ABSTRACT. Climate change projections indicate that mosquito distributions will expand to include new areas of North America, increasing human exposure to mosquito-borne disease. Controlling these vectors is imperative, as mosquito-borne disease incidence will rise in response to expansion of mosquito range and increased seasonality. One means of mosquito control used in the USA is the biocontrol agent, Toxorhynchites rutilus. Climate change will open new habitats for its use by vector control organizations, but the extent of this change in habitat is currently unknown. We used a maximum entropy approach to create species distribution models for Tx. rutilus under 4 climate change scenarios by 2070. Mean temperature of warmest quarter (22.6°C to 29.1°C), annual precipitation (1,025.15 mm to 1,529.40 mm), and precipitation seasonality (≤17.86) are the most important bioclimatic variables for suitable habitat. The center of current possible habitat distribution of Tx. rutilus is in central Tennessee. Depending upon the scenario, we expect centroids to shift north-northeast by 97.68 km to 280.16 km by 2070. The extreme change in area of greater than 50% suitable habitat probability is 141.14% with 99.44% area retained. Our models indicate limited change in current habitat as well as creation of new habitat. These results are promising for North American mosquito control programs for the continued and potential combat of vector mosquitoes using Tx. rutilus.

KEY WORDS Biological control, climate change, ecological niche model, Maxent, Toxorhynchites rutilus

INTRODUCTION

The incidence of mosquito-borne illness is expected to increase in the future as vector populations expand due to climate change (Bouzid et al. 2014, Savic et al. 2014, Carvalho et al. 2017, IPCC 2018, Kraemer et al. 2019), increasing globalization (Kilpatrick 2011, Powell 2016), changes in land use, and urbanization (Bowden et al. 2011, Rogalski et al. 2017). As of 2017, the estimated number of annual cases of the major mosquito-vectored diseases (malaria, dengue, lymphatic filariasis, chikungunya, Zika virus, yellow fever, Japanese encephalitis, and West Nile virus) was over 347 million, with nearly 448,000 estimated deaths (WHO 2018). Controlling mosquito populations is critical in the prevention and elimination of the diseases they vector. Chemical pesticides (Faraji and Unlu 2016), entomopathogenic bacteria, viruses, and fungi (Atyame et al. 2011, Kean et al. 2015), sterilized male mosquitoes (Alphey et al. 2010), reproduction-inhibiting bacteria, genetically modified adults, and natural enemies (Benelli et al. 2016) are employed to kill or otherwise prevent the reproduction of these insects and limit mosquito-borne illness.

One such natural enemy, the mosquito Toxorhynchites rutilus (Coq.), is a biocontrol agent used in the USA (Focks et al. 1982). The use of Tx. rutilus as a biocontrol involves mass breeding of the predator and inundative releases of adults. Also known as the elephant mosquito and the mosquito assassin, the larvae prey on aquatic invertebrates in tree holes and artificial containers (Dodge 1964, Focks 2007, Schiller et al. 2019). Adults feed on nectar and never blood and are thus incapable of transmitting human or animal pathogens (Collins and Blackwell 2000, Burkett-Cadena 2013). Toxorhynchites rutilus is widely distributed across eastern North America, ranging from northern Mexico to New England and the Atlantic coast to the Great Plains (Darsie and Ward 2005).

Many studies have modeled the potential distributions of vector mosquitoes due to climate change (Epstein et al. 1998, Hongoh et al. 2012, Brown et al. 2015). However, recent work has suggested that some native and established natural enemy populations may be at risk of extinction due to climate change (Thurman et al. 2017). The current study represents the only of its kind for Tx. rutilus and addresses a critical gap in knowledge, since biocontrol deployments of Tx. rutilus will be less effective in habitats where climatic variables limit oviposition and embryonic and larval development (Campos and Lounibos 2000, Focks 2007; Anita Schiller, personal communication). Similar models found that warmer and wetter habitats are projected to move northward in North America (McKenney et al. 2007, Butler et al. 2016). Over the next 50 years higher latitudes and higher elevations will likely experience greater numbers of mosquitoes for longer periods each year (Ryan et al. 2019). Affected regions will benefit from increased Tx. rutilus habitat, and vector control organizations in these areas may begin using the predator as a biocontrol agent. Areas already using Tx. rutilus as a biocontrol will likely have to deploy the predator for longer periods throughout the year.
due to increased vector seasonality. Breeding adequate numbers of these mosquitoes to achieve vector control requires considerable effort in both labor and resources (Schiller et al. 2019; Schiller, personal communication). To maximize production and release efficiency, vector control organizations require new and more accurate information to make better-informed decisions on the release of *Tx. rutilus*. Additionally, the possibility that natural populations of the predator may experience extinction events due to climate change needs to be addressed, as releases of *Tx. rutilus* will be ineffective in those conditions. We used Maxent to model the niches of *Tx. rutilus* and then modeled future niches under 4 climate change scenarios in order to identify areas that will be suitable for this biocontrol agent by 2070.

**MATERIALS AND METHODS**

Occurrence data were downloaded from Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/). We mapped these data and visually identified and removed aberrant occurrences. Data were resampled using ENMTools (Warren et al. 2019) such that 1 record occurred per 100 km$^2$ (Warren et al. 2010). Elevation and bioclimatic variables were obtained from WorldClim (http://www.worldclim.org/; Table 1) at 5 arc minutes resolution (Hijmans et al. 2005). We trimmed the spatial extent of elevation and climatic variables from central Mexico to northern Canada using ArcGIS v.10.4; 2016 (Environmental Systems Research Institute, Redlands, CA). A total of 258 *Tx. rutilus* occurrence records were downloaded from GBIF. After resampling, we used a total of 123 records for constructing our species distribution model.

We modeled the current and projected distributions of *Tx. rutilus* using the maximum entropy (Maxent) approach (Phillips et al. 2006). All bioclimatic variables were modeled initially. We retained the variables that had the greatest effect on the gain in order to observe the strongest predictive model (Butler et al. 2016). This included variables that greatly increased the gain as well as those that caused the greatest decrease in gain. We avoided overfitting by penalizing increased model complexity using a regularization approach (Phillips et al. 2006, Merckx et al. 2011). We evaluated regularized models with Akaike’s information criterion (AIC; Warren and Seifert 2011) using variables that did not exhibit high multicollinearity (Jones et al. 2010). Sensitivity versus specificity were plotted to create receiver operating characteristic (ROC) curves. We used cross-validation area under the curve (AUC) scores to evaluate accuracy of the model along with AIC scores and model weights (So and Sham 2010).

Predicted climatic models from the Intergovernmental Panel on Climate Change (IPCC) were used to project the potential distribution of *Tx. rutilus* by 2070. We obtained these climatic models from WorldClim (Hijmans et al. 2005). Intergovernmental Panel on Climate Change scenarios include representative concentration pathway (RCP) 2.6, RCP 4.5, RCP 6.0, and RCP 8.5. Each RCP represents a possible climatic future in which the change in radiative forcing increases 2.6, 4.5, 6.0, and 8.5 W/m$^2$ from preindustrial levels by the year 2100. Radiative forcing is a measure of the difference between the solar radiation absorbed by the Earth and the amount of energy radiated into space at the tropopause. The amount of change in radiative forcing is indicative of greenhouse gas concentrations in the atmosphere. These scenarios do not represent greenhouse gas emissions, but rather represent possible radiative forcing scenarios as a result of predicted greenhouse gas emissions (IPCC 2018). In the RCP 2.6 scenario greenhouse gas emissions peak by 2020 and then decline, these emissions peak by 2040 in the RCP 4.5 scenario, and by 2080 in RCP 6.0. Emissions continue to rise throughout the 21st century in RCP 8.5. We used model averages under each RCP scenario to create projected suitable habitat models.

**RESULTS**

The best model for *Tx. rutilus* (i.e., with the lowest AIC$_c$ score) included the variables mean temperature of warmest quarter, annual precipitation, and precipitation seasonality (Table 2). The AUC for this model was 0.960 ± 0.006. Areas that were predicted to have suitability >50% had a mean temperature of warmest quarter of 22.6°C to 29.1°C, annual precipitation of 1,025.15 mm to 1,529.40 mm, and precipitation

| Variable | Definition |
|----------|------------|
| BIO 1    | Annual mean temperature |
| BIO 2    | Mean diurnal range (Mean of monthly [max temp–min temp]) |
| BIO 3    | Isothermality (BIO 2/BIO 7) × 100 |
| BIO 4    | Temperature seasonality (standard deviation × 100) |
| BIO 5    | Max temperature of warmest month |
| BIO 6    | Min temperature of coldest month |
| BIO 7    | Temperature annual range (BIO 5–BIO 6) |
| BIO 8    | Mean temperature of wettest month |
| BIO 9    | Mean temperature of driest month |
| 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 (coefficient of variation) |
| BIO 16   | Precipitation of wettest quarter |
| BIO 17   | Precipitation of driest quarter |
| BIO 18   | Precipitation of warmest quarter |
| BIO 19   | Precipitation of coldest quarter |
| Elevation| Elevation above sea level |
seasonality of less than 17.86. The current modeled suitable distribution ranges from northern Mexico to southern Canada through central and eastern USA (Fig. 1). Highly suitable areas (i.e., those of >50% suitability) were restricted to south Texas through central Illinois and southern Georgia to central Pennsylvania excluding Appalachia.

The median projected increase in highly suitable conditions for all *Toxorhynchites rutilus* was 84.03% (range 9.61–141.14%), although there was considerable variation among RCP scenarios (Table 3). Under the RCP 2.6 scenario, the amount of suitable habitat increased by only 9.61%. In contrast, under RCP scenarios 4.5, 6.0, and 8.5, the amount of suitable habitat increased by 70.76%, 114.62%, and 141.14%, respectively. The amount of currently highly suitable habitat retained in future projections for this species was 89.78% to 99.65%, with a median of 96.92%.

Table 2. A comparison of the top 5 model runs for *Toxorhynchites rutilus*. Log-likelihood is the natural log of the probability of the data given in the model. AIC is the corrected Akaike’s Information Criterion (AIC) score, used for a small sample size by increasing the cost for each parameter. The difference between the model with the lowest score (the “best” model) and the AIC score for each model is given by ΔAIC. The model weight (wAIC) is the relative likelihood for each model, divided by the total relative likelihood for all models that were considered. AUC (area under the curve) is a measure of the accuracy of the model.

| Variables                                | Log likelihood | AIC score | ΔAIC | wAIC | Mean AUC |
|------------------------------------------|----------------|-----------|------|------|----------|
| BIO 10, BIO 12, BIO 15                   | −1,286.863     | 2,608.211 | 0.000| 0.955| 0.960    |
| Elevation, BIO 1, BIO 12, BIO 15, BIO 1  | −1,285.202     | 2,615.783 | 7.572| 0.022| 0.958    |
| BIO 9, BIO 10, BIO 12, BIO 15            | −1,275.230     | 2,617.085 | 8.874| 0.011| 0.964    |
| Elevation, BIO 10, BIO 12, BIO 15        | −1,286.878     | 2,619.135 | 10.924| 0.004| 0.959    |
| BIO 10, BIO 14, BIO 15                   | −1,290.101     | 2,620.031 | 11.82| 0.003| 0.957    |
The RCP 2.6 scenario had the least suitable habitat retention with range losses mostly in Mississippi, Alabama, and Kentucky (Fig. 2). Under RCP scenarios 4.5 and 6.0, 99.65% and 98.80% suitable habitat was retained, respectively. These scenarios indicate highly suitable conditions will expand into southern Canada and peninsular Florida. The RCP 8.5 scenario retains 99.44% of current habitat. The probable range under this scenario extends further south than previous models and also expands in geographic distribution around the Great Lakes and New England.

The centroid of the current suitable \( \textit{Toxorhynchites rutilus} \) distribution according to our best model is in central Tennessee (Fig. 3). Centroids shifted generally north-northeast in successive scenarios. The median projected centroid shift for each scenario was 29.0 km per decade (range 16–47 km/decade), but variability exists in the response rate. The centroids for the RCP 2.6 and 4.5 scenarios were relatively close together, only 97.68 km north and 126.91 km

### Table 3.

| Scenario   | Area (km²) | % change in area from current | Area common to current (km²) | % current distribution retained |
|------------|------------|-------------------------------|-----------------------------|-------------------------------|
| Current    | 1,359,647.02 |                               |                             |                               |
| RCP 2.6    | 1,490,357.88 | 9.61                          | 1,220,641.98                | 89.78                         |
| RCP 4.5    | 2,321,781.88 | 70.76                         | 1,354,870.71                | 99.65                         |
| RCP 6.0    | 2,918,007.51 | 114.62                        | 1,343,359.31                | 98.80                         |
| RCP 8.5    | 3,278,635.34 | 141.14                        | 1,352,042.22                | 99.44                         |

Table 3. The total area predicted to have >50% probability of suitable conditions for \( \textit{Toxorhynchites rutilus} \) under each Representative Concentration Pathway (RCP) scenario by 2070. Percent area of retention and change of highly suitable habitat relative to the current predicted distribution.

Fig. 2. Predicted suitable habitat of \( \textit{Toxorhynchites rutilus} \) for (A) RCP2.6, (B) RCP4.5, (C) RCP6.0, and (D) RCP8.5 scenarios. Habitat suitability probability is indicated by black intensity, areas of white are unsuitable. RCP, representative concentration pathway.
north-northeast from the current probable centroid, respectively (Table 4). Centroids for RCP 6.0 and 8.5 scenarios were farther apart, in southern and northern Kentucky, respectively. Scenarios RCP 6.0 and RCP 8.5 were 194.52 km north-northeast and 280.16 km north-northeast from the current probably centroid, respectively.

**DISCUSSION**

Our models show that the current range of *T. rutilus* will expand northward by 2070. The RCP 2.6 scenario shows a slight north and northwestward increase into the southern Great Lakes region and central New England. Scenarios RCP 4.5 and RCP 6.0 demonstrate a moderate increase in northward and westward ranges. The RCP 8.5 scenario indicates a strong northward and westward expansion from the current range into southern Quebec and Ontario and northern New England. Plotted centroids show a north-northeastward trend moving from central Tennessee to the Kentucky–Indiana border in the extreme scenario. These centroids show a small change in potential *T. rutilus* habitat. *Toxorhynchites rutilus* response to mean temperature of warmest quarter, annual precipitation, and precipitation seasonality is likely due to an increase in suitable vegetation and prey, a greater number of individuals reaching maturity, and a reduced length of overwintering seasons. Because *T. rutilus* is sylvatic, it may be that increased potential habitat is due partially to an increase in suitable woody vegetation in which its oviposition sites are located. Generally, temperate forests will benefit from increased temperatures and precipitation (Saxe et al. 2001). Eastern North American forests are less

| Scenario | Distance (km) and direction from current | Rate, km per decade |
|----------|----------------------------------------|---------------------|
| RCP 2.6  | 97.68 (N)                              | 16                  |
| RCP 4.5  | 126.91 (NNE)                           | 21                  |
| RCP 6.0  | 194.52 (NNE)                           | 32                  |
| RCP 8.5  | 280.16 (NNE)                           | 47                  |
sensitive to climate change than their western counterparts (Phipps 1982) which, ignoring land use changes, explains the extent of habitat retention in our models. Additionally, increased precipitation will keep tree holes and other oviposition sites filled with water, thereby increasing larval habitat. An increased length of warmer portions of the year will result in increased food abundance (i.e., vector mosquitoes and flowering plants). This greater seasonality also contributes to an increased number of generations per year of both *Tx. rutilus* and vector mosquitoes as well as reduced diapause periods. Insectary temperatures recommended for optimal growth of *Tx. rutilus* are between 21°C and 29°C (Schiller et al. 2019). The increase in mean temperature of warmest quarter to 22.6°C to 29.1°C will allow more mosquitoes to reach maturity.

Vector control organizations currently using *Tx. rutilus* in the southern USA will be unaffected by climate change, as the 4 RCP scenarios had little effect on the species’ southern habitat. This is good news for mosquito control organizations, since deployments of *Tx. rutilus* will remain effective as vector populations increase and temperatures rise (Collins and Blackwell 2000). However, the need for bolstered control methods is apparent when considering the potential for increased vector populations and seasonality. Increased length of mosquito season will require greater numbers of captive *Tx. rutilus* bred annually. This puts an increasing financial burden on control organizations in both resources and labor to effectively combat mosquitoes. Novel mosquito controls, particularly integrated vector management, will undoubtedly be necessary in the near future (WHO 2012, Fernandes et al. 2018).

Some research has indicated that native biocontrols are at risk of extinction (Thurman et al. 2017). This does not appear to be the case for *Tx. rutilus*. We do not anticipate extinction events of *Tx. rutilus*, since our models indicate high retention of current habitat under the 4 climate change scenarios. This may be due in large part to the generalist feeding habits of this predator (Collins and Blackwell 2000). Additionally, Deutsch et al. (2008) found that nontropical insect species will exhibit limited negative responses to increased global temperatures through the 21st century. Collier and Steenwyk identified environmental conditions that are unfavorable for augmentative biocontrol releases (Collier and Van Steenwyk 2004). They found that, generally, too hot and dry conditions lowered efficacy in agricultural settings. These findings should be of concern to mosquito control professionals, but our models show that this will not be of concern in eastern North America. Most research on biocontrol responses to climate change have focused on agricultural pests. More work is needed to evaluate the efficacy of biocontrols of mosquitoes and other vectors of emerging and reemerging infectious disease.

Much research has focused on vector-borne disease risk under climate change. Vector-borne disease occurrence will broadly increase due to increasing globalism (Berrang-Ford et al. 2009) and vector dependence on the warmer and wetter conditions predicted by climate change models (Lafferty 2009). In areas where these conditions will occur, native populations are at risk of exposure to emerging and reemerging vector-borne diseases such as dengue fever and malaria (Berrang-Ford et al. 2009, Bouzid et al. 2014). Increased seasonality is another concern for establishment of endemic vector-borne disease. In areas where autochthonous infections are rare, increased seasonality will heighten the risk of establishment by lengthening the time of the year in which vectors are active. Areas on the fringe of endemic transmission areas and those with occasional outbreaks are of particular concern for establishment of vector-borne disease (Butterworth et al. 2017).

These models consider bioclimatic variables under climate change scenarios. They do not account for habitat loss due to anthropogenic factors such as deforestation and urbanization. Further study is needed to adequately identify potential future habitats based on bioclimatic variables, urbanization, and vegetation modelling (Bowden et al. 2011, Khazan et al. 2015, Rogalski et al. 2017, Kraemer et al. 2019). Occurrence records tend to be clustered around areas easily accessed near roadways, towns and cities, and bodies of water near homes or areas of interest to collectors and observers (Newbold 2010). Low sample size coupled with potentially biased occurrence records may have resulted in skewed habitat predictions (Feeley and Silman 2011). However, Maxent is more effective than other species distribution modeling approaches across all sample sizes (Wisz et al. 2008). Effective models have been generated with 25 or fewer occurrence records (van Proosdij et al. 2016). We did not account for interspecific and conspecific competition when creating our models. These factors are of great importance when projecting potential distributions of organisms, and further study will be needed to maximize these models in accordance with interspecific and conspecific competition (Yoshioka et al. 2012, Wasserman et al. 2014, Lounibos and Juliano 2018). In the case of *Tx. rutilus*, we expect introduction into new habitats to be by anthropogenic means in the form of inundative control releases. Mass releases of predatory mosquitoes will suffer losses by competition but will likely not be limiting due to the sheer numbers of individuals released.

All 4 scenarios show the potential for the use of *Tx. rutilus* as a biocontrol in an expanded range over the next 50 years. Notably, communities in New England and the American Midwest will be able to take advantage of this increase in habitat suitability. Under the RCP 8.5 scenario, cities as far north as Montreal, Quebec, could support populations of *Tx. rutilus*. In these northern climes where the incidence...
of vector-borne disease is projected to rise, sustainable *Tx. rutilus* habitat and the benefits of natural vector reduction will certainly be welcome (Berrang-Ford et al. 2009, Hongoh et al. 2012). Additionally, retention of *Tx. rutilus* habitat in the southern USA is a reassuring sign in a time when the future of mosquito-borne illness in North America is of great concern.

ACKNOWLEDGMENTS

We thank the University of Central Oklahoma College of Math and Science for allowing us the use of ArcGIS. We thank Anita Schiller of the Harris County Precinct 4 Biocontrol Initiative for her insight into *Tx. rutilus* biology and mass rearing.

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