The Company of Biologists

RESEARCH ARTICLE

Acclimatization in the physiological performance of an introduced ectotherm

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ABSTRACT

Phenotypic flexibility may facilitate range expansion by allowing organisms to maintain high levels of performance when introduced to novel environments. Phenotypic flexibility, such as reversible acclimatization, permits organisms to achieve high performance over a wide range of environmental conditions, without the costly allocation or acquisition tradeoffs associated with behavioral thermoregulation, which may expedite range expansion in introduced species. The northern curly-tailed lizard, *Leiocephalus carinatus*, was introduced to the USA in the 1940s and is now established in southern Florida. We measured bite force and the thermal sensitivity of sprinting of *L. carinatus* during the winter and spring to determine how morphology and performance varied seasonally. We found evidence of seasonal variation in several aspects of physiological performance. Lizards sampled in spring sprinted faster and tolerated higher temperatures, while lizards sampled in winter had high performance over a wider range of temperatures. Furthermore, seasonal differences in physiology were only detected after generating thermal reaction norms. Both sprint and bite force performance did not differ seasonally when solely comparing performance at a common temperature. No seasonal relationships between morphology and performance were detected. Our results suggest that *L. carinatus* may use reversible acclimatization to maintain high levels of performance across seasons not typically experienced within their native range. Thermal physiology plasticity may ameliorate the impacts of sub-optimal temperatures on performance without the cost of behavioral thermoregulation. Our work highlights the importance of utilizing reaction norms when evaluating performance and the potential ecological impacts of introduced species.

KEY WORDS: Acclimation, Plasticity, Invasive species, Seasonality, Thermal performance curves

INTRODUCTION

The ranges of most species are not static, but expand and contract throughout their evolutionary history (Davis and Shaw, 2001). A special case of range expansion is when introduced species become invasive, expanding into a previously unoccupied geographic area and impacting native flora and fauna. One critical aspect governing range limits is a species' ability to adapt and/or acclimatize to novel environmental conditions, and this is particularly true during range expansions (Hoffmann and Sgrò, 2011; Parker et al., 2003; Somero, 2010; Tepolt and Somero, 2014; Wright et al., 2010). Organisms undergoing range expansions, especially successful invasive species, often possess phenotypes that are well suited for exploiting a wide variety of resources and niche spaces (Crowder and Snyder, 2010; Huang et al., 2010; Layman and Allgeier, 2012; Snyder and Evans, 2006).

Successful invasive species, including brown anoles (*Anolis sagrei*), fire ants (*Solenopsis invicta*), brown tree snakes (*Boiga irregularis*) and gray squirrels (*Sciurus carolinensis*), can often outcompete native species because they possess traits such as generalist habitat requirements and diet, decreased susceptibility to native parasites, pathogens and predators, and high fecundity, relative to natives (Gurnell et al., 2004; Losos et al., 1993; Rodda et al., 1992; Tompkins et al., 2003; Vogt et al., 2002). Another trait likely employed by successful invasive species is an increased ability to acclimatize to a broader range of environmental conditions (Funk, 2008). This acclimatization requires that organisms possess sufficient phenotypic plasticity to expand their geographic range. However, surprisingly little is known about how seasonal variation in temperature or rainfall influences the relationship between morphology and physiological performance for species undergoing range expansion.

Phenotypic flexibility (i.e. reversible phenotypic plasticity, acclimatization or acclimation) refers to the within-individual variation that occurs in response to predictable (e.g. seasonal) or stochastic environmental fluctuations (Piersma and Drent, 2003; Seebacher, 2005; Wilson and Franklin, 2002). Seasonal acclimatization is likely a useful mechanism employed by both successful native (Stellatelli et al., 2018; Sun et al., 2018) and invasive (Braby and Somero, 2006; Tepolt and Somero, 2014; Xu et al., 2007) species to optimize physiological performance in novel environments. However, the benefit of plasticity depends on the magnitude of the environmental change and the resources required to exhibit the acclimation response (DeWitt et al., 1998; Gabriel and Lynch, 1992). Subsequently, tradeoffs (e.g. allocation, acquisition, specialist–generalist) constrain the phenotypes that can be expressed by a given genotype (Angilletta et al., 2003). Therefore, the extent of phenotypic flexibility typically varies and is often modest rather than fully compensatory (Kingsolver and Huey, 1998). Thermal reaction norms are commonly used to determine the sensitivity of performance (e.g. locomotion, assimilation, survivorship, etc.) to changes in temperature and are proximately constrained by biochemical processes (Hochachka and Somero, 1968; Somero, 1978). Acclimation in temperature-dependent physiological traits such as membrane fluidity, action potential generation, protein synthesis, heat-shock protein expression and protein thermal stability can lead to adaptive shifts in thermal optima and thermal tolerance limits (Hochachka and Somero, 1968; Somero, 2002). When experiencing environmental variation, such as during a range

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expansion, increased phenotypic flexibility is likely under strong natural selection (Davidson et al., 2011; Kingsolver and Huey, 1998; Somero, 2010). Despite the evolutionary and ecological relevance of acclimatization for biological invasions, the acclimatory capabilities of many introduced species remain unstudied.

Many organisms align important fitness-influencing activities with optimal environmental conditions available in a certain season. For example, plants and animals often reproduce during warmer months in higher latitudes or during wetter months in lower latitudes (Bauer, 1992; Castilho et al., 2007; Taylor and Tulloch, 1985). Morphological traits can also exhibit phenotypic flexibility. Irschick and Meyers (2007) found that during the breeding season, *Urosaurus* lizards with relatively narrow heads and low bite forces increase head width, which increases bite force; conversely, lizards with large heads and high bite forces early in the breeding season exhibited narrower heads and low bite forces late in the breeding season. In that study, the researchers hypothesized that head width plasticity dictates social interactions in the breeding season, as head width (and bite force performance) largely impacts territory defense and mate acquisition (Irschick and Meyers, 2007). However, the correlative relationship between morphological and physiological traits undergoing reversible acclimatization remains largely enigmatic. We studied phenotypic flexibility in two performance traits and the performance morphology axis to better understand the potential for acclimatization to increase annual performance in an introduced, potentially invasive species.

The northern curly-tailed lizard, *Leiocephalus carinatus*, was introduced into the southeastern USA in the 1940s and is now established in southern Florida. Curly-tailed lizards outcompete and prey upon other lizards when introduced, including another introduced species, *Anolis sagrei* (Losos et al., 2004), and their presence may disrupt the ecology of many native species in this region (e.g. *Anolis carolinensis*). We evaluated (1) how the thermal sensitivity of sprinting and bite force performance changes across seasons, and (2) how the relationship between morphology and performance might change across seasons in the introduced range of *L. carinatus*. We asked the following questions. (1) Does performance at a common temperature vary seasonally for different performance traits? (2) Do thermal performance curves for sprint performance vary seasonally? (3) Does the relationship between morphology and physiological performance vary seasonally? We hypothesized that sprint speed and bite force performance would have similar thermal optima because these traits influence survivorship and/or fecundity and therefore have substantial fitness consequences (Husak et al., 2006; Lappin and Husak, 2005; Miles, 2004). Monthly average ambient temperatures differed by 2.5°C between seasons during our sampling period (NOAA, National Centers for Environmental Information: https://www.ncei.noaa.gov/; Menne et al., 2012). We expect curly-tailed lizards to align thermal optima for performance with the differing environmental temperatures available during the spring and winter seasons. Hence, thermal optima for bite force and sprint performance would be higher in the spring and lower in the winter. We predicted that differing thermal optima could alter the morphology–performance axis.

MATERIALS AND METHODS
Study system
The northern curly-tailed lizard (*Leiocephalus carinatus* Gray 1827) natively occupies rocky, open, coastal habitats in The Bahamas, the Cayman Islands and Cuba. The regions where curly-tailed lizards occur natively and non-natively are close geographically

and therefore experience similar climates. However, introduced populations in Florida are concentrated in urban areas where temperatures are likely inflated as a result of urban heat island effects (Winchell et al., 2016; Yuan and Bauer, 2007). Introduced curly-tailed lizards were sampled separately (i.e. not mark–recaptured) in the winter (November 2015 and January 2016) and spring (March 2016) in urban West Palm Beach, FL, USA (26.743939, −80.049544). Lizards were captured using a slip noose and temporarily stored in cloth bags in a cool environment while in the field. Lizards were then transferred to the animal care facility at Georgia Southern University for collection of physiological and morphological data. All applicable institutional and/or national guidelines for the care and use of animals were followed. All methods were approved by the Georgia Southern University Institutional Animal Care and Use Committee (protocol #I15011 and #I15012).

Critical thermal limits
Critical thermal maxima (CT_{max}) and critical thermal minima (CT_{min}) are indices of the highest and lowest temperatures at which an animal loses basic locomotor function (Lutterschmidt and Hutchison, 1997) and define tolerance limits in ectotherms (Huey and Stevenson, 1979). To measure CT_{max}, lizards were placed in a deep container under heat lamps, so the temperature increased at a constant rate ($\sim$1°C min^{-1}). Attached to the venter of each animal was a small thermocouple that continuously measured ventral body temperature. Every minute, a lizard's 'righting response' was checked by gently flipping the lizard onto its back and observing whether it could regain an upright position. If the lizard flipped over within 15 s, the trial continued. The temperature at which an animal lost its righting response was recorded as CT_{max}. For CT_{min} trials, lizards were cooled on an icepack, and the righting response was checked each minute. The temperature at which an animal lost its righting response was recorded as the CT_{min}. Thermal sensitivity and thermal tolerance data were only collected from male animals, as varying levels of gravidity are known to impact female thermal preference in a wide range of ectotherms and specifically many lizards (Beuchat, 1986; Braña, 1993; Le Galliard et al., 2003; Rock and Cree, 2003). Egg laying typically begins for *L. carinatus* in early May (Meshaka et al., 2006), so we could not determine female reproductive status during our spring sampling period.

Sprinting thermal sensitivity
Male sprint speed was quantified at five ecologically relevant temperatures (28, 32, 34, 37 and 40°C) that span the critical thermal limits of the northern curly-tailed lizard to generate thermal performance curves. Prior to each sprinting trial, lizards were placed in an incubator until the desired body temperature was reached. Lizard body temperature was measured with a cloacal thermometer prior to the start of each trial. After ensuring a lizard was at the desired trial temperature, it was encouraged by the experimenter to sprint down a 2 m racetrack. We did not include trials in statistical analyses if they occurred more than 30 s after the lizard was removed from the incubator because of the rapid rate of equilibration with environmental temperature. Infrared photocells lined the track (9 paired photocells spaced 0.25 m apart), allowing us to collect data for calculation of velocity using custom LabView software (see Angilletta et al., 2002; Bauwens et al., 1995; Miles, 2004). Each lizard was run 3–4 times at each temperature, and the maximum sprint value from each trial was retained for analysis. We considered a lizard's sprint speed to be 0 m s^{-1} if the individual was unable to run continuously for 25 cm (the distance between each photocell pair). Lizards were sprinted at the same temperature on the

2

same day, and the order of temperature trials was randomized. Between the various temperature trials, lizards were kept in terraria at ~33–35°C for ≥24 h between sampling days to minimize stress and ensure lizards were ready for the next sprint trial at a different temperature. If sprint data could not be collected for at least three-quarters of the trial temperatures for an individual (excluding the upper and lower trial temperatures), they were omitted from the curve-fitting process.

The thermal performance curve of each individual lizard was estimated by fitting a set of left-skewed parabolic equations to sprint data using the program TableCurve 2D (Systat Software, Inc.) (Angilletta, 2006; Logan et al., 2014; Neel and McBrayer, 2018). Equations were chosen based on the typical left-skewed shape of ectotherm thermal performance curves, which are thought to be structured by the thermodynamics of enzyme function (Somero, 1978). A line of best fit for the data for each individual was selected using Akaike's information criterion (AIC) (Akaike, 1987; Logan et al., 2014). When two equations did not significantly differ in their AIC score, the equation with the fewest parameters was chosen. When curves did not differ in AIC score or in the number of parameters, the curve with the highest R^2 value was chosen. Thermal performance curves were anchored with the critical thermal limits for an individual. The upper and lower temperature where an individual lost its righting response were considered the thermal limit. The loss of a righting response would clearly hinder locomotor performance, and thus it makes biological sense to incorporate this measure into the thermal performance curve for sprint performance.

Thermal performance curves were used to estimate three traits associated with thermal performance. First, the predicted maximum sprint speed (P_{max}) was estimated from each curve. Second, the thermal optimum (T_{opt}), or the temperature at which performance is predicted to be maximal, was estimated for each individual from their thermal performance curve. Finally, the range of body temperatures over which the lizard can run at 80% of its P_{max} or faster (B_{80}) was estimated for each individual via the thermal performance curve. These three traits were all used to describe and compare the shapes of the thermal performance curve (Huey and Stevenson, 1979).

Bite force performance
Bite force was measured every other day for 6 days (i.e. three trial days per lizard). On days in which bite force was measured, lizards were removed from terraria, placed in individual cloth bags, and stored in a thermal chamber at 37°C for at least 30 min before measurements were recorded. The temperature of each lizard was taken with a cloacal thermometer immediately prior to the start of the trial. We measured bite force performance at a single temperature, as previous studies have found it to be relatively insensitive to changes in temperature (Herrel et al., 2007). We selected 37°C as our common temperature to compare seasonal variation in sprint and bite performance because physiological optima are expected to be co-adapted with preferred body temperature in nature (Angilletta, 2009; Lande and Arnold, 1983). We expected this trial temperature to be closest to preferred body temperature, which Phillips and Howes (1988) found to be 37.1±0.8°C in L. carinatus.

Bite force was measured using dual cantilever bite plates fitted with a piezoelectric force transducer (Kistler 9203; see Herrel et al., 1999). The bite plates consisted of two metal plates, spaced 2 mm apart, and wrapped in small pieces of duct tape to avoid damaging the lizards' teeth during measurements. The position of the plates in a lizard's mouth was standardized such that the furthest edges of the metal bars aligned with the third scale posterior to the nostril.

Lizards were encouraged to bite the bite force meter 3 times per trial day. Lizards were held in the hand and placed into position to bite the plates immediately upon mouth opening. If more than a minute passed or if the lizard escaped and had to be recaptured, we did not take any more measurements on that animal on that trial day. We generated a standard curve by regressing the force (in newtons, N) displayed on the readout of the calibrated charge amplifier (Kistler 5995A) while hanging weights of known mass on the bite bars to determine the actual bite force in newtons (Anderson et al., 2008). For each individual, we used the maximum bite force across all trials for all subsequent statistical analyses.

Morphological measurements
All collected lizards were euthanized with MS-222. We used digital calipers to measure the following morphometric traits to the nearest 0.01 mm: snout–vent length (SVL), jaw length, jaw width, humerus length, antebrachium length, metacarpal length, longest digit from both the hindlimb (tarsal phalange) and forelimb (phalange) length, femur length, shank length, metatarsus length and tail length. We excluded individuals with broken or autotomized tails from further analyses, as this may have affected performance.

Body temperature model
We derived estimates of lizard body temperature using the ectotherm model in the R package NicheMapR v.2.0.0 (Kearney and Porter, 2020). For this, we first estimated microclimates (air temperature, wind speed, zenith angle of sun, relative humidity, solar radiation, sky radiation and substrate temperatures) for West Palm Beach, FL, USA, using the NicheMapR microclimate model (Kearney and Porter, 2017). The NicheMapR microclimate model generates hourly above- and below-ground conditions from meteorological, terrain, vegetation and soil data at a resolution of 15 km^2 (Kearney and Porter, 2017; New et al., 2002). We ran the microclimate model assuming a shade level of 50% to compare estimated lizard body temperatures between seasons. The NicheMapR ectotherm model uses the output produced from the microclimate model as the driving environmental input to compute the range of body temperatures animals would experience (Kearney and Porter, 2017). We ran the ectotherm model for a diurnal lizard with a mass of 40 g. We turned off behavioral parameters (i.e. postural changes, shade-seeking, climbing and retreating underground) to minimize the potential effects of behavioral thermoregulation on computed body temperatures. The data we present here are for the middle days of each month during the winter (15 November, 15 December and 15 January) and spring (15 March, 15 April and 15 May).

Statistical analysis
To statistically determine the relationship between bite force, sprint performance, morphology and season, we used general linear models with a normal distribution. All dependent variables were log-transformed prior to statistical analysis. Data were size-adjusted by including body size (log-transformed SVL) in all models tested as covariates. To test for seasonal differences in the relationship between morphology and performance, initial analyses included sex×season interactions and interactions between the morphological trait of interest and season, but none were significant, so interaction terms were not included in the final analyses. To test for heterogeneity of slopes in our thermal performance curve statistics, initial analyses included SVL×season interaction effects, but none were significant so the interaction terms were not included in the final analyses. To determine whether seasonal acclimatization in sprint performance was beneficial, we analyzed sprint speed at

Table 1. Seasonal variation in the relationships between snout–vent length (SVL) and sprint performance at 37°C between sexes in *Leiocephalus carinatus*

Variable	F	P
Sex	61.78	<0.0001*
Season	2.87	0.10
SVL	6.64	0.014*

*Significant difference.

our lowest (28°C) and highest (40°C) temperature trials with a temperature×season interaction. All data were evaluated for the assumption of normality and equal variances prior to using parametric tests. For parametric analyses, we obtained P-values using the 'Anova' function (car package; Fox and Weiserg, 2019) with type III sum of squares. If assumptions of parametric tests were not met, non-parametric alternatives were used. All linear models were fitted and tested using R Statistical Software (http://www.R-project.org/). Means are reported ±1 s.e.m., and significance was established at α=0.05.

RESULTS
Seasonal variation in sprinting and bite force performance at a common temperature
We found that sprint speed did not vary seasonally, when sexes were analyzed either separately or together. Log-transformed sprint speed at 37°C did not differ between seasons (N=14 winter, N=28 spring) but did differ between sexes (N=15 females, N=27 males) and with SVL (ANCOVA: season: $F_{4,32}$=2.87, P=0.10; sex: $F_{4,32}$=61.78, P≤0.0001; SVL: $F_{4,32}$=6.64, P=0.014; see Tables 1–3, Fig. 1A). Log-transformed sprint speed did not vary seasonally for males (ANCOVA: $F_{3,18}$=1.72, P=0.20) or females (ANCOVA: $F_{3,12}$=1.56, P=0.24).

Similarly, we found that bite force did not vary among seasons (N=18 winter, N=29 spring), when sexes were analyzed either separately or together (N=26 females, N=21 males). Log-transformed bite force did not differ between seasons, but did differ between sexes and with SVL (ANCOVA: season: $F_{4,43}$=1.68, P=0.20; sex: $F_{4,43}$=4.19, P=0.046; SVL: $F_{4,43}$=611.24, P≤0.001; Fig. 1B). Log-transformed bite force did not vary seasonally for males (ANCOVA: $F_{3,18}$=0.47, P=0.50) or females (ANCOVA: $F_{3,23}$=1.30, P=0.26).

Seasonal variation in thermal performance curve shape
We found that CT_{max} was greatest in the spring, but CT_{min} did not vary seasonally. Log-transformed CT_{max} was greater in the spring (41.62±0.24°C, N=17) than in the winter (39.75±0.79°C, N=9; ANCOVA: $F_{3,23}$=7.72, P=0.010). CT_{min} did not vary between spring (19.38±0.50°C, N=17) and winter (17.73±0.95°C, N=10; ANCOVA: $F_{3,23}$=3.67, P=0.07).

We found that P_{max} and B_{80} varied seasonally, with greater P_{max} in spring and greater B_{80} in the winter. Log-transformed P_{max} was greater in lizards during the spring (1.17±0.06 mm s^{-1}) than during
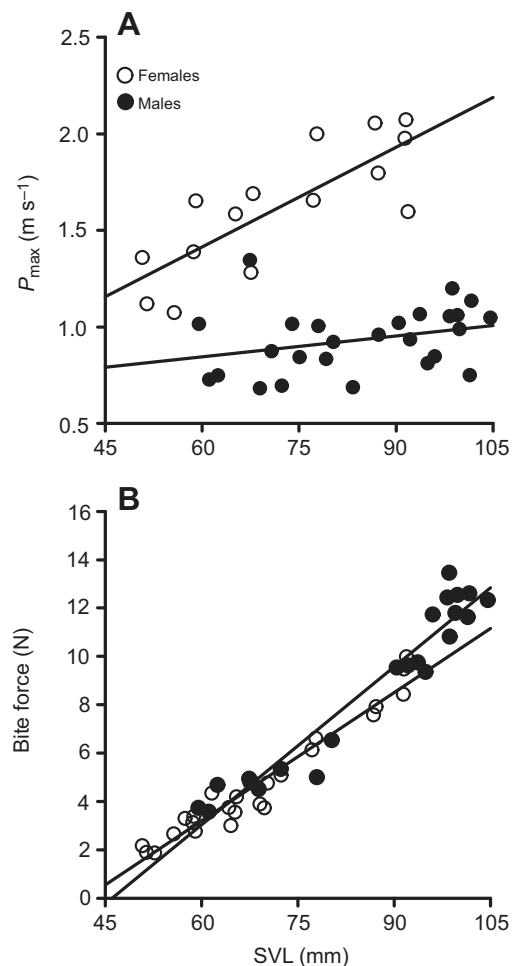
Table 2. Thermal sensitivity of mean (±1 s.e.m.) sprint speed in male *L. carinatus*

	Sprint speed (m s^{-1})			
Temperature (°C)	Winter		Spring	
28	0.76±0.05	N=11	0.75±0.03	N=17
32	0.79±0.04	N=11	0.96±0.03	N=17
34	0.67±0.08	N=3	0.84±0.04	N=17
37	0.84±0.04	N=10	1.01±0.04	N=17
40	0.73±0.04	N=11	1.10±0.03	N=17

Table 3. Seasonal variation in thermal performance curve parameters and thermal tolerance limits

Variable	F	P
CT_{min}	3.67	0.06
CT_{max}	7.72	0.010*
T_{opt}	43.5	0.15
B_{80}	11	0.044*
P_{max}	13.93	0.002*

CT_{min}, critical thermal minimum; CT_{max}, critical thermal maximum; T_{opt}, thermal optimum; B_{80}, thermal performance breadth; P_{max}, maximal performance.
Note that for T_{opt} and B_{80}, we used non-parametric Wilcoxon tests and report the corresponding W-statistics for those data rows in the F column. *Significant difference between seasons.
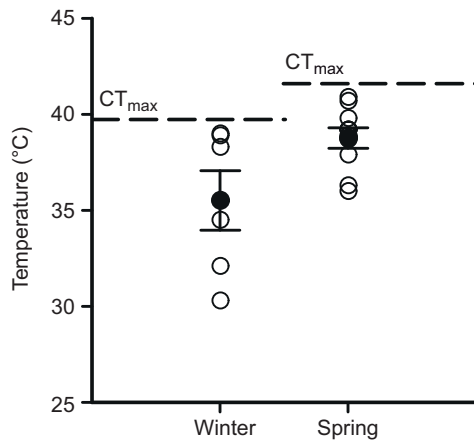
the winter (0.85±0.05 mm s^{-1}; ANCOVA: $F_{3,13}$=13.93, P=0.002). Log-transformed T_{opt} was 3°C warmer in the spring (38.76±0.52°C) than in the winter (35.85±1.52°C), although this difference was not statistically significant (non-parametric Wilcoxon–Mann–Whitney: $W_{1,14}$=43.5; P=0.15; Fig. 2). Log-transformed B_{80} was greater in lizards sampled in the winter (10.13±0.96°C; non-parametric Wilcoxon–Mann–Whitney: $W_{1,14}$=11; P=0.044) than in the spring (7.42±0.52°C; see Table 3). Sprint speed was relatively low at both

Fig. 1. Sprint speed performance and bite force of *Leiocephalus carinatus* at a common temperature (37°C) as a function of body size. (A) Sprint speed (P_{max}; N=27 males, N=15 females) and (B) bite force (N=22 males, N=27 females) potted against snout–vent length (SVL).

Fig. 2. Thermal optima (T_{opt}) for sprint performance in *L. carinatus* sampled in the winter and spring. CT_{max}, critical thermal maximum. Means±1 s.e.m. are shown (N=6 winter, N=10 spring).

the coolest and warmest temperature trials in the winter, although it increased between our coolest and warmest temperature trials in the spring, suggesting that seasonal acclimatization in sprint performance was beneficial (ANCOVA: $F_{5,27}=9.49$, $P=0.004$).

Seasonal variation in the relationship between morphology and performance

Despite seasonal variation in P_{max} and B_{80} for locomotion, we did not detect any corresponding seasonal variation in the morphology–performance axis. There were no significant differences between seasons in the relationships between morphological traits and physiological performance (see Table 4; Table S1).

DISCUSSION

Our results suggest that phenotypic flexibility may be an important factor in facilitating the invasion of new habitats. We found evidence of seasonal acclimatization in several aspects of physiological performance, including differences in T_{opt}, B_{80}, P_{max} and CT_{max}. Differences in T_{opt} and CT_{max} between winter and spring (2.9 and 1.8°C, respectively) closely tracked seasonal environmental variation during that time. Monthly average ambient temperature increased by 1.8°C between winter (November, December and January) and spring (March, April and May) during sampling periods in 2015–2016. Average daily minimum

and maximum ambient air temperature spanned 19.4–26.4°C in our winter sampling period, and 20.7–28.6°C in our spring sampling period (NOAA, National Centers for Environmental Information 2019: https://www.ncei.noaa.gov/; Fig. S1). However, ectotherms can achieve body temperatures that differ greatly from air temperatures as a result of complex interactions between the organism and environmental factors (e.g. air and surface temperature, solar radiation, wind, precipitation, etc.) (Angilletta, 2009; Bakken, 1992; Heath, 1964). Lizard body temperature generated with NicheMapR (Kearney and Porter, 2020) spanned 11.6–32.1°C during the winter and 15.1–37.3°C during the spring (Fig. S2). In winter months, the average highest body temperature lizards could attain during the day was 30.5°C, compared with 35.1°C in the spring (Fig. S2). Consistent with our predictions, higher temperatures enabled higher P_{max} in the spring (Figs 3A and 4). We also found that during the winter, when temperatures are lower and more heterogeneous (Fig. S1), lizards had wider B_{80} (Fig. 3B). These results suggest an alignment between physiological traits and the predictable, seasonal fluctuations in environmental temperature that occur within the non-native range of curly-tailed lizards.

Importantly, we were only able to detect seasonal variation in locomotion by generating the reaction norms of thermal performance (Fig. 4; Fig. S3). Reaction norms describe the relationship between continuous environmental and phenotypic variables (Gotthard and Nylin, 1995; Stearns, 1989). Reaction norms describing the thermal sensitivity of performance metrics such as locomotion, assimilation, survivorship, etc., are commonly referred to as thermal performance curves because of their characteristic non-linear and left-skewed shape (Huey and Stevenson, 1979). By generating thermal reaction norms, curve parameters (T_{opt}, B_{80}, CT_{min}, CT_{max} and P_{max}) can be used to capture and interpret variation in the relationship between temperature and performance (Huey and Stevenson, 1979) that may otherwise be missed when solely comparing performance at a common temperature. Our results highlight the value of considering performance over a range of temperatures when seeking to evaluate the potential for introduced species to invade novel environments.

Phenotypic flexibility has been proposed as the main mechanism employed by species across a broad taxonomic range for continued persistence under projected warming scenarios (Charmantier et al., 2008; Chown et al., 2007; Seebacher et al., 2015) and also when encountering novel environmental conditions during range expansion (Baker, 1965; Molina-Montenegro and Naya, 2012; Parker et al., 2003; Wright et al., 2010). The performance breadth, or range of temperatures that permits high performance (80% of P_{max}), has direct

**Table 4. Seasonal variation in the relationships between morphology and performance at a common temperature (37°C)**

	d.f.	Sex		Season		SVL		Morphology	
		F	P	F	P	F	P	F	P
Bite force									
Jaw length	5,42	3.83	0.06	0.50	0.48	50.31	<0.0001*	0.36	0.55
Jaw width	5,42	3.52	0.07	1.38	0.24	42.40	<0.0001*	1.25	0.26
Sprint speed									
Tail length	5,31	63.32	<0.0001*	2.65	0.11	6.48	0.02*	2.00	0.16
Humerus	5,31	68.02	<0.0001*	0.16	0.68	0.32	0.57	3.31	0.08
Antebrachium	5,31	86.71	<0.0001*	0.14	0.70	0.02	0.88	8.48	0.006*
Metacarpal	5,31	52.27	<0.0001*	1.88	0.17	2.41	0.13	0.30	0.58
Phalange	5,31	61.05	<0.0001*	2.66	0.11	3.42	0.07	0.0001	0.99
Femur	5,31	90.87	<0.0001*	0.27	0.60	1.91	0.17	10.18	0.003*
Shank	5,31	74.48	<0.0001*	0.31	0.58	0.65	0.42	5.02	0.03*
Metatarsus	5,31	60.88	<0.00001*	1.91	0.17	1.69	0.20	0.07	0.78
Tarsus phalange	5,31	66.24	<0.00001*	3.22	0.08	0.34	0.56	2.60	0.11

*Significant difference.
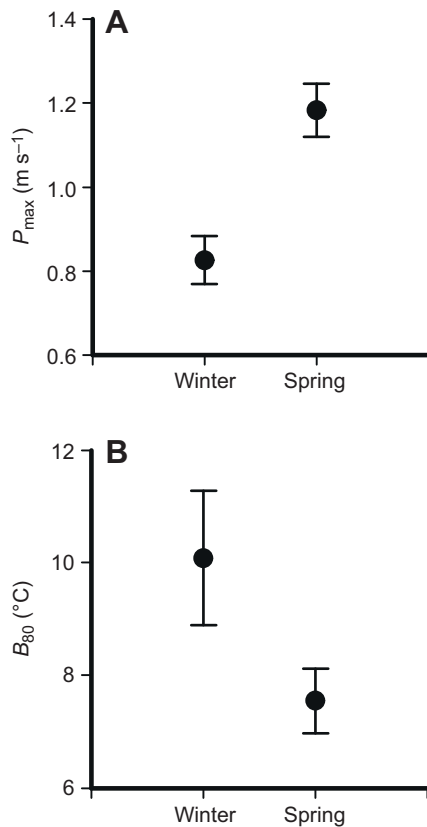
Fig. 3. P_{max} and thermal performance breadth in *L. carinatus* sampled in the winter and spring. (A) P_{max} and (B) thermal performance breadth (B_{80}). Means±1 s.e.m. are shown (N=6 winter, N=10 spring).

implications for organismal performance and fitness in novel or fluctuating environments (Huey and Stevenson, 1979; Kingsolver et al., 2004). In winter, when a wider range of environmental temperatures is experienced daily, expanding performance breadth enables animals to maintain relatively high levels of activity, despite experiencing increased environmental variation.
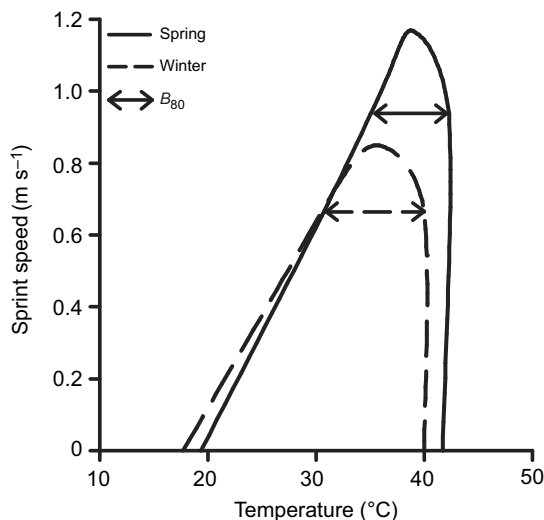
Fig. 4. Thermal performance curves for *L. carinatus* sampled in the winter and spring. Mean curve parameter values: thermal optimum (T_{opt}), B_{80}, critical thermal minimum (CT_{min}), CT_{max} and P_{max} (N=6 winter, N=10 spring).

Given the proximate biochemical mechanisms limiting performance at the organismal level, models of thermal sensitivity assume that tradeoffs between maximum performance and performance breadth (e.g. specialist–generalist tradeoffs) constrain variation in performance curves (Gilchrist, 1995; Huey and Kingsolver, 1989). However, several recent studies conflict with the predictions of this model, suggesting current theories may be too simplistic or not applicable to a broad range of taxa (Angilletta et al., 2003; Butler et al., 2013). Our results provide potential support for a specialist–generalist tradeoff. We observed lower P_{max} and wider B_{80} in the more-varied winter sampling period and higher P_{max} and narrower B_{80} in the spring (Fig. 4; Fig. S4). Moreover, thermal performance breadth likely contributes to determining a species' or population's fundamental niche, which describes a hypervolume of environmental states that enable survival (Colwell and Futuyma, 1971; Hutchinson, 1959). Research has shown a positive relationship between niche breadth and geographical range size in a wide range of both plant and animal taxonomic groups (Slatyer et al., 2013). Niche breadth, and specifically the breadth for thermal performance, as well as thermal tolerance likely play an important role in determining the potential for geographic range expansion in invasive and introduced species.

Limitations of this study include that we did not sample throughout ontogeny (i.e. juveniles and hatchlings were not sampled), only measured thermal sensitivity of male lizards, and only studied lizards in two different seasons. However, to better understand how phenotypic flexibility can impact invasive species biology, future work should measure phenotypic variation across the full range of environmental variation. Thermal tolerance can differ among the sexes and life stages in ectotherms (Bowler and Terblanche, 2008; Krebs and Loeschcke, 1995), and it cannot be assumed that adult male physiology alone determines the fundamental niche space or the potential for range expansion. While our results demonstrate temporal variation in physiological performance, future research across multiple seasons in both sexes across multiple life stages is necessary to elaborate how phenotypic flexibility is associated with seasonal changes in the environment.

Species undergoing rapid range expansion should experience selection for phenotypic flexibility in a variety of traits. Specifically, when phenotypic flexibility brings a population close to a new phenotypic optimum that aligns with current environmental conditions, directional selection should increase fitness in individuals with greater plasticity (Ghalambor et al., 2007). Beyond the adaptively plastic response of single traits, evolutionary theory suggests that alterations in behavior should accompany acclimation in a co-adapted genotype (Lande and Arnold, 1983). In the context of thermal biology, thermal co-adaptation could entail thermal optima aligning with preferred temperatures, which has been observed in several ectotherms including crocodiles (Glanville and Seebacher, 2006) and lacertid lizards (Bauwens et al., 1995). This alignment occurs because, as thermoregulation becomes cost-prohibitive in unfavorable environments, animals should maximize the net benefit of thermoregulation by shifting preferred temperatures to align with available temperatures (Angilletta, 2009; Huey and Slatkin, 1976). In the broadest context, phenotypic flexibility like that in curly-tailed lizards could ultimately induce physiological shifts that lead to genetic adaptation, thereby facilitating a cycle of invasion and range expansion.

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Supplementary materials

Table S1. Seasonal variation in morphology.

|	df	Sex		Season		SVL		SVL*Season		Sex*Season	
		F	P	F	P	F	P	F	P	F	P
Jaw Length	5,41	2.71	0.11	0.22	0.63	4.01	0.055	0.44	0.64	2.98	0.09
Jaw Width	5,41	0.17	0.67	0.08	0.78	0.05	0.81	2.03	0.14	0.09	0.76
Tail length	5,41	0.01	0.90	0.85	0.36	2.42	0.13	1.38	0.26	0.07	0.79
Humerus	5,41	1.30	0.26	0.27	0.60	1.55	0.22	0.53	0.59	5.96	0.02*
Antebrachium	5,41	3.05	0.09	2.40	0.13	6.43	0.016*	2.19	0.12	0.0004	0.98
Metacarpal	5,41	1.31	0.26	0.43	0.51	0.64	0.42	0.12	0.87	1.18	0.28
Phalange	5,41	0.15	0.69	0.34	0.56	8.48	0.006*	2.63	0.08	0.13	0.71
Femur	5,41	0.47	0.49	0.01	0.90	4.79	0.03*	1.56	0.22	1.61	0.21
Shank	5,41	0.19	0.66	0.57	0.45	7.25	0.01*	1.08	0.35	0.12	0.72
Metatarsus	5,41	0.22	0.64	5.83	0.02*	5.32	0.02*	0.2.23	0.12	0.14	0.70
Tarsus phalange	5,41	0.48	0.49	1.55	0.22	5.32	0.02*	2.22	0.12	1.65	0.20
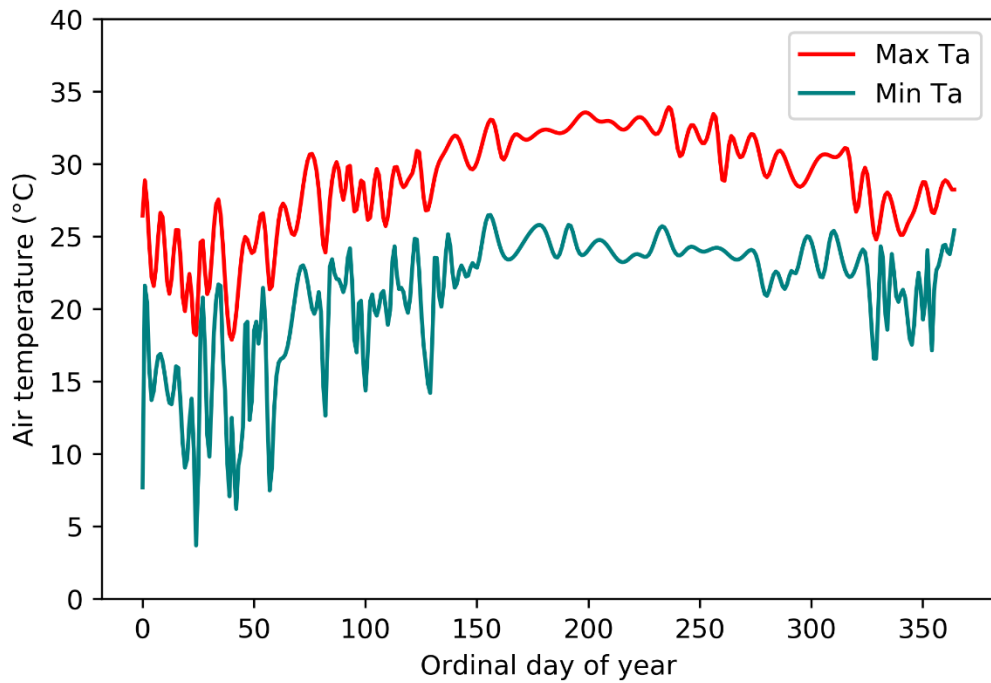
Figure S1. Annual minimum and maximum air temperatures interpolated from available weather station data for West Palm Beach, FL in July 1, 2015 through June 30, 2016 (NOAA, National Centers for Environmental Information, 2019). Weather station data were fit to a nonlinear spline function ($k = 4$) to generate predicted minimum and maximum air temperature data.
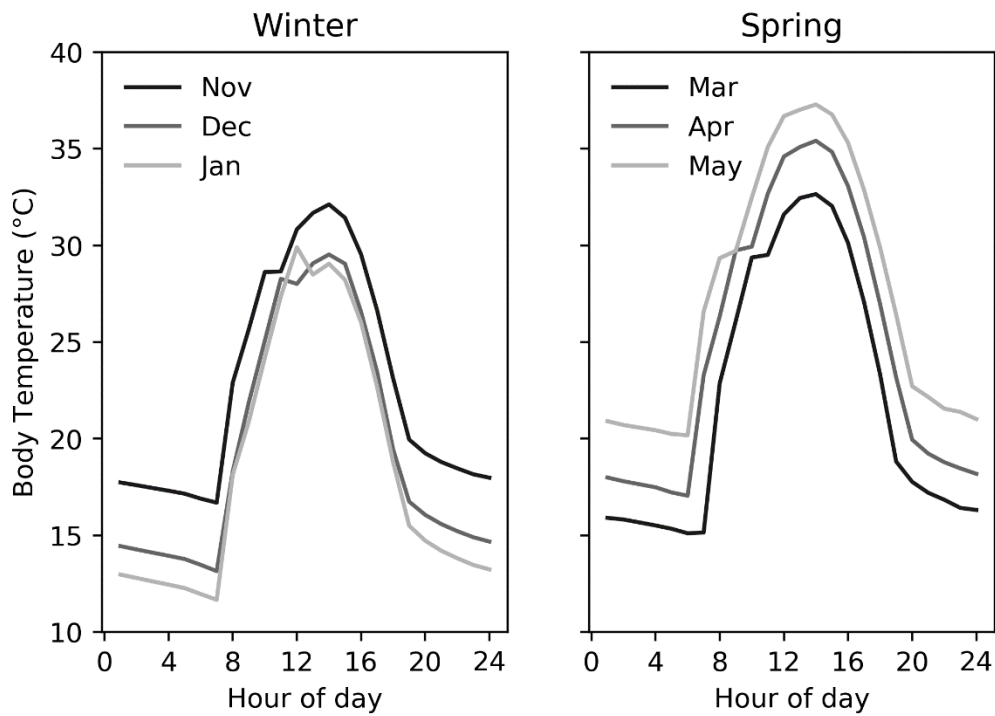
Figure S2. Estimated lizard body temperatures generated using NicheMapR ver. 2.0.0 (Kearney and Porter, 2020). Body temperatures were predicted for the middle day of each month in the winter and spring for lizards in West Palm Beach, FL.
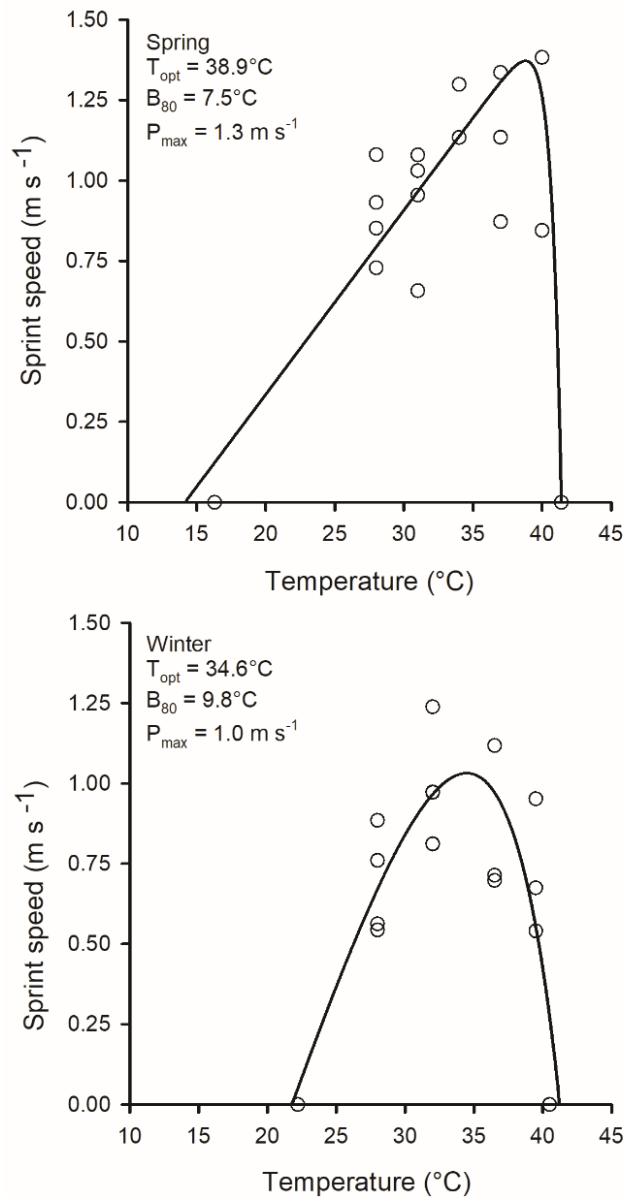
Figure S3. Thermal performance curves for two representative *Leiocephalus carinatus* lizards sampled during the spring (top) and winter (bottom) seasons. The selected curves illustrate seasonal variation in thermal performance curve shape. Both individual's thermal optima (T_{opt}), performance breadth (B_{80}), and maximum performance (P_{max}) are shown.
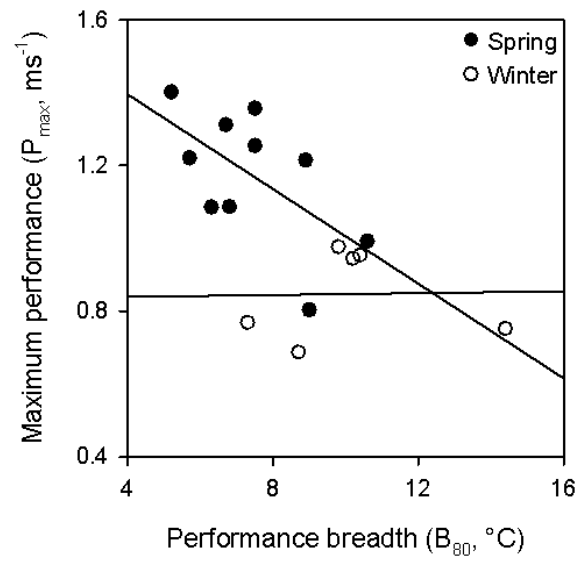
Figure S4. Maximum performance shown as a function of performance breadth suggests that a tradeoff may exist between high maximal performance and performance breadth in the spring.