Invaders from islands: thermal matching, potential or flexibility?

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Native-range thermal constraints may not reflect the geographical distributions of species introduced from native island ranges in part due to rapid physiological adaptation in species introduced to new environments. Correlative ecological niche models may thus underestimate potential invasive distributions of species from islands. The northern curly-tailed lizard (Leiocephalus carinatus) is established in Florida, including populations north of its native range. Competing hypotheses may explain this distribution: Thermal Matching (distribution reflects thermal conditions of the native range), Thermal Potential (species tolerates thermal extremes absent in the native range) and/or Thermal Flexibility (thermal tolerance reflects local thermal extremes). We rejected the Thermal Matching hypothesis by comparing ecological niche models developed from native vs. native plus invasive distributions; L. carinatus exists in areas of low suitability in Florida as predicted by the native-distribution model. We then compared critical thermal limits of L. carinatus from two non-native populations to evaluate the Thermal Potential and Flexibility hypotheses: one matching native range latitudes, and another 160 km north of the native range that experiences more frequent cold weather events. Critical thermal minima in the northern population were lower than in the south, supporting the Thermal Flexibility hypothesis, whereas critical thermal maxima did not differ.

ADDITIONAL KEYWORDS: ecological niche model – invasive species – physiology – reptile – thermal limits.

INTRODUCTION

Invasive species are often studied in the context of islands, where their introduction from mainland to insular environments can have severe and often irreversible ecological effects (Sax & Gaines, 2008). Fewer studies have been performed on invaders originating on islands and introduced to mainland environments. These island-sourced species may be released from native-range constraints such as geographical barriers and narrow thermal regimes when introduced to new areas. As such, predicting the potential spread of invasive species sourced from islands based on native-range data poses challenges.

It is important to understand these limitations when predicting the spread of invasive species and planning management actions.

A common tool for predicting the spread or introduction of invasive species is the correlative ecological niche model (ENM). Many correlative ENMs use climate and habitat data from a target species’ native range to predict the relative likelihood of invasion in a given area (Thuiller et al., 2005; Peterson & Soberón, 2012). These models have varying levels of utility for different types of invasive species (Peterson, 2003; Liu et al., 2020), but may be particularly applicable to ectotherms (Liu et al., 2017), which primarily regulate body temperature via behaviour and are constrained by available temperatures. Climate-matching ENMs can be useful when predicting locations suitable for establishment...
of non-native ectotherms such as snakes and lizards, but may widely under- or overestimate the potential geographical spread of invaders after initial establishment (e.g. Rodda et al., 2011; Mothes et al., 2019). When considering invasion risk by species native to islands, this underestimation may be exacerbated, as predicting suitable sites is based primarily on extrapolation of environmental space due to the restricted geography and habitats on islands (Wiens et al., 2019). Another problem is that correlative ENMs cannot reconstruct the fundamental niche of species in the native range; niche estimates are often underestimated by an unknown amount depending on other biotic factors and dispersal limitations (Peterson, 2003; Peterson et al., 2011; Rodda et al., 2011; Jarnevich et al., 2015). Island species in particular may have plasticity in certain traits that are not adequately reflected in correlative ENMs, such that model outputs may underpredict potential invasion sites. For example, Wiens et al. (2019) reported substantial thermal niche shifts in 15 species of introduced reptiles and amphibians sourced from island native ranges. Thus, it is important to consider the plasticity or subsequent evolution of island species’ traits after release from native range constraints when attempting to understand their potential distributions.

An important component for integrating plasticity into predicting range expansion of invasive reptiles is an understanding of target species’ thermal physiology and behaviour (Kearney & Porter, 2009). In part, reptiles rely on behavioural thermoregulation to adjust body temperature based on available temperatures and can tolerate a range of body temperatures (Seebacher & Franklin, 2005). These tolerance thresholds and associated behavioural mitigation (i.e. thermal flexibility) may depend on adaptation to the local environment. For example, areas such as the tropics or restricted island ranges may have relatively fewer extreme thermal selection events such that thermal plasticity is not as pronounced as in reptiles with wider ranges and greater variation in thermal conditions (Shine & Madsen, 1996). In species with wide latitudinal ranges, such as Argentine black and white tegu (Salvator merianae Duméril & Bibron, 1839), selective basking and burrowing during the cold season can create effective thermal buffers in invasive and native ranges (e.g. McEachern et al., 2015; Sanders et al., 2015). Ultimately and despite behavioural thermal buffers, survival of ectotherms depends on physiological thermal tolerance, as demonstrated by Burmese python (Python bivittatus Kuhl, 1820) deaths in cold weather despite selective basking and sheltering (Dorcas et al., 2011), iguanas (Iguana iguana Linneaus, 1758) falling from trees during cold snaps in South Florida (Campbell, 2011; Chappell, 2020), and green sea turtle (Chelonia mydas Linneaus, 1758) strandings and cold-stunnings (Roberts et al., 2014).

Physiological limits determine survival at thermal extremes, but rapid physiological adaptation may also occur in species introduced to new environments (e.g. Kolbe et al., 2012; Leal & Gunderson, 2012; Card et al., 2018; Campbell-Staton et al., 2020). Critical thermal minima and maxima (CT_min and CT_max, respectively), which represent the lower and upper body temperatures at which an animal can function, are important variables for understanding range expansion in introduced ectotherms and estimating future range limits due to climate change (Wiens et al., 2019; but see Sofae et al., 2018 for a discussion on endothermic animals). It is also important to consider the role of adaptation to new thermal environments for invasion success. Non-native Anolis lizards demonstrate adaptation for greater cold tolerance in invaded vs. native island ranges (A. cristatellus Duméril & Bibron, 1837; Kolbe et al., 2012; Leal & Gunderson, 2012), and in the northern vs. southern portions of the invaded North American range (A. sagrei Duméril & Bibron, 1837; Kolbe et al., 2014). Thermal lability may be characteristic of this well-studied clade, as evolution of both heat tolerance and cold tolerance occur rapidly among native Anolis when behavioural thermoregulation does not provide an adequate buffer (Muñoz et al., 2014; Campbell-Staton et al., 2020, respectively). Aside from Anolis spp., little research has been performed on thermal tolerance plasticity vs. adaptation of established populations of other non-native lizard species (Haro, 2018; Litmer & Murray, 2019; Mothes et al., 2019; Neel et al., 2020), begging the question as to whether this phenomenon is broadly applicable to other island-sourced reptile invasions.

The continuing range expansion of the northern curly-tailed lizard, Leiocephalus carinatus Gray, 1827, across Florida presents a fortuitous opportunity to evaluate physiological adaptation to novel thermal environments in an island-sourced invasive lizard. This small omnivorous iguanid lizard belongs to the family Leiocephalidae with subspecies native to the Bahamas and Cuba, and also occurs on various other Caribbean islands, although native status is uncertain (McCrane, 2015). This species is well suited for assessing the thermal influences on invasion of ectothermic invaders from restricted ranges because it (1) comes from a restricted island range; (2) has many confirmed established populations in Florida, including those at higher latitudes than its native Bahamian range (e.g. Engeman et al., 2011; Thomason et al., 2020; Fig. 1); and (3) occurs in great enough numbers to collect sufficient samples for generating physiological information within a short timespan.
to avoid short-term acclimation influences on data (N. M. Claunch pers. obs.). *Leiocephalus carinatus* thus represents a compelling case study for testing various thermal hypotheses for predicting areas of establishment for an island-sourced invader. While there are non-thermal factors that may also limit its current distribution, the following thermal-environment-focused hypotheses are key ones for explaining the broad invasive distribution of *L. carinatus*: (1) distribution in both the native and the invaded ranges is constrained by the thermal conditions of the native range (Thermal Matching); (2) distribution in the native range is constrained by geographical barriers rather than thermal conditions, in that the species can tolerate thermal extremes beyond those observed in the native range (Thermal Potential); or (3) lizards may exhibit Thermal Flexibility such that introduction to environments with differing thermal extremes leads to physiological acclimatization and/or subsequent adaptation of thermal limits to one or both extremes. We tested the Thermal Matching hypothesis by comparing the results of two different correlative ENMs using temperature and precipitation variables (Jarnevich et al., 2015): one incorporating only native presence data (native model) and one including both native and invasive presences (full model). We chose to use correlative ENMs rather than mechanistic models given that they are much easier to parameterize, a common challenge when assessing potentially invasive species (Jiménez-Valverde et al., 2011). If Thermal Matching is supported, we predict *L. carinatus* populations will not occur outside the predicted suitable areas of the native-only ENM. Further, the predicted climatic suitability across invaded range occurrences is expected to be roughly equal to the climatic suitability across native range occurrences. Based on our ENM results, we then tested the Thermal Potential and Thermal Flexibility hypotheses by comparing critical thermal limits of *L. carinatus* from each of two established Florida populations: Key Largo (25.1°N; established between the late 1990s and early 2000s; Duquesnel, 1998; Krysko et al., 2005), which matches latitudes in the native range, and Cocoa Beach (28.3°N; established in the mid-to-late 1990s; Krysko & King, 2002), which is 160 km north of the native range. If the Thermal Potential hypothesis is supported, we predict no observable differences between thermal limits in Key Largo and Cocoa Beach, indicating a species-level ability to tolerate extreme temperatures. If the Thermal Flexibility hypothesis is supported, we predict that one or both critical thermal limits differ.

Figure 1. Ecological niche models predicting relative suitability for *Leiocephalus carinatus* using native-range-only presence points (A, yellow circles) and including both native and verified invaded Florida range presence points (B, white circles) to construct the models. Lighter colours indicate higher relative suitability. Hatching leading down to the right indicates areas extrapolated by the model (MESS), while areas without cross-hatching indicate interpolated areas. Hatching leading down to the left indicates areas where minimum winter land surface temperature (LST \(_{\text{min}}\)) is equal to or below 12 °C (calculated from the 14 °C minima reported herein and subtracting a 2 °C thermal buffer in burrows). Highest suitability areas for *L. carinatus* in both models generally fall outside of areas where LST \(_{\text{min}}\) is below CT \(_{\text{min}}\) for the species. Arrows indicate Cocoa Beach (north) and Key Largo (south) populations sampled in this study, which are in areas predicted as low and high relative suitability, respectively. Inset are the marginal response curves for LST \(_{\text{min}}\) in each model, with the average CT \(_{\text{min}}\) of the northern population (14 °C) marked by a vertical line. The native range model’s LST \(_{\text{min}}\) curve reaches its lowest value at the measured CT \(_{\text{min}}\) but at the same value, the full model predicts higher relative suitability.
between populations. Because thermal maxima are less labile than minima (reviewed by Gunderson & Stillman, 2015), we specifically predict that although CT max may not differ, the Cocoa Beach population (160 km north of the native range) will have lower CT min than the southern Key Largo population (within the native range).

MATERIAL AND METHODS

ENMs
We generated two separate ENMs using Maxent: one using only native range data for L. carinatus to predict onto Florida (native model with projection to native and invaded range), and the other adding invasive range data (verified by the authors) to predict onto Florida (full model). The native model is a hypothesis of the possible invasive distribution of a species from a restricted island range that had either recently established or for which very limited invasion information is available (e.g. Jarnevich et al., 2015), while the full model is a test of this hypothesis. Although it is hypothesized that L. c. armouri is the established subspecies in Florida (Meshaka et al., 2005), not all invasive populations have been identified to subspecies, and genetic delineation to confirm subspecies status is not yet available. Additionally, restriction of native range data to L. c. armouri (i.e. Little Bahama Bank; Buckner et al., 2012) leads to more extreme limitation of ecological space available for conducting ENMs (Wiens et al., 2019). Thus, when downloading native range occurrence localities from the Global Biodiversity Information Facility (GBIF), we included all subspecies within L. carinatus. All occurrence localities that were not georeferenced, had ambiguous georeferences or that were derived from fossil records were removed. We included occurrence localities from the invaded range based on field surveys confirming established populations for another study conducted in the summers of 2017–2019 by the authors (unpubl. data). We considered invaded range populations verified as established if we were able to detect all age classes at locations indicated by range extension notes (Layne, 1987; Duquesnel, 1998; Hauge & Butterfield, 2000; Krysko & King, 2002; McCoid, 2002; Godley & Godley, 2011; Connor et al., 2013; Enge, 2018; Thomason et al., 2020), other studies (Weigl et al., 1969; Smith et al., 2004; Meshaka et al., 2005), observations on reporting platforms (e.g. iNaturalist and EDDmapS) or colleagues (Florida Museum of Natural History). To reduce bias in predictions resulting from the spatial autocorrelation of occurrence data, we used the package ‘spThin’ to ensure that all localities were a minimum of 10 km apart (Aiello-Lammens et al., 2015). This resulted in a total of 49 localities in the native range and 27 localities in the invaded range. Maxent relies on presence-only data, and as such, the selection of background data is of high importance (Barve et al., 2011). Given the relatively restricted area, we selected native range background localities from the entirety of Cuba and The Bahamas. To establish the background area in the invaded range, we downloaded all verified occurrence records from EDDmapS, removing ambiguous or missing georeferenced records as above; however, we did not restrict background data to verified populations. ENMs assume that the species being modelled is in equilibrium with its environment, and this is often not the case with ongoing invasions (Václavek & Meentemeyer, 2012). To account for this, we used smaller, 10-km buffers around all verified background localities within the Florida invaded range. For both the full model and the native model, we randomly selected 5000 points from across each model’s respective accessible area to serve as background points in the models.

We downloaded Bioclimatic variables used as predictors in models from two sources: 19 WorldClim (v.2; 1970–2000, Fick & Hijmans, 2017), and land surface temperature data from the Moderate Resolution Imaging Spectroradiometer (MODIS, Wan et al., 2015). Because establishment dates for L. carinatus are somewhat ambiguous and because we predicted thermal minima would be most important when considering invasion, we limited land surface temperature data to minimum temperatures in January from 2000 to 2018 (hereafter, LST min). Data for LST min were only available in 8-day intervals, so we generated 32-day composites representing the mean minimum daily temperature of January (analogous to WorldClim BIO6, minimum temperature of the coldest month). This was accomplished using ArcGIS 10.7.1 (ESRI 2019, Redlands, CA, USA). All variables used were at ~1.27-km resolution at the equator. We used a pairwise approach to select variables; when two variables had a Pearson correlation coefficient greater than 0.86 (Dormann et al., 2013; Ihlow et al., 2016), we retained the variable we predicted to be more biologically relevant (e.g. Rödder et al., 2009). The final reduced set of variables consisted of mean diurnal temperature range (BIO2), maximum temperature of the warmest month (BIO5), precipitation seasonality coefficient of variation (BIO15), precipitation of wettest quarter (BIO16), precipitation of driest quarter (BIO17) and LST min.

All ENMs were run using the package ‘ENMeval’ (Muscarella et al., 2014) in R v.3.6.1 (R Core Team, 2019), which itself depends on the package ‘dismo’ (Hijmans et al., 2017), and Maxent. To minimize model complexity, we used only linear, linear +
quadratic, linear + product, and linear + product + quadratic features in models. Additionally, we tested regularization multipliers – which use smoothing to penalize model complexity (Elith et al., 2006) – of 0.5 (least penalizing), 1 and 2 (most penalizing). We used all combinations of the above for the full and native models, resulting in a total of 24 separate models tested. To calibrate ENMs, we split the background and occurrence localities into training and testing data, using the checkerboard2 method in ‘ENMeval’. This method splits all localities into $k = 4$ spatial bins at two different spatial scales. For each model set, we selected only the model with the lowest Akaike information criterion score ($\text{AIC}_c$) for further processing (Burnham & Anderson, 2002). In the case of competing models (i.e. models within 2 $\Delta\text{AIC}$), the model with the fewest parameters was selected.

Using only the top model across both sets, we calculated the area under the curve (AUC), from the receiver operating characteristic (ROC) curve for both the training and the testing data, and then compared the difference. This difference is predicted to be greater in overfitted models (Warren & Seifert, 2011). We then generated a continuous probability surface ranging from 0 to 1, representing the relative probability of presence, using the logistic output from Maxent. Additionally, we generated presence/absence surfaces thresholded at the maximum sum of specificity and sensitivity ($\text{SSS}_{\text{max}}$; Liu et al., 2016) and a 10% omission threshold ($\text{TP}_{0.1}$; Norris, 2014). To assess model transferability, we generated multivariate environmental similarity surfaces (MESS) for both the native and the full models. MESS compares the values of environmental variables throughout the training region to the projection region, such that negative values represent extrapolation outside the range of what is in the training region. Finally, we evaluated the predicted probability of presence in the invaded and native ranges by comparing the median relative suitability values generated by each model. Because correlational models are sensitive to method, we also used an ensemble approach to verify that similar results are produced regardless of approach. Both performance and results of our Maxent approach were comparable to the ensemble approach (see ‘ensemble model approach’, Supporting Information); we report and discuss Maxent results in the main text for brevity.

**LOCAL TEMPERATURES**

To give local context to the two *L. carinatus* populations sampled herein, we compiled local ambient temperature data from NOAA from two timespans. To assess if animals were potentially acclimated to significantly different temperatures before measurement we evaluated ambient temperatures at each location encompassing the previous autumn and winter (1 October 2019 to 9 March 2020). Maximum and minimum ambient temperatures were collected from the nearest weather station (Cocoa Beach: Melbourne Beach USC0085603, ~33 km south of sampling site; Key Largo: John Pennekamp State Park USC0084412, ~16 km north of sampling site). To assess whether long-term differences in local temperatures may have influenced adaptation of thermal tolerance at each site, we used datasets spanning from July 1991 to March 2020. Due to gaps in available data and hurricane destruction of older weather stations, multiple weather stations were used. For Cocoa Beach, the Melbourne Weather Forecast station (USC0085612, ~26 km south of sampling sites) was used for the entire time period. For Key Largo, the Tavernier station (USC0088841, ~12.5 km south of sampling sites) was used from 1995 to January 2004, and John Pennekamp State Park (USC0084412) used for February 2004 to the present. To assess ambient temperature differences, $t$-tests were conducted for minimum and maximum ambient temperatures between populations for both potential acclimatization (October 1990 to March 2020) and potential adaptation (1991–2020) timescales in R v.3.4.0 Patched (R Core Team, 2019). Because temperature minima and maxima are more extreme in winter and summer, respectively, and these thermal extremes may exert local selective pressures on the thermal limits of *L. carinatus*, we conducted $t$-tests as above on adaptation timescale data in subsets of winter (December–March) or summer (June–Sept) months.

**THERMAL LIMITS**

We captured 35 adult *L. carinatus* from each of two populations (Key Largo and Cocoa Beach, FL, USA), via an extendable pole with loop or glue board between the hours of 0900 and 1400. We sampled lizards after winter (3 March to 8 March 2020) when lizards become regularly active above ground for capture. To limit acclimation effects associated with captivity, we assessed all lizards for thermal limits on the same day of capture (limits measured mean ±SD = 4.39 ± 2.1 h after capture for $\text{CT}_{\text{min}}$; 7.94 ± 2.25 h after capture for $\text{CT}_{\text{max}}$). We first assessed all lizards for $\text{CT}_{\text{min}}$, then $\text{CT}_{\text{max}}$, we placed lizards in the same trial groups for $\text{CT}_{\text{min}}$ and $\text{CT}_{\text{max}}$ to minimize variation in time between $\text{CT}_{\text{min}}$ and $\text{CT}_{\text{max}}$ tests, which averaged 3.99 ± 1.5 h. Due to time constraints, only 28 of 35 lizards were tested for $\text{CT}_{\text{max}}$ in Cocoa Beach.

We assessed thermal limits with a device engineered at California Polytechnic State University, the Gas Analysis Temperature Oxygen Regulation System (GATORS; described in detail in Haro, 2018;
Ivey et al., 2020). Briefly, we inserted resistance thermometers into lizard cloacae held in place with medical tape, and then placed lizards into individual, flippable thermal chambers. After lizard body temperature had equilibrated with the ambient temperature (set to 30 °C), GATORS cooled (to assess CT_{min}) or heated (to assess CT_{max}) ambient temperature in the chambers by 1 °C/min. CT_{min} and CT_{max} are defined as the low and high body temperatures at which lizards were no longer able to right themselves when the chamber was flipped. Additionally, before CT_{max} was reached, we noted body temperature at which lizards gaped (held mouth open for longer than 3 s; T_{gape}) and panted (laboured breathing while gaping; T_{pant}). Immediately after righting response was lost following CT_{min}, we removed lizards from chambers to recover righting response and normal behaviour. After CT_{max} was reached, lizards were also allowed to recover (to ensure lethal temperatures had not been reached), after which we anaesthetized each with isoflurane followed by euthanasia via intracardiac injection of potassium chloride (150 mg/kg). Gravidity is known to affect female thermal limits in some lizards (Virens & Cree, 2019). To account for this, we dissected females and measured the largest follicles and eggs within all individuals to assess potential differences in reproductive stage among populations. Procedures were conducted in accordance with approved University of Florida IACUC protocol no. 201910938.

Analyses of covariance (ANCOVAs) were conducted in R v.3.4.0 Patched (R Core Team, 2019). Mass was log-transformed to meet assumptions for ANCOVA. Sex distribution was similar between populations (Cocoa Beach: female N = 15, male N = 20; Key Largo: female N = 16, male N = 19). The distribution of follicle/egg sizes in females was also similar between populations (t_{128.74} = −0.55, P = 0.59), and thus we did not include gravidity in analyses. Mass is known to affect cloacal heating rates and critical thermal limit interpretations in lizards (Claunch et al., 2021), so we included it as a covariate in analyses. Thermal breadth (T_{breadth}) was calculated as the CT_{max} − CT_{min} for each individual. Reported models were constructed with response variables of CT_{min}, CT_{max}, T_{breadth}, T_{pant} or T_{gape}, with predictor variable of population, and with covariates mass, population by mass interaction and sex.

RESULTS

ENMs

The top-performing model for the native set was the model that used linear + quadratic + product and had a regularization multiplier value of 1. There were three competing models within 2 ΔAIC_c, but the selected model had the fewest (six) parameters (Supporting Information, Table S1). The top-performing model for the full set was the model that used only linear + quadratic features and had a regularization multiplier value of 0.5. There were no competing models in this set. For simplicity, we use the model with the lowest AIC_c (top model) from each set for comparative analyses. The top models across both sets had moderate discriminatory power, with the native model having a greater AUC_{train} (0.81) than the full model (0.78). Both models had average AUC_{test} values close to their respective AUC_{train} values (native model: 0.78; full model: 0.76), suggesting neither model was overfit (Table S1). Both models had disparate threshold values; the SSS_{max} was 0.61 for the native model and 0.47 for the full model. The native model had a TP_{0.10} threshold value of 0.21, and the full model 0.25. The incorporation of invasive range occurrence localities substantially reduced the amount of extrapolation, with most of Florida being out of the training range for the native model (Figs 1, 2). The only variables within the training range for the entirety of Florida in both models were precipitation of the wettest and driest quarters.

The full model predicted higher suitability across all invaded range occurrence localities (Fig. 3), with the median value of invaded occurrences from the full model being 0.67, and the median value of invaded occurrences from the native model being 0.38 (Table 1). However, both models predicted similar relative suitability across native range occurrences, with a median value of 0.76 for the full model and 0.77 for the native model (Table 1; Fig. 3).

In both native and full ENMs, Cocoa Beach occurs in an area predicted to be relatively lower in suitability for L. carinatus than Key Largo, which occurs in an area with the highest relative suitability (Fig. 1). Comparing the native and ENMs, Cocoa Beach slightly increases in relative suitability in the full ENM, while the relative suitability of Key Largo remains unchanged (Fig. 3). The ensemble model had comparable results (Supporting Information, Tables S2, S3, Figs S1, S2).

LOCAL TEMPERATURES

Statistics for local temperature analyses are reported in Table 2. In the 5 months leading up to our sampling (potential acclimatization timescale), maximum ambient temperature was 0.96 °C higher in Key Largo than in Cocoa Beach, and minimum ambient temperature was on average 1.93 °C higher in Key Largo (Table 2; Fig. 4). Since 1991 (potential adaptation timescale), maximum ambient temperature across all months was on average 0.35 °C higher in Key Largo,
while minimum ambient temperatures was on average 4.53 °C higher in Key Largo (Table 2; Fig. 5). In summer (June–September), maximum ambient temperatures from 1991 to the present were higher in Cocoa Beach than in Key Largo by 0.45 °C, and minimum ambient temperatures were higher in Key Largo by 3.06 °C. In winter (December–March), maximum ambient temperatures from 1991 to the present were 1.60 °C higher in Key Largo, and minimum ambient temperatures were 6.42 °C higher in Key Largo.

**THERMAL LIMITS**

Statistics and models for thermal limits are reported in Table 3. For CT$_{\text{min}}$, there was a main effect of mass, with larger lizards having higher CT$_{\text{min}}$, and there was a population by mass interaction wherein large lizards from Key Largo exhibited higher CT$_{\text{min}}$ values than those from Cocoa Beach (Table 3; Fig. 6). Population also affected CT$_{\text{min}}$, with the invasive population north of the native range (Cocoa Beach) having a CT$_{\text{min}}$ nearly 1 °C lower than the invasive Key Largo population with a latitude similar to that of the native range (Cocoa Beach: mean ± SD = 14.04 ± 1.25 °C; Key Largo: 14.97 ± 1.5 °C; Fig. 7). Sex did not influence CT$_{\text{min}}$.

We observed no appreciable difference in CT$_{\text{max}}$ between populations (all lizards 43.02 ± 1.00 °C; Fig. 7). We observed a marginally non-significant interaction between mass and population; large lizards from Key Largo exhibited a weak trend towards lower CT$_{\text{max}}$ while mass did not appear to influence CT$_{\text{max}}$ in Cocoa Beach lizards (Fig. 6). We did not detect a correlation between mass and CT$_{\text{max}}$, nor did we detect an effect of sex. Similarly, we did not observe significant associations with any variables for T$_{\text{gape}}$ (38.12 ± 1.34 °C) or T$_{\text{pant}}$ (38.74 ± 1.33 °C; Table 3). Regarding T$_{\text{breath}}$, we observed a significant interaction between mass and population, with large Key Largo lizards exhibiting narrower T$_{\text{breath}}$ than large Cocoa Beach lizards as a result of the lower CT$_{\text{min}}$ in large Cocoa Beach lizards. Overall, larger lizards had narrower T$_{\text{breath}}$. T$_{\text{breath}}$ differed between populations, with Cocoa Beach 1.21 °C wider than Key Largo (29.07 ± 1.43 °C and 27.86 ± 2.19 °C, respectively; Fig. 7). We did not detect a difference in T$_{\text{breath}}$ between sexes.

**DISCUSSION**

Our correlative ENM results reject the Thermal Matching hypothesis for *Leiocephalus carinatus*, as they have established in environments with climatic values outside of the native range. We found that the ENM constructed using only native-range data underpredicted suitable habitat in Florida as compared to the full model, and the native ENM predicted low suitability in areas with confirmed established invasive populations. It is important to note that while precipitation variables and hydration...
status are important to consider when characterizing lizard distributions (Sannolo & Carretero, 2019), the precipitation variables were not substantially different among native and invaded ranges, and the improvement in the full model can probably be attributed to addition of thermal information from the invaded range. In this case, the native ENM with restricted island geographical and environmental space had limited value when predicting suitable habitats for establishment by an island-sourced invader. Inclusion of invaded range information in the full model improved the predictive power of the model, as it predicted higher relative suitability and an increased proportion of thresholded suitable areas

Table 1. The respective 10% omission threshold (TP$_{10}$) and median suitability scores for ecological niche models predicting relative suitability of Leiocephalus carinatus based on presence points from the native range (native) or native-and-invasive Florida range (full model). Values represent the suitability scores relating to either the native presence points or invasive range presence points

| Model  | Points  | TP$_{10}$ | Median |
|--------|---------|-----------|--------|
| Full   | Native  | 0.19      | 0.76   |
| Native | Native  | 0.22      | 0.77   |
| Full   | Invasive| 0.41      | 0.67   |
| Native | Invasive| 0.16      | 0.38   |

Figure 3. Shifts in relative suitability for Leiocephalus carinatus based on incorporation of invasive Florida range localities into ecological niche models. Orange indicates increases in relative suitability with inclusion of invasive range data, yellow indicates low or no differences in relative suitability, and blue indicates decreases in relative suitability. Points represent the invasive locality presence points (white) and native locality points (yellow). Arrows indicate populations sampled for thermal limits. Overall, the inclusion of invasive range data prompted increases in relative suitability throughout most of Florida.
in areas where *L. carinatus* are established (Figs 1, 2). As a case study, our results are important as they highlight the limited ability of correlative ENMs to accurately predict suitable habitat for species from restricted native ranges that have either not yet been introduced or were just recently established. Even when using mainland species, native-range ENMs can underpredict the suitability of invaded habitat, as found in a study predicting invasion of islands by four mainland snake species (*Silva-Rocha et al.*, 2019). As a contrast, a study on slider turtles (*Trachemys scripta* Schoepff, 1792), a species with a wider mainland native distribution, used a similar method of applying biologically relevant climatic variables in a correlative ENM to predict invasive populations (*Rödder et al.*, 2009). Their ENM produced relatively accurate projections of known invasive populations, which may partly be due its wide native range and thus larger proportion of environmental space incorporated in their model as compared to ours. Considering that screening tools are largely used when information about a potential invader is limited (reviewed by *Lyons et al.*, 2019), our study indicates that use of ENMs with limited information is a major shortcoming.

Linking between critical thermal limits studies and spatially coarse-scale ENMs can often be challenging. For example, while ambient temperatures may exceed critical thermal limits in a given area, lizards may not experience body temperatures near these limits due to microhabitat availability and thermoregulatory behaviour (reviewed by *Taylor et al.*, 2020). In addition, some lizards are able to survive several days at or below their CT<sub>min</sub> (*Huang & Tu*, 2008; *Lin et al.*, 2019). Some have argued that the right approach is inclusion of physiological data in ENMs (e.g. mechanistic ENMs) as a means to improve the accuracy of predictions (e.g. *Kearney & Porter*, 2004, 2009; *Rödder et al.*, 2009; *Wilms et al.*, 2011; reviewed by *Taylor et al.*, 2020), but fully fitting these models still often requires fine-grain microclimatic data. Our work shows, however, that there can be interesting parallels between physiological measurements and correlative ENM predictions. For example, we found that the curves for winter land surface temperatures (LST<sub>min</sub>) for *L. carinatus* asymptote near the CT<sub>min</sub> documented in this study. Additionally, LST<sub>min</sub> largely predict the areas of highest suitability in both native and full models. Subsetting the LST<sub>min</sub> at the average CT<sub>min</sub> of *L. carinatus* reported herein and subtracting a 2 °C buffer by soil to account for burrowing (e.g. *Paul et al.*, 2004) shows that the highest suitability areas fall outside of this threshold (Figs 1, 2). Of note, LST<sub>min</sub> is the average daily low of the coldest month, itself averaged across years, so cold snaps may still cause die-offs within suitable areas. Taken as a whole, we argue that our and others’ data demonstrate that interpreting correlative ENMs based on independently derived critical thermal limits can be useful for understanding the actual or potential ranges of invasive species (*Rödder et al.*, 2009; *Kolbe et al.*, 2010; *Mothes et al.*, 2019). Thus, we echo calls that a more formal inclusion of physiological data can improve the interpretation and implementation of ENMs in invasion biology (i.e. mechanistic ENMs; *Jiménez-Valverde et al.*, 2011; *Lennox et al.*, 2015; *Taylor et al.*, 2020).

Our physiological tolerance data reject the Thermal Potential Hypothesis in favour of the Thermal Flexibility Hypothesis, as we observed inter-population differences in CT<sub>min</sub>. Curly-tailed lizards from the Cocoa Beach population, 160 km north of the native range, had nearly 1 °C lower CT<sub>min</sub> compared with the population (Key Largo) within the latitude of the native range, meaning that lizards are either acclimatized or adapted to the lower temperatures in Cocoa Beach. While it is difficult to truly discern between acclimatization and adaptation of CT<sub>min</sub> without long-term multi-generation experimentation, we discuss evidence for both to inform future study.

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**Table 2.** Results from *t*-tests assessing maximum and minimum ambient temperatures at different timescales from locations nearest to populations of *Leiocephalus carinatus* sampled in Cocoa Beach and Key Largo, Florida

| Timescale | Measurement       | d.f.  | *t*      | *P*     | Mean temperature Cocoa Beach (°C) | Mean temperature Key Largo (°C) |
|-----------|-------------------|-------|----------|---------|----------------------------------|----------------------------------|
| Acclimation (5 months prior) | Max. ambient temp. | 1, 288.45 | 2.44 | 0.02<sup>*</sup> | 25.15 | 26.11 |
| | Min. ambient temp. | 1, 315.14 | −3.73 | 0.0002<sup>*</sup> | 17.42 | 19.35 |
| Adaptation 1991 to present (all months) | Max. ambient temp. | 1, 19074 | −6.15 | < 0.0001<sup>*</sup> | 27.95 | 28.30 |
| | Min. ambient temp. | 1, 19225 | −61.60 | < 0.0001<sup>*</sup> | 17.55 | 22.08 |
| Adaptation 1991 to present (summer only) | Max. ambient temp. | 1, 6568 | 16.79 | < 0.0001<sup>*</sup> | 32.09 | 31.45 |
| | Min. ambient temp. | 1, 5568 | −65.25 | < 0.0001<sup>*</sup> | 22.75 | 25.57 |
| Adaptation 1991 to present (winter only) | Max. ambient temp. | 1, 3073 | −13.30 | < 0.0001<sup>*</sup> | 23.65 | 25.14 |
| | Min. ambient temp. | 1, 3336.6 | −38.49 | < 0.0001<sup>*</sup> | 11.99 | 18.33 |

<sup>*Significant at *P* < 0.05 threshold.</sup>
A cold spell in January 2020 closely preceded our sampling (Fig. 4), which was relevant to other invasive lizard species; weather reporters accurately predicted green iguanas (Iguana iguana) falling from trees (Chappell, 2020) as ambient temperatures apparently dropped below their CT$_{\text{min}}$. Other non-native arboreal lizards in Miami, Florida, that survived the same cold snap converged on a similar CT$_{\text{min}}$ that was evident 10 weeks after sampling (Stroud et al., 2020). While it is possible that our results were influenced by this cold event, both of our sampled areas experienced similar minimum temperatures at the same times (Fig. 4). We therefore doubt that our observed difference in CT$_{\text{min}}$ between populations is explained by the cold event alone. Improved cold tolerance in the Cocoa Beach population could be attributed at least in part to acclimatization to lower temperatures over the preceding winter (Fig. 4). Within 18 weeks of acclimation to cool conditions, brown anole (Anolis sagrei) CT$_{\text{min}}$ decreased by 2–4 °C (Kolbe et al., 2014), and Italian wall lizard (Podarcis sicula Rafinesque, 1810) CT$_{\text{min}}$ was 3 °C lower in an introduced New York population after 12 weeks (but did not change in a California population; Haro, 2018). In brown and crested anoles (A. sagrei and A. cristatellus) assessed in the summer, population differences in CT$_{\text{min}}$ were only detected after cold acclimation in the laboratory; differences due to seasonal acclimatization were apparent in winter (Kolbe et al., 2012). Neel et al. (2020), however, found that CT$_{\text{min}}$ in L. carinatus from a population geographically intermediate to ours (West Palm Beach) did not differ between winter and spring, so seasonal acclimatization of cold tolerance may be minimal, or had already occurred and persisted through spring. Of note, we found CT$_{\text{min}}$

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**Figure 4.** Daily maximum (red) and minimum (blue) ambient temperatures and trends for Cocoa Beach (crosses, solid line) and Key Largo (circles, dashed line) in the days prior to sampling of *Leiocephalus carinatus* thermal limits. Lines indicate a smoothed average of the point data. Dates include the winter prior to sampling (1 October 2019 to 9 March 2020). The horizontal lines indicate the CT$_{\text{min}}$ measured in this study for Cocoa Beach (solid line) and Key Largo (dashed line). Note overlapping crosses and circles, which indicate days when both populations experienced similar ambient temperatures.

**Figure 5.** Ambient temperature minima (blue) and maxima (red) for Cocoa Beach and Key Largo areas from 1991 to the present sourced from NOAA weather stations. Dotted lines indicate averaged CT$_{\text{min}}$ (blue) and CT$_{\text{max}}$ (red) from both populations of *Leiocephalus carinatus* in this study.
values lower than those reported by Neel et al. (2020). However, we caution against direct comparison of these results, because in Neel et al. (2020) lizards were held in captivity for an undisclosed amount of time and potentially had acclimated to captive conditions. We anticipate negligible acclimation effects due to captivity in our study (Kolbe et al., 2012; Pintor et al., 2016; reviewed by Hutchison & Maness, 1979), because we tested individuals on the day of capture. Additionally, their study used conductive cooling and measured surface body temperature of lizards, whereas we used convective cooling and measured internal body temperatures. Regardless, both studies report CTmin in *L. carinatus* as higher than those of other non-native lizard species established in South Florida (Kolbe et al., 2012, 2014; Leal & Gunderson 2012; Mothes et al., 2019), even after accounting for potential differences in methodology and acclimation effects. This observation is also not limited to comparisons of smaller tree-dwelling lizards (e.g. most *Anolis* sp.), but stands for established non-native lizards that reach comparable or larger sizes and may burrow or shelter in cavities to some extent (e.g. *Agama picticauda* Linnaeus, 1758; *Basiliscus vittatus* Weigmann, 1828; *Ameiva ameiva* Linnaeus 1758; Mothes et al., 2019). Thus, with such high CTmin, *L. carinatus* may be uniquely suited to future study on the selective pressure of cold events.

Our observation of improved cold tolerance in Cocoa Beach lizards could be a result of adaptation to lower temperatures, with selection caused by hard freeze events or exposure to lower temperatures over generational timespans. Cool conditions cause death in some lizard species (e.g. Gorman & Hillman, 1977). Notably, a record cold spell in 2010 caused deaths of many native and non-native reptiles in southern Florida (Mazzotti et al., 2011, 2016). Both *L. carinatus* populations in this study probably became established well before 2010 and within 10 years of one other (Duquesnel, 1998; Krysko & King, 2002; Krysko et al., 2005). Each has persisted despite cold snaps and hard freeze events including the aforementioned 2010

### Table 3.

Results from ANCOVA assessing thermal limits in *Leiocephalus carinatus* from two invasive populations in Florida. Coefficients for variables in the linear models are given under the ‘value’ column. Post-hoc tests with Bonferroni corrections at $P < 0.05$ threshold (italicized) were conducted when population or the interaction between population and mass were significant; $P$-values are given in the $P$ column. Differences between population means and mean slopes (for interactions with mass) are reported in the ‘value column’.

| Measurement | Variable                                      | d.f. | $F$   | $P$     | Value  | SE   |
|-------------|-----------------------------------------------|------|-------|---------|--------|------|
| **CTmin**   | Population (Key Largo)                        | 2, 65| 13.41 | 0.0005* | 9.75   | −1.97 |
|             | *Cocoa Beach – Key Largo*                     | –    | –     | –       | –      | –    |
|             | *Sex*                                         | 1, 65| 0.04  | 0.87    | −0.07  | 0.36 |
|             | *Mass*                                        | 1, 65| 42.97 | < 0.0001* | 1.45  | 0.41 |
|             | Population (Key Largo) × Mass                 | 1, 65| 5.29  | 0.025*  | 1.44   | 0.63 |
|             | *Cocoa Beach – Key Largo*                     | –    | –     | –       | –      | –    |
|             | *Sex*                                         | 1, 58| 1.68  | 0.20    | 0.28   | 0.25 |
|             | *Mass*                                        | 1, 58| 3.32  | 0.08    | −0.05  | 0.46 |
|             | Population (Key Largo) × Mass                 | 1, 58| 3.72  | 0.06    | −1.18  | 0.61 |
| **CTmax**   | Population (Key Largo)                        | 2, 58| 1.54  | 0.22    | 39.10  | 1.95 |
|             | *Sex*                                         | 1, 58| 1.28  | 0.26    | 0.37   | 0.35 |
|             | *Mass*                                        | 1, 58| 2.88  | 0.09    | −0.45  | 0.64 |
|             | Population (Key Largo) × Mass                 | 1, 58| 0.69  | 0.35    | −0.81  | 0.86 |
| **Tgape**   | Population (Key Largo)                        | 2, 58| 3.23  | 0.08    | 0.45   | 2.75 |
|             | *Sex*                                         | 1, 58| 0.88  | 0.35    | 0.34   | 0.36 |
|             | *Mass*                                        | 1, 58| 0.62  | 0.43    | −0.51  | 0.64 |
|             | Population (Key Largo) × Mass                 | 1, 58| 0.005 | 0.94    | 0.06   | 0.87 |
| **Tpant**   | Population (Key Largo)                        | 1, 58| 10.66 | 0.002*  | 5.80   | 2.99 |
|             | *Cocoa Beach – Key Largo*                     | –    | –     | –       | –      | –    |
|             | *Sex*                                         | 1, 58| 1.75  | 0.19    | 0.43   | 0.39 |
|             | *Mass*                                        | 1, 58| 38.08 | < 0.0001* | −1.97  | 0.71 |
|             | Population (Key Largo) × Mass                 | 1, 58| 5.23  | 0.03*   | −2.18  | 0.95 |
| **Tbreadth**| Population (Key Largo)                        | 1, 58| 0.03* | 0.95    | −2.18  | 0.95 |

*Significant at $P < 0.05$ threshold. CTmin = critical thermal minimum; CTmax = critical thermal maximum; Tgape = temperature at gaping; Tpant = temperature at panting; Tbreadth = thermal breadth.
freeze, but cold snaps have occurred less frequently in the southern Key Largo population (Fig. 5). In Cocoa Beach, the average ambient minimum temperature in winter is below the CT_{min} of *L. carinatus*. *Leiocephalus carinatus* shelters in self-made burrows, which probably buffer them from short-term temperature extremes, as in other burrow-dwelling reptiles (McEachern et al., 2015; Ivey et al., 2020). However, with a CT_{min} as high as 14 °C, behavioural thermoregulation alone may not serve as an adequate buffer (Buckley et al., 2015), inducing selection for improved cold tolerance in northern populations. The capacity for evolution of improved cold tolerance has been investigated in other lizard species, which found similar results to ours (Leal & Gunderson, 2012; Kolbe et al., 2014; Haro, 2018). Brown anoles (*A. sagrei*) with overall reduced CT_{min} after acclimation showed consistent among-population differences in CT_{min} after 18 weeks; higher CT_{min} was observed in the population closer to the equator (Kolbe et al., 2014). Similarly, crested anoles (*A. cristatellus*) from a population ~800 km north of its native range showed improved cold tolerance relative to the native range, even after 3 weeks of laboratory acclimation of both populations (Leal & Gunderson, 2012). A next step based on the work presented here is determining the relatedness among individual *L. carinatus* populations within the invasive range, because genetic factors could determine the limits of physiological plasticity for each population (Kolbe et al., 2012; Gerken et al., 2015; Haro, 2018). For example, it is possible that, by chance, the Cocoa Beach population was sourced from a northern island in the Bahamas that was already selected for greater cold tolerance, while the Key Largo population was sourced from a more southerly island. However, as noted earlier, the Cocoa Beach population is 160 km north of the most northern potential native source population. It is possible that a combination of acclimation and adaptation in relation to source population drives cold tolerance, rather than effects of source population alone. To this end, future genetic work, assessment of additional populations with differing origins and acclimation experiments would be informative.

Our findings that CT_{max} did not differ between populations does not invalidate our support of the Thermal Flexibility Hypothesis for non-native populations of *L. carinatus*, because our data still support population differences in thermal tolerance. The lack of difference in CT_{max} is not surprising. CT_{max} is not a very labile trait compared with CT_{min}; CT_{max} is generally closer to the upper lethal temperature than CT_{min} is to the lower lethal temperature (Araújo et al., 2013; Hoffmann et al., 2013; Gunderson & Stillman, 2015). The relatively narrow plasticity in CT_{max} is likely because tissue damage and/or enzyme malfunction caused at high temperatures are difficult to abate physiologically (Paulson & Hutchinson, 1987; Frederich & Pörtner, 2000; Gangloff & Telemecco, 2018). Additionally, behavioural heat avoidance in the form of burrow use may prevent selection for higher CT_{max} in
natural populations (Huey et al., 2003; Buckley et al., 2015; Ivey et al., 2020), while non-burrowing species may have greater selection pressure on CT$_{\text{max}}$, such as Anolis cristatellus in urban heat islands (Campbell-Staton et al., 2020). We found that differences in maximum ambient temperatures between Key Largo and Cocoa Beach are historically and recently consistently lower than the differences between minimum ambient temperatures. Leiocephalus carinatus, which lives in hot, sunny environments in both native and introduced ranges, may have already reached peak heat tolerance for its species (Gilbert & Miles, 2017).

While repeated exposure to upper thermal limits can affect future measurements of CT$_{\text{max}}$ (reviewed by Hutchison & Maness, 1979), there is little evidence to suggest same-day exposure to low temperatures, as in our study, affects CT$_{\text{max}}$ (Menke & Claussen, 1982). Additionally, we noted an effect of body size on CT$_{\text{min}}$, with larger lizards in Key Largo showing higher CT$_{\text{min}}$, but as the size distributions between populations were similar and we did not observe an overall effect of size on CT$_{\text{max}}$, we believe this reflects a difference in tolerance between populations that is made more obvious by thermal inertia of larger lizards, rather than effects of inertia alone (Claunch et al., 2021; Fig. 6). With these potential caveats in mind, our finding that the T$_{\text{breadth}}$ of lizards in Cocoa Beach is about 1 °C greater than in Key Largo is best explained by the difference in CT$_{\text{min}}$ between the two populations. A recent study echoes our results in that CT$_{\text{max}}$ did not vary among populations of invasive Italian wall lizards (P. muralis), while CT$_{\text{min}}$ was lowest in the highest latitude population, affecting T$_{\text{breadth}}$ (Litmer & Murray, 2019). Interestingly, Neel et al. (2020) reported seasonal thermal lability for CT$_{\text{max}}$ in L. carinatus. They found that the increase in CT$_{\text{max}}$ nearly mirrored the increase in ambient temperatures from winter to spring, indicating that acclimatization to local thermal environments may occur. We measured CT$_{\text{max}}$ in the spring and found 1.4–3.27 °C higher CT$_{\text{max}}$ than reported by Neel et al. (2020) (winter and spring, respectively) for populations north and south of theirs. For the reasons described above, we hesitate to draw conclusions from directly comparing our results to theirs, but as is the rule of any good science, repetition of these studies with improved sampling would be necessary to understand the responses of island-sourced species to novel habitats and climatic regimes.

**CONCLUSIONS**

Our results support the Thermal Flexibility hypothesis for L. carinatus, even if technically limited to the CT$_{\text{min}}$. While our understanding of the role of adaptation vs. acclimatization to cold is incomplete,
our combined approach of using an ENM with experimental data on just two populations of lizards gave insight into the thermal lability of island-sourced invaders. Additionally, our application of a buffered \( CT_{\text{min}} \) value as a ‘filter’ of \( LST_{\text{min}} \) data for Florida (Figs 1, 2) gave a reasonable approximation of the areas of highest suitability as predicted by a correlative ENM constructed from the current invasive distribution of these lizards. This demonstrates that relatively simple, low-cost physiological data collected in a reasonable amount of time (in our case, 1 week) may have similar predictive power regarding the highest suitable areas for establishment as time-intensive surveys over wide areas combined with correlative ENMs. We anticipate that a greater understanding of physiological limits and performance will aid the predictive power of ENMs, especially for invasive species sourced from restricted native ranges. Integrative modelling would probably provide much more accurate (and potentially smaller) targets for managers; thus, additional investigation of \( L. \ carinatus \) thermal performance across its invaded and native ranges would be beneficial. These data could ultimately be further integrated into mechanistic ENMs and linked to finer scale microclimate data. We anticipate that continued study of this system would yield interesting results for invasion ecology and evolution.

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DATA AVAILABILITY

Data collected for this study and code are available at https://doi.org/10.5066/P9XGK1GG (Claunch & Reed, 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Top ecological niche models and outputs predicting Leiocephalus carinatus (northern curly-tailed lizard) based on presence points from the native range or native-and-invasive range (full model), determined by selection of models within Δ2 Akaike information criterion score (AICc).

Table S2. ROC scores for each modelling algorithm used in the ensemble approach, as well as the top-model from the tuned Maxent approach.

Table S3. Relative suitability scores of both native (N = 49) and invaded range localities (N = 27) used in models.

Figure S1. Mean relative suitability across all algorithms used in ensemble models.

Figure S2. Mean presence–absence consensus across ensemble models.