectares)	Presence	864.38	2.43-12,137	222.38
	Absence	423.32	1.62-1,896	216.41
Mean depth (meters)	Presence	5.56	1.5-32.6	4.3
	Absence	6.18	0.6-14	5.65
pH	Presence	6.98	5.98-7.65	7.05
	Absence	6.99	6.05-7.48	7.06
Surface temperature (°C)	Presence	22.46	19.41-25.25	22.75
	Absence	22.28	18.96-24.04	22.59
Shoreline development	Presence	2.83	1.16-5.94	2.42
	Absence	2.47	1.07-7.52	2.10
Shoreline per stream (kilometers)	Presence	2.58	0.32-8.29	1.98
	Absence	2.10	0.24-8.58	1.28
Proportion of surrounding wetland area	Presence	0.04	0-0.20	0.03
	Absence	0.04	0-0.23	0.02

Table 4. Logistic regression slope estimates, standard errors and p-values of habitat parameters affecting snake presence.

Parameter	Estimate	Standard Error	$Pr(>\|z\|)$
Shoreline Development	0.185	0.183	0.313
Streams	0.118	0.126	0.350
Area	9.81E-5	1.06E-4	0.353
Mean Depth	-0.030	0.061	0.623
Surface temperature	0.089	0.204	0.664
Surrounding Wetland	-1.701	5.305	0.749
pH	-0.070	0.747	0.926

DISCUSSION

The models indicate that bioclimatic variables can help explain why *N. s. sipedon* has a disjunct range. Most of these bioclimatic variables involve temperature and indicate that warmer locations are more likely to have *N. s. sipedon*, but some are also partly driven by precipitation patterns, especially seasonality.

Presence and absence at lakes in the potential range

Mean temperature of the wettest quarter drove the model explaining the presence and absence within the potential range of *N. s. sipedon* in Maine. In contrast, our results showed that the lake characteristics we tested (e.g., area and shoreline development) did not help explain *N. s. sipedon* presence and absence.

While these absences cannot be completely verified, MARAP records for turtles, *C. p. picta*, in over half of the Absence lakes strengthen the assumption that those lakes do not have *N. s. sipedon*. Both *C. p. picta* and *N. s. sipedon* exhibit similar basking behaviors, both in time of day that they bask and objects that they will bask on (Lovich 1988, Burger et al. 2014). It is quite likely that if a MARAP volunteer found a *C. p. picta* basking they would have found a *N. s. sipedon* basking, although turtles are somewhat more conspicuous and easier to identify than snakes. A majority of Absence lakes were found in the range gap of *N. s. sipedon* further strengthening the assumption that these lakes did not have *N. s. sipedon*.

Lakes within the potential range of *N. s. sipedon* showed great variation in terms of the tested characteristics but Presence and Absence lakes were not significantly different except for their bioclimates. This suggests that lake characteristics are not important for *N. s. sipedon* and, more generally, that *N. s. sipedon* is a habitat generalist. The ability of *N. s. sipedon* to persist in diverse urban and natural settings (Pattishall and Cundall 2009) supports this idea. More specifically, two characteristics that shaped *N. s. sipedon* habitat selection in previous studies were streams (Cecala et al. 2010) and surrounding wetlands (Roe et al. 2003), but they were not statistically significant in this analysis. Stream quality may be more important than the amount of streams, particularly if one large stream can support all the juveniles from a lake's population (Cecala et al. 2010). The lack of significance for the surrounding wetland parameter may be due to lake size. Lakes may provide enough habitat that the snakes do not need to use adjacent wetlands. It is also possible that the key habitat characteristics for *N. s. sipedon* involved features we did not measure such as aquatic vegetation (Roth II and Greene 2006), prey (Robertson and Weatherhead 1992) and hibernacula (Pattishall and Cundall 2008).

The best bioclimatic variable within the model predicting the presence and absence of *N. s. sipedon* within their potential range indicated that presence was positively correlated with mean temperature of the wettest quarter (Bio8), which is September, October, and November. By September *N. s. sipedon* are going into their hibernacula or have already done so. Temperature is very important for any species while hibernating, especially for ectotherms, in order for them not to freeze and die. *N. s. sipedon* use large rocks as hibernacula (Pattishall and Cundall 2008), but may also use crawfish burrows like the copperbelly water snake (*Nerodia erythrogaster neglecta*) (Kingsbury and Coppola 2000). Mean temperature at this time is important as it can limit the length of their growing period. A longer growing period can allow snakes to be more active and take in energy increasing their ability to survival hibernation. The top model did not have much support from McFadden's r-squared, which shows that while this is the best model that we tested there may be better predictors of *N. s. sipedon* within its potential range.

<u>Comparing the bioclimate of gap and the eastern range</u>

An analysis of bioclimatic variables in the gap compared to the eastern range found that the best model was driven by mean temperature of the warmest quarter (Bio

10), annual precipitation (Bio 12), and annual mean temperature (Bio 1). This model had a large McFaddens r-squared value showing that these variables are the main difference between the gap and the eastern population. Annual mean temperature had a positive slope estimate meaning that the annual mean temperature was higher in the eastern range than in the range gap which is consistent with *N. s. sipedon* being at their northern range limit and thermal limit (Table 5). The inability to operate within a thermal optimum can lead to snakes becoming inactive, which can limit their growing period and therefore affect their winter survival and fecundity. Apparently the eastern range is a slightly warmer refugium than the gap. Mean temperature of the warmest quarter and annual precipitation had negative slope estimates meaning that they were lower in the eastern range compared to areas in the range gap (Table 5). Mean temperature of the warmest quarter may be an anomaly within the model. High summer temperatures could affect the activity of snakes in the middle of the day if it gets to warm, but this is unlikely in Maine. Annual precipitation could be correlated with cloudiness while the snakes are active, and thus linked to reduced opportunities for basking. The negative slope indicates that the effect of summer precipitation may be more important to *N. s. sipedon* than winter precipitation. Nevertheless, snowpack is known to be important to many other species because it insulates them from cold temperatures (Simmons et al. 2010, O'Connor and Rittenhouse 2016).

Table 5. Parameter estimates of the top model predicting the influence of bioclimatic variables within the range gap of *N. s. sipedon* compared to the eastern population in Maine, USA.

Bioclimatic variable	Slope estimate	Standard Error
Mean temperature of warmest quarter	-0.091	0.017
Annual precipitation	-0.003	0.001
Annual mean temperature	0.052	0.021

Northern range limit

The best model predicting the northern range limit of *N. s. sipedon* incorporates five variables (Figure 5): four of these were lower north of the *N. s. sipedon*'s range (annual mean temperature, mean temperature and precipitation of the driest quarter [Jan.-March], and precipitation of the warmest quarter [June-Aug.]), while one was greater north of the *N. s. sipedon*'s range (precipitation of the wettest quarter [Sept.-Nov.]). This model had a large McFaddens r-squared value showing that these variables are a large part of explaining the northern range limit of *N. s. sipedon*. The importance of temperature parameters were discussed above and are presumably similar to their effects on the eastern range of *N. s. sipedon*. Precipitation during the driest quarter may be correlated with increased snowpack which may be linked to greater survival of hibernating snakes. Precipitation during the wettest quarter may limit the growing period of *N. s. sipedon* because this is when snakes move to their hibernacula. Areas with increased precipitation may start having snowfall earlier forcing snakes into hibernacula. Areas with lower precipitation could allow snakes to be active for a longer period. Higher rainfall in the warmest quarter doesn't have any obvious biological significance and may be an anomaly.

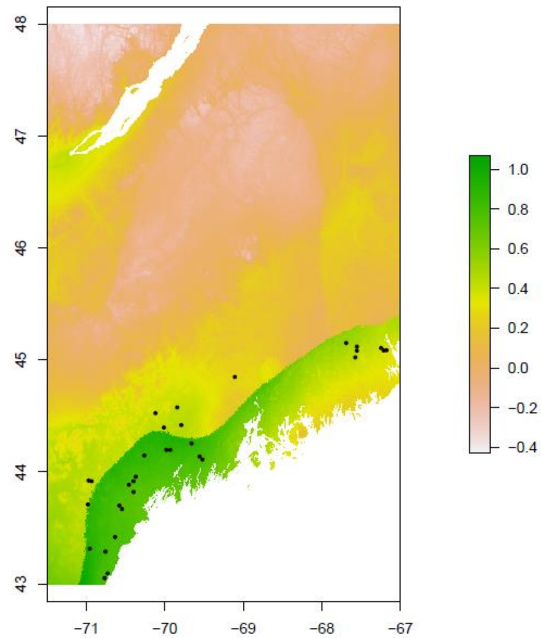

Figure 5. Projection map of the top model used to predict the northern range limit of northern water snakes (*Nerodia sipedon sipedon*) in Maine, USA, with known locations marked.

FUTURE RESEARCH

N. s. sipedon habitat characteristics needs further study before we can understand why a range gap persists. More work needs to be done on *N. s. sipedon* hibernacula and diet to see what they are selecting for and if part of their habitat selection is determined by prey. A study on dispersal of *N. s. sipedon* in Maine could also be illuminating as limited dispersal may also help explain why the gap persists.

CONCLUSIONS

The reason why the gap persists is puzzling, but the reason why it began seems simpler. Both the eastern ribbon snake (*Thamnophis sauritus sauritus*) and *E. blandingii* have disjunct ranges in the northeastern United States and Canada. It appears that they expanded their geographic range during a warm period in the mid-Holocene and were reduced to refugia during later cool periods (Spooner et al. 2014). It seems likely that *N. s. sipedon* went through a similar process and that they were reduced to eastern Maine and were excluded farther north.

Our results suggest that warmer temperatures play a large role in determining the presence of *N. s. sipedon* in some lakes and their overall range in Maine, with precipitation playing a smaller role, perhaps influencing basking opportunities. With a warming climate we would expect to see snakes starting to occupy the gap. We would expect the movement into the gap to be slower than movement north as *N. s. sipedon* may use rivers as travel corridors and the major rivers in Maine run north-south. Lake characteristics, at least those analyzed, did not affect the presence of *N. s. sipedon*.

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APPENDIX

Appendix 1. Bioclimatic variables from WorldClim (http://worldclim.org)

Bio 1: Annual mean temperature

Bio 2: Mean diurnal range

Bio 3: Isothermality

Bio 4: Temperature seasonality

Bio 5: Max temperature of warmest month

Bio 6: Min temperature of coldest month

Bio 7: Temperature annual range

Bio 8: Mean temperature of wettest quarter

Bio 9: Mean temperature of driest quarter

Bio 10: Mean temperature of warmest quarter

Bio 11: Mean temperature of coldest quarter

Bio 12: Annual precipitation

Bio 13: Precipitation of wettest month

Bio 14: Precipitation of driest month

Bio 15: Precipitation seasonality

Bio 16: Precipitation of wettest quarter

Bio 17: Precipitation of driest quarter

Bio 18: Precipitation of warmest quarter

Bio 19: Precipitation of coldest quarter

AUTHOR'S BIOGRAPHY

Anthony J. Pawlicki was born in Buffalo Grove, Illinois, on July 16, 1995. He was raised in the Chicago suburb where he attended Buffalo Grove High School and was a goalkeeper on the soccer team until graduation in 2013. He matriculated to the University of Maine to pursue a B.S. in Wildlife Ecology with a concentration in Conservation Biology and a minor in Political Science. He was active in the University of Maine Student Chapter of the Wildlife Society and was Vice President in 2016. He presented posters on this research in 2016 at the annual meetings of the Northeast Partners in Amphibian and Reptile Conservation and the Wildlife Society. He received two scholarships from the Penobscot County Conservation Association. He also received a distinguished student service award from the University of Maine Department of Wildlife, Fisheries, and Conservation Biology. Upon graduation he hopes to gain more field experience working with herpetofauna and to pursue a Master's degree in wildlife ecology with a focus on herpetology and/or policy.