

# Thermal stability of an adaptable, invasive ectotherm: Argentine giant tegus in the Greater Everglades ecosystem, USA

ANDREA F. CURRYLOW <sup>1,†</sup> MICHELLE A. M. COLLIER,<sup>1,4</sup> EMMA B. HANSLOWE,<sup>1,5</sup> BRYAN G. FALK,<sup>1,4</sup> BRIAN S. CADE <sup>2</sup>, SARAH E. MOY,<sup>1,6</sup> ALEJANDRO GRAJAL-PUCHE,<sup>1,7</sup> FRANK N. RIDGLEY <sup>3</sup>, ROBERT N. REED,<sup>2,8</sup> AND AMY A. YACKEL ADAMS<sup>2</sup>

<sup>1</sup>U.S. Geological Survey, South Florida Field Station, Fort Collins Science Center, 40001 SR 9336, Homestead, Florida 33034 USA

<sup>2</sup>U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue Building C, Fort Collins, Colorado 80526 USA

<sup>3</sup>Conservation and Research Department, Zoo Miami, 12400 SW 152nd Street, Miami, Florida 33177 USA

**Citation:** Currylow, A. F., M. A. M. Collier, E. B. Hanslowe, B. G. Falk, B. S. Cade, S. E. Moy, A. Grajal-Puche, F. N. Ridgley, R. N. Reed, and A. A. Yackel Adams. 2021. Thermal stability of an adaptable, invasive ectotherm: Argentine giant tegus in the Greater Everglades ecosystem, USA. *Ecosphere* 12(9):e03579. 10.1002/ecs2.3579

**Abstract.** Invasive species globally threaten biodiversity and economies, but the ecophysiological mechanisms underlying their success are often understudied. For those alien species that also exhibit high phenotypic plasticity, such as habitat generalists, adaptations in response to environmental pressures can take place relatively quickly. The Argentine giant tegu (*Salvator merianae*; tegu) is a large omnivorous lizard from South America that is prolific, long-lived, vagile, and highly adaptable to disturbed environments. They are well suited to the climate of southeastern United States, introduced to several disjunct areas, including the Everglades, where their voracious appetite threatens native wildlife. Tegus undergo winter dormancy (hibernation) to cope with colder temperatures, and while this behavior may facilitate invasion into more temperate regions, it may also present management opportunities. We studied the thermal habits of wild *S. merianae* within their invaded range in southern Florida, USA. We used radiotelemetry and trail cameras to verify aboveground behaviors, and temperature dataloggers to monitor surface (sun-exposed [ $T_e$ ] and shaded [ $T_s$ ]), ambient ( $T_a$ ), subsurface ground ( $T_h$ ), and internal body ( $T_b$ ) temperatures of a population of free-ranging tegus over several seasons. We evaluated thermal and behavioral data and identified five biologically significant periods: pre-hibernal, hibernal, cold snaps, hibernal-basking, and post-hibernal. We found tegus maintained thermal stability throughout the hibernal period, frequently at temperatures above available thermal microhabitats. Variation in  $T_b$  was lowest during hibernation and cold snaps and was less variable than subsurface temperatures despite not leaving their hibernaculum. Hibernal ingress and egress were best predicted by temperature differentials between exposed soil and ambient daily mean temperatures ( $T_e - T_a$ ) and daylength. Though we detected no sex differences, larger animals started hibernation sooner, stayed in hibernation longer, and retained higher fat stores over the study period. One individual did not hibernate, representing only the second record of this behavior. Despite limitations of these descriptive data, this is the first study finely detailing  $T_b$  of a population of wild, free-ranging *S. merianae* over multiple biologically significant time periods and to associate  $T_b$  with thermal habitats within its invasive range. Tegus' apparent ability for thermal stability expands the adaptability breadth of this species and underscores the invasion threat.

**Key words:** Argentine black and white tegu; biological invasion; brumation; ecological impacts; hibernation; invasive species; plasticity; reptile; *Salvator merianae*; thermal ecology; *Tupinambis merianae*.

**Received** 5 November 2020; accepted 1 February 2021. Corresponding Editor: George Middendorf.

**Copyright:** © 2021 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of Ecological Society of America. This article is a U.S. Government work and is in the public domain in the USA. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

<sup>4</sup>Present address: Everglades National Park, National Park Service, 40001 SR 9336 Homestead Florida 33034 USA.

<sup>5</sup>Present address: Department of Environmental Studies, University of Illinois Springfield, One University Plaza, Springfield Illinois 62703 USA.

<sup>6</sup>Present address: 1030 North 78th Street Omaha Nebraska 68114 USA.

<sup>7</sup>Present address: Department of Biological Sciences, Northern Arizona University, 617 S. Beaver Flagstaff Arizona 86011 USA.

<sup>8</sup>Present address: U.S. Geological Survey, Pacific Island Ecosystems Research Center, Building 344 Hawaii National Park Hawaii 96718 USA.

† E-mail: [acurrylow@usgs.gov](mailto:acurrylow@usgs.gov)

## INTRODUCTION

Invasive species negatively impact ecosystems and economies in myriad ways (Pimentel et al. 2005, Simberloff et al. 2013), but to predict and address those impacts requires an understanding of how the species and the system interact. The primary factors restricting species distributions are environmental conditions, underscoring the importance of understanding population-level tolerance and limitations (Jimenez-Valverde and Lobo 2011). Temperature is among the most valuable predictors of invasion potential (Zerebecki and Sorte 2011, Mohan and Kariyanna 2018), particularly for ectothermic species that rely on thermal regimes for their physiological processes (Jimenez-Valverde and Lobo 2011, Sunday et al. 2014). Ectotherms are dependent on available thermal habitats and behavioral thermoregulation for normal physiological functions (Hertz et al. 1982, Huey and Kingsolver 1989). Thermal regimes dictate diel and seasonal activity such as ectotherm locomotion, foraging, digestion, dormancy, and reproduction (Huey 1982, Webb and Shine 1998). During the active season, terrestrial ectothermic vertebrates behaviorally thermoregulate, differentially using available thermal habitats throughout the daytime hours (e.g., basking), and often retreat to thermally stable underground refuges in periods of thermal extremes (high midday heat or cold nights). During colder months, many ectotherms hibernate (undergo winter dormancy), often sheltering below ground in hibernacula as a buffer against temperature extremes (Currylow et al. 2013). The thermal suitability of available habitats determines not only the microclimates across an ecosystem that ectotherms can inhabit, but also their range limits and, in some cases, population sex ratios (Viets et al. 1994, Shine 1999, Pringle et al. 2003, Pike et al. 2011). The

phenotypic plasticity exhibited among individuals in response to differing environmental conditions can predict invasive establishment success (Kraus 2009).

The Greater Everglades ecosystem in southern Florida is known for its diversity of habitats and abundance of wildlife, particularly ectotherms such as herpetofauna that flourish in its subtropical climate. Many species of non-native herpetofauna have established populations in this ecosystem (Krysko et al. 2011, 2016), including well-publicized examples such as the invasive Burmese python (*Python bivittatus*; Snow et al. 2007, Dorcas et al. 2012, Hanslowe et al. 2018, Krysko et al. 2019). The Argentine giant tegu (*Salvator merianae*; tegu) is a large (up to 5 kg) teiid lizard native to South America's tropical to temperate environments (Andrade et al. 2004) that was brought to southern Florida because of its popularity in the pet trade (Enge et al. 2006, Krysko et al. 2016). Tegus are omnivorous habitat generalists that have quickly established populations in natural, urban, and agricultural areas of southern Florida and now threaten the persistence of native ground-dwelling and ground-nesting vertebrate populations (Barraco 2015, Mazzotti et al. 2015). They are prolific breeders (Pernas et al. 2012, Meshaka et al. 2019), and intensive ongoing harvest in the native range for the skin trade appears to be sustainable (Fitzgerald et al. 1991, Fitzgerald 1994). This suggests that control in an introduced range will prove challenging. For these reasons, tegus may be considered a significant threat to the Greater Everglades ecosystem. Because they can capitalize on altered ecosystems and anthropogenic features for shelter and dispersal, these lizards have the potential to invade much of the southern United States (Winck and Cechin 2008, Chiarello et al. 2010, Klug et al. 2015, Jarnevich et al. 2018). Indeed, recent evidence shows at least one

population is established north of Florida (Haro et al. 2020), contributing to the broad establishment success of introduced lizard taxa (Kraus 2009).

Argentine giant tegu distribution and activity are closely tied to temperature (Lanfri et al. 2013, Ferreguetti et al. 2018, Jarnevich et al. 2018) limiting its invasion expansion. Though southern Florida has generally high annual temperature and humidity levels, the Greater Everglades ecosystem is known for shallow, often flooded soils and/or exposed bedrock. Much of the area offers few deep-soil thermal refuges for burrowing animals, especially during winter months when the animals hibernate (McEachern et al. 2015). However, this species was recently shown to exhibit seasonal reproductive endothermy in captivity (Tattersall et al. 2016). Evidence of similar facultative endothermy (metabolic heat production above ambient temperatures) during hibernation and in response to evolutionarily unfamiliar microhabitat features could change our understanding of its invasion potential and management. Yet, no studies have detailed the thermal ecology of wild *S. merianae* within their invasive range, and we could only find a single mention of a small, unpublished study in the native range (Andrade et al. 2004).

In order to provide managers a better understanding of the thermal tolerance and invasion capacity of a free-ranging invasive ectotherm with the potential to impact populations of sympatric species, we investigated the thermal biology of wild *S. merianae* in Florida, USA. We used temperature dataloggers to monitor shaded and exposed substrate temperatures, ambient air temperature, subsurface ground and burrow temperatures, and internal body temperature of free-ranging tegus for more than 10 months encompassing hibernation. We aimed to (1) describe the thermal habitats available to ectotherms overwintering in southern Florida; (2) identify the physical or environmental factors that contribute to tegu ingress into, or egress from, hibernation; (3) determine how tegus respond to cold temperatures and the shallow burrow depths in the wild; and (4) understand how thermal responses influence invasion risk of this species for climates in North America.

## STUDY AREA

We conducted this study in the Greater Everglades ecosystem of southern Florida, USA. Our study site was primarily located in the Southern Glades Wildlife Environmental Area (WEA), which is co-managed by the Florida Fish and Wildlife Conservation Commission (FWC) and the South Florida Water Management District (SFWMD; described in McEachern et al. 2015). The habitat is predominantly freshwater sawgrass (*Cladium jamaicense*) slough interspersed with marl prairies and tree islands dominated by broadleaf and cypress trees (*Taxodium* spp.). The area is highly anthropogenically altered; agriculture and commercial tree groves border the site, and the hydrology is managed by a system of canals, levees, gates, and locks. Invasive plant species such as Brazilian pepper (*Schinus terebinthifolius*) and native, early-successional species such as poisonwood (*Metopium toxiferum*) often dominate these disturbed areas. Soil depths average 28–30 cm over limestone bedrock with an isohyperthermic temperature regime (i.e., mean annual soil temperature  $\geq 22^{\circ}\text{C}$  with  $< 6^{\circ}\text{C}$  seasonal variation; Mount and Brannon 2007). Monthly groundwater level ranges from +1.06 to  $-0.80$  feet (NAVD88; often submerging exposed ground) and ranges in temperature from  $23.5^{\circ}\text{C}$  to  $27.1^{\circ}\text{C}$  in the region (USGS 2020). The region is classified as having a subtropical savanna climate with a distinct hot, humid wet season in the summer and slightly cooler, less-humid dry season mid-fall through late spring (Hela 1952, Duever et al. 1994). Occasional winter cold fronts can cause rapid temperature drops, which last for short periods.

## METHODS

### Tegu monitoring

We live-trapped 35 *S. merianae* (18♂, 17♀) from across the study site and recorded sex, snout-vent length (SVL), mass, and capture location for each individual. We surgically implanted coated temperature dataloggers (Thermochron iButton, model number DS1921G-F5#, Maxim Integrated, San Jose, California, USA, coated in PlastiDip and then paraffin/beeswax mixture) that had been gas-sterilized with ethylene oxide. We implanted the dataloggers into the coelom using

sterile technique through a lateral flank incision. We held animals for 4–6 d for post-surgical recovery before release at the point of capture.

We programmed dataloggers to record tegu internal body temperature ( $T_b$ ) every 60 min from as early as 23 June 2015 to as late as 2 May 2016 (up to 46 weeks depending on capture dates) to completely encompass hibernation. Immediately prior to release at their point of capture, we equipped each tegu with a VHF radio transmitter (Advanced Telemetry Systems model A2930B, Advanced Telemetry Systems, Isanti, Minnesota, USA) over the pelvis using a harness of stainless-steel ball chain. We subsequently tracked individuals three times per week until hibernation had commenced (following McEachern et al. 2015) and then once per week to monitor hibernation. We deployed a motion-detection trail camera (Moultrie models M990i, M880, PRADCO, Birmingham, Alabama, USA; Bushnell model 119468, Bushnell Outdoor Products, Overland Park, Kansas, USA or similar) near each burrow to sample aboveground behavior. At the conclusion of each study animal's hibernal period, we hand-captured or live-trapped individuals as they egressed their burrow hibernaculum. We humanely euthanized all recaptured study animals, recorded post-hibernation morphometric and necropsy data, and recovered thermal dataloggers.

#### *Thermal habitat monitoring*

To document the thermal habitats used by tegus surrounding and throughout the hibernal period, we deployed 43 temperature dataloggers (coated in PlastiDip for weatherproofing) at several locations across the study site. Once a study animal commenced hibernation, we deployed a temperature datalogger inside the burrow corridor of the occupied burrow hibernacula within arm's length (averaging 31 cm) to record available subsurface/hibernacula temperatures ( $T_h$ ). Animals chose overwintering burrows of various materials (bedrock caverns, cavities in massive limestone spoil; see McEachern et al. 2015). It was impractical to attempt excavation of hibernacula, and the irregularity and complexity of the rock spoil prevented us from describing the extent of tegu-accessible dimensions. Where an entrance to the hibernacula could not be determined (e.g., in a large rock pile with multiple

possible entrances), temperature dataloggers were buried (subsurface 13–45 cm) at the location of the animal's strongest transmitter signal. We programmed  $T_h$  dataloggers to record temperatures every 60 min and deployed the majority by November 2015. These were recovered by April 2016 for a total of approximately 27 weeks of records.

In addition to the 34 subsurface/hibernacula dataloggers, we chose three replicates of each of three environmental microclimatic types (ambient, full sun-exposed substrate, and shaded substrate;  $n = 9$  total) and deployed temperature dataloggers at those locations across the study region in order to represent available thermal habitats. We suspended the three ambient temperature dataloggers ( $T_a$ ) inside clear plastic cups (to prevent moisture and wind from influencing readings) at 1 m above ground in shaded areas, covered the three exposed soil temperature dataloggers ( $T_e$ ) with approximately 1 cm of substrate in areas fully exposed to the sun during the entire day, and concealed the three shaded soil temperature dataloggers ( $T_s$ ) with approximately 1 cm of substrate in areas fully shaded during the entire day. All thermal habitat dataloggers recorded temperatures every 60 min from 2 July 2015 through 18 April 2016 (approximately 45 weeks).

#### *Data analyses*

To characterize the hibernal ecology of *S. merrianae* and detect thermal patterns across the study site, we analyzed thermal data at multiple levels. We processed the raw thermal data using RStudio (version 1.2.5033; 2009–2019 RStudio, Boston, Massachusetts, USA), and because subsurface temperatures we present may not represent the potentially deeper burrow temperatures that the animals could have been experiencing, we calculated daily means, medians, minimums, and maximums (temperature dailies) for each of the temperature dataloggers and then binned them by locations ( $T_b$ ,  $T_h$ ,  $T_a$ ,  $T_e$ , and  $T_s$ ) to describe the population and landscape. At the coarser sampling intervals of days and hours (opposed to minutes) and with our lack of operative temperature models, we did not attempt to address fine-scale behavioral thermoregulation or thermal inertia (Taylor et al. 2020). Instead, we binned data by location and calculated daily variation in

temperature (daily  $T_{(\max)}$  – daily  $T_{(\min)}$ ) to help analyze and interpret general tegu behavior relative to available thermal habitats. To investigate differences in temperature and seasonal timing, we used univariate split-plot approaches with the restricted maximum-likelihood method fit for linear mixed models with daily  $T_{(\max)}$ , daily  $T_{(\min)}$ , daily  $T_{(\text{mean})}$ , daily  $T_{(\text{median})}$ , and daily  $T_{(\max-\min)}$  as dependent variables, and month, week, SVL, mass, body condition score (BCS), sex, and location as the predictors with individual temperature datalogger ID as the random effect on the intercept and all predictor variables to account for repeated measures. We used fixed effect regression models when evaluating hibernation start and end dates and hibernation duration by SVL, mass, BCS, and sex. We followed model tests by least squares means Tukey-Kramer post hoc pairwise comparisons or Student's  $t$  tests to detect significant differences among fixed effect groups.

We determined individual hibernal ingress and egress dates for each study animal using thermal data supplemented with telemetry and images from trail cameras. We defined ingress date as the first date a study animal did not subsequently exit the hibernacula for three or more consecutive days, and egress date as the first date it was tracked away from the hibernacula or began basking daily, whichever behavior occurred first. We used hibernal ingress and egress dates and hibernation duration to generate general biologically significant seasonal time periods (pre-hibernal, hibernal, and post-hibernal), and we compared daily and weekly temperatures across datalogger locations during each of these periods. We also analyzed all daily temperatures within the hibernal period for cold snaps and basking events. We defined cold snaps based on the frequency of dramatic temperature variation with an emphasis on negative deviation from microclimatic mean (Pirhalla et al. 2015). We calculated this as a 24-h period meeting two conditions: (1) The variation in ambient temperature ( $\Delta[T_{a(\max)} - T_{a(\min)}]$ ) was more than two standard deviations (SD) above the mean variation ( $\text{mean}[T_{a(\max)} - T_{a(\min)}]$ ), and (2) included low temperatures that were at least two standard deviations below the ambient mean (i.e.,  $-2\text{SD} \leq \text{mean}(T_a)$ ; a rapid fall to cold temperature within 24 h). Similarly, we calculated basking events as 24-h periods under two conditions: (1) Days when  $\Delta(T_{b(\max)} - T_{b(\min)})$  was greater than

two standard deviations above mean( $T_{b(\max)} - T_{b(\min)}$ ), and (2) included high temperatures that were  $2\text{SD} \geq \text{mean}(T_b)$ .

We used ANOVA tests or nominal logistic regression chi-square analyses (where appropriate and depending on data type) when examining variation among individuals in morphometrics and associated dates. As an index of body condition, we used residuals from a regression of log-transformed body mass on log-transformed SVL where zero represents the mean value (Falk et al. 2017). We evaluated the potential for metabolic heat regulation and behavioral thermoregulation by comparing hourly, daily, and time period actual, range, and variation in  $T_b$  to  $T_{bv}$  and against available environmental thermal habitats ( $T_a$ ,  $T_e$ , and  $T_s$ ). We used median temperatures when appropriate to best represent associated temperatures and reduce the influence of outliers. Preliminary datafile processing was carried out in R (R Foundation for Statistical Computing, Vienna, Austria), while further data processing and all statistical analyses were carried out using JMP statistical software (version 14.2.0; 2018 SAS Institute, Cary, North Carolina, USA).

## RESULTS

Over a total of 46 weeks, we recorded 215,143 individual temperatures (8911 daily summaries) from 22 tegus (9♂, 13♀), 19 subsurface/hibernaculum, and six environmental locations. We were not able to find or recapture 13 of the study animals (9♂, 4♀) and recovered neither their temperature dataloggers nor final morphometric information; subsurface/hibernacula data for these individuals were not used in subsequent analyses. One male tegu did not hibernate (remained active all season; Appendix S1: Figs. S1, S2) and was excluded from hibernation-specific analyses. Two other subsurface/hibernacula dataloggers (associated with 2♀) and three of the thermal habitat dataloggers (one exposed soil and two shaded soil) were lost or damaged; images from trail cameras suggest that most of this disturbance can be attributed to small mammals.

### *Thermal ranges and biologically significant time periods*

We identified five periods that were linked to the thermal ecology of tegus in southern Florida

Table 1. Median temperatures (°C) from all grouped datalogger locations by biologically significant time period across 46 weeks of monitoring during 2015–2016 in the Greater Everglades ecosystem, Florida, USA.

Datalogger location and statistic	Pre-hibernation	Hibernation	Cold snap	Hibernal-basking	Post-hibernation
<i>Salvator merianae</i> internal ( $T_b$ )	30.9 <sup>a</sup> (28.6, 36.5)	24.5 <sup>a</sup> (24.2, 24.7)	19.1 <sup>a</sup> (18.7, 19.4)	27.1 <sup>a</sup> (25.3, 35.6)	25.9 <sup>a</sup> (22.8, 33.3)
Subsurface/Hibernaculum ( $T_h$ )	24.3 <sup>c</sup> (23.1, 26.1)	23.0 <sup>b</sup> (22.2, 23.6)	17.1 <sup>b</sup> (15.6, 17.9)	24.1 <sup>a</sup> (24.0, 25.1)	21.5 <sup>b</sup> (20.7, 22.4)
Ambient air ( $T_a$ )	27.2 <sup>bc</sup> (23.8, 32.1)	22.3 <sup>b</sup> (19.3, 26.6)	15.5 <sup>b</sup> (9.4, 23.7)	24.8 <sup>a</sup> (21.5, 29.7)	23.2 <sup>ab</sup> (19.5, 28.4)
Exposed soil ( $T_e$ )	29.7 <sup>ab</sup> (24.5, 39.9)	22.8 <sup>ab</sup> (18.8, 29.9)	16.6 <sup>ab</sup> (9.0, 29.5)	25.7 <sup>a</sup> (21.0, 35.0)	25.4 <sup>ab</sup> (19.3, 37.1)
Shaded soil ( $T_s$ )	26.4 <sup>bc</sup> (25.6, 27.3)	22.7 <sup>ab</sup> (22.0, 23.7)	17.4 <sup>ab</sup> (15.9, 19.6)	24.4 <sup>a</sup> (23.7, 25.3)	22.9 <sup>ab</sup> (21.9, 24.2)
$F$	16.6001	5.5518	2.9199	1.9662	9.224
df	4, 25.19	4, 38.95	4, 29.57	4, 11.17	4, 27.32
$P$	<0.0001	0.0012	0.0378	0.1685	<0.0001
SD	1.06	1.15	2.12	1.26	1.83

Notes: SD, standard deviation. Datalogger location temperatures within columns not connected by the same letter are statistically different. For reference, mean minimum and mean maximum temperatures for those locations by time periods appear in parentheses.

(pre-hibernal, hibernal, cold snaps, hibernal-basking, and post-hibernal) using the compiled tracking, thermal, and photodocumentary data. These periods represent times when tegus are active (pre-hibernation, hibernal-basking, and post-hibernation) and inactive (hibernation and cold snaps), and the internal body temperature variation detected during those periods is reflective of the associated behaviors. We found that 13 individual study animals actively basked 24 times over the course of their hibernation (1–5 times each). Combined median  $T_b$  differed between all periods except post-hibernation ( $F_{4, 121.8} = 136.1062$ ,  $P < 0.0001$ ). However,

average daily internal temperature variation (e.g.,  $\Delta[T_{b(\max)} - T_{b(\min)}]$ ) was only different between active and inactive periods ( $F_{4, 119.6} = 11.0052$ ,  $P < 0.0001$ ; see Tables 1, 2 for  $T_b$  values).

Grouped by biologically significant time periods (pre-hibernal, hibernal, and post-hibernal), each  $T_b$  measurement bin (daily mean, daily median, daily minimum, and daily maximum) was higher than every associated  $T_h$  measurement bin (all  $P \leq 0.0063$ ). Over cold snaps and hibernal-basking events, daily  $T_b$  measurement bins were again higher than associated  $T_h$  measurement bins (all  $P \leq 0.0397$ ) except mean and

Table 2. Mean temperature variation ( $\Delta[T_{(\max)} - T_{(\min)}]$ ) from grouped datalogger locations by biologically significant time period across 46 weeks of monitoring during 2015–2016 in the Greater Everglades ecosystem, Florida, USA.

Datalogger location and statistic	Pre-hibernation	Hibernation	Cold snap	Hibernal-basking	Post-hibernation
$T_b$	7.76 <sup>a</sup>	0.51 <sup>a</sup>	0.78 <sup>a</sup>	10.68 <sup>ab</sup>	10.23 <sup>a</sup>
$T_h$	3.07 <sup>ab</sup>	1.42 <sup>b</sup>	2.35 <sup>b</sup>	1.22 <sup>c</sup>	1.80 <sup>b</sup>
$T_a$	8.34 <sup>a</sup>	7.34 <sup>c</sup>	14.33 <sup>c</sup>	8.17 <sup>b</sup>	8.87 <sup>ac</sup>
$T_e$	15.41 <sup>c</sup>	11.11 <sup>d</sup>	20.48 <sup>d</sup>	14.04 <sup>a</sup>	17.74 <sup>d</sup>
$T_s$	1.63 <sup>b</sup>	1.69 <sup>ab</sup>	3.76 <sup>ab</sup>	1.56 <sup>c</sup>	2.30 <sup>bc</sup>
$F$	23.7217	249.6848	178.2060	23.0898	30.7078
df	4, 26.76	4, 39.30	4, 28.77	4, 14.97	4, 22.47
$P$	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
SD	1.28	0.54	1.10	1.73	2.22

Notes: SD, standard deviation. Datalogger locations were tegu (*Salvator merianae*) body ( $T_b$ ), subsurface/hibernacula ( $T_h$ ), ambient air ( $T_a$ ), exposed soil ( $T_e$ ), and shaded soil ( $T_s$ ). Datalogger location temperature variations within columns not connected by the same letter are statistically different.

minimums on basking days and maximum on cold snaps (differences were not significant). During each season, median  $T_b$  was generally higher than all other thermal habitats regardless of the differences in locations (underground vs. soil surface; see Table 1). Prior to hibernation, daily  $T_b$  variation averaged 7.8°C, closest to the aboveground variation for  $T_a$ , but remained higher overall than any other median temperature for the period (Table 1). During inactive periods, hibernating tegus maintained stable median  $T_b$ , exhibiting very little daily temperature variation at only 0.5°C and 0.8°C for hibernation and cold snap bins, respectively, about a third of the daily variation seen in the associated subsurface/hibernaculum bin (Table 2). Average  $T_{b(\min)}$  remained higher (18.7°C) during cold snaps than other minimum temperatures (15.9°C;  $F_{4,30.07} = 16.4289$ ,  $P < 0.0001$ ) except  $T_{s(\min)}$ . Throughout inactive periods underground, median  $T_b$  was not distinguishable from those of surface soil temperatures ( $T_e$  and  $T_s$ ; Table 1), though the animals were not detected aboveground. However, during basking events within the hibernal period,  $\Delta(T_{b(\max)} - T_{b(\min)})$  increased to 10.7°C, reflecting the active behavioral thermoregulation also detected on camera traps (Table 2). Post-hibernation, aboveground  $T_b$  remained higher than temperatures found in remaining subsurface/hibernaculum and the average daily  $T_b$  again aligned closest to changes in  $T_a$ , reflecting the active behavioral thermoregulation. Though not always statistically different, median  $T_b$  tended to remain higher than  $T_{(\text{median})}$  recorded from any other datalogger location during every period (Table 1).

#### Seasonal thermal profiles, ingress, and egress

For 31–46 weeks (June 2015–April 2016), we obtained thermal profile data from up to 22 tegus (13♀ and 9♂; mean number of weeks individuals were monitored = 39.6). There was no difference in overall  $T_b$  bins by SVL, mass, or sex. During hibernation, male  $T_b$  (22.6°C) was slightly different from female  $T_b$  (21.1°C;  $F_{1,19,71} = 4.4143$ ,  $P = 0.0487$ ) only in the month of January 2016. There were only three weeks during which male and female  $T_b$  differed (week 37 in September 2015; 29.7°C ♂, 31.2°C ♀;  $F_{1,19,05} = 4.4420$ ,  $P = 0.0485$ , week 6 late January–early February, 23.1°C ♂, 21.5°C ♀;  $F_{1,18} = 4.6676$ ,  $P = 0.0445$ ,

and week 13 in late March, 24.3°C ♂, 26.9°C ♀;  $F_{1,3,168} = 15.0308$ ,  $P = 0.0275$ ).

Throughout the study, weekly  $T_{b(\text{median})}$  was typically warmer than all other ( $T_a$ ,  $T_e$ ,  $T_s$ , and  $T_h$ ) median temperatures by week, even during hibernal weeks (Fig. 1). For every month,  $T_{b(\min)}$  averages were higher than all other datalogger minimum temperatures, and statistically so for all  $T_{a(\min)}$  and  $T_{e(\min)}$  (all  $P < 0.0205$ ). Further, in every hibernal month, all  $T_b$  measurement groups (daily mean, daily median, daily minimum, and daily maximum) were higher than associated  $T_h$  hibernation locations (all  $P < 0.0053$ ), except in February (~weeks 6–9) when most basking occurred and in the daily temperature maximums in October (~weeks 41–44) and December (~weeks 49–53). We detected general temperature upticks during those months (Fig. 1) and note that daylength starts to increase again in February (Fig. 2).

We documented ingress dates for 21 of 22 tegus (8♂, 13♀; one male did not hibernate). Ingress date did not vary by sex but was correlated with capture mass and SVL (mass  $F_{1,19} = 15.1235$ ,  $P = 0.0010$  and SVL  $F_{1,19} = 6.4538$ ,  $P = 0.0200$ ), where larger individuals started hibernating sooner (Fig. 3). In agreement with those analyses, we found that individuals with higher body condition started hibernation earlier ( $F_{1,19} = 7.7939$ ,  $P = 0.0116$ ), hibernated for longer durations ( $F_{1,19} = 5.9309$ ,  $P = 0.0249$ ), and had higher fat mass recovered at necropsy ( $F_{1,19} = 5.1287$ ,  $P = 0.00354$ ). Fat mass was negatively correlated with days since hibernation end ( $F_{1,19} = 12.6053$ ,  $P = 0.0021$ ) and date euthanized ( $F_{1,20} = 23.0649$ ,  $P < 0.0001$ ).

Overall, ingress dates ranged between 23 August and 29 October 2015, with 75% of tegus entering hibernation by mid-October 2015 (~week 42 of 2015); average duration of hibernation was 138 d (SD = 30.0, range = 48–183 d). Hibernation egress dates ranged from 16 December 2015 to 24 March 2016, and 75% of study animals egressed by early March 2016 (~week 9 of 2016). The temperature differential in daily median  $T_e$  and  $T_a$  predicted general timing of ingress and egress across all individuals (occurrence of pre-hibernal, hibernal, and post-hibernal periods;  $\chi^2 = 245.4743$ , df = 1,  $P < 0.0001$ ; Fig. 2). Most tegus were active when weekly median  $T_e - T_a$  was positive (i.e., sun-exposed soil temperatures

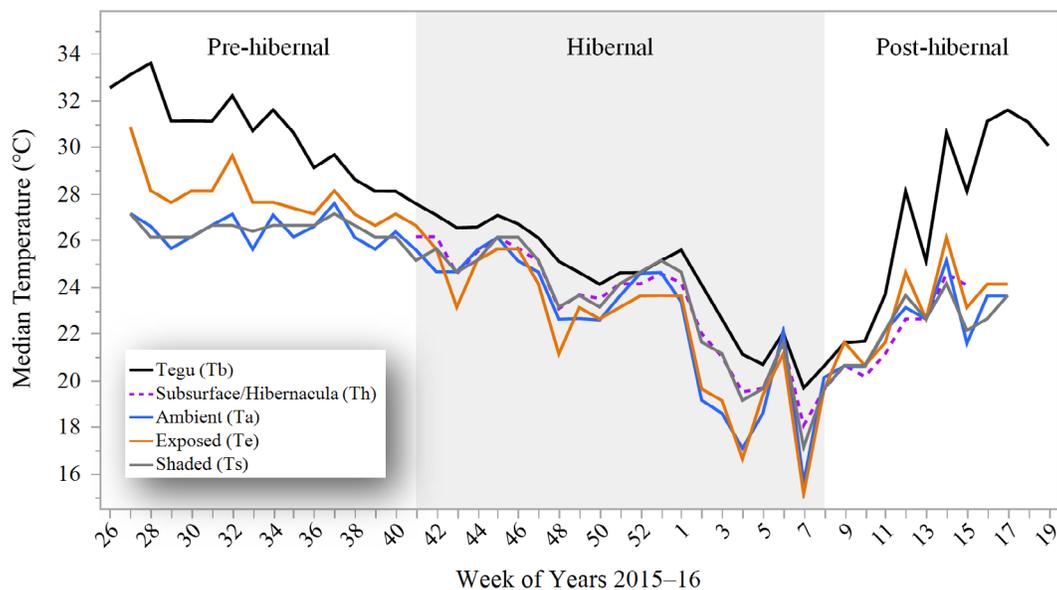


Fig. 1. Median temperatures ( $^{\circ}\text{C}$ ) across weeks from 23 June 2015 through 2 May 2016 in the Greater Everglades ecosystem, Florida, USA. Temperature lines represent internal *Salvator merianae* (tegu) body temperatures ( $T_b$ , black), subsurface/hibernacula temperatures ( $T_{hv}$ , dotted purple), and environmental temperatures of ambient air at 1 m ( $T_a$ , blue), exposed soil (full sun;  $T_e$ , orange), and shaded soil (deep shade;  $T_s$ , gray). Gray section between weeks 42 and 9 (~mid-October 2015 and early March 2016) represents general tegu hibernation timing from this study.

were higher than ambient temperatures), while hibernation commenced when sun-exposed soil temperatures were the same or below ambient (weekly median  $T_e - T_a \leq 0$ ; Fig. 2).

Diel  $T_b$  patterns were unimodal during seasonal activity, peaking during the hottest part of the day between 13:00 and 15:00 hours (pre-hibernation  $\sim 33.9^{\circ}\text{C}$ ,  $F_{23, 477.2} = 37.3140$ ,  $P < 0.0001$ ; and post-hibernation  $\sim 31.0^{\circ}\text{C}$ ,  $F_{23, 390.2} = 23.6812$ ,  $P < 0.0001$ ; Fig. 4) as expected for behavioral thermoregulation. That pattern held for activity during hibernation where those animals that basked did so in the middle of the day, peaking around 13:00 hours (Fig. 5) when  $T_e$  was also highest (Fig. 4). However, there were relatively few individual basking events during the entirety of each individual's hibernation period (0–5), hourly  $T_b$  remained constant (all  $P = 0.34$ – $0.99$ ) and was usually above available thermal environments (Fig. 4). Overnight,  $T_b$  continued to remain constant during hibernation (did not decline as other temperatures did from overnight cooling) and even remained notably higher ( $24.5^{\circ}\text{C}$ ) than thermal habitats ( $19.7$ – $22.7^{\circ}\text{C}$ ;  $F_{4, 39.55} = 15.2821$ ,

$P < 0.0001$ ) except for shaded soil ( $22.5^{\circ}\text{C}$ ) in the few hours just before sunrise (03:00–06:00 hours).

## DISCUSSION

Over nearly a year of in situ monitoring, we were able to identify three major (pre-hibernal, hibernal, and post-hibernal) and two minor (cold snaps and hibernal-basking events) thermal and biologically significant periods for wild *S. merianae* in their invasive range in southern Florida, USA. During all three major periods, study animals generally exhibited high body temperatures, often maintaining body temperatures above those available in thermal habitats. Weekly  $T_{b(\text{mean})}$ ,  $T_{b(\text{median})}$ ,  $T_{b(\text{minimum})}$ , and  $T_{b(\text{maximum})}$  recorded from study animals during hibernation were all higher than associated temperatures recorded from subsurface/hibernaculum. Though metabolic rate generally scales with body size and temperature, the thermal sensitivity in tegus of any body size has been shown to be low over a broad range of temperatures (e.g.,  $17$ – $30^{\circ}\text{C}$ ; Abe 1995, Milsom et al. 2008, Toledo et al. 2008, Sanders et al. 2015). Still,

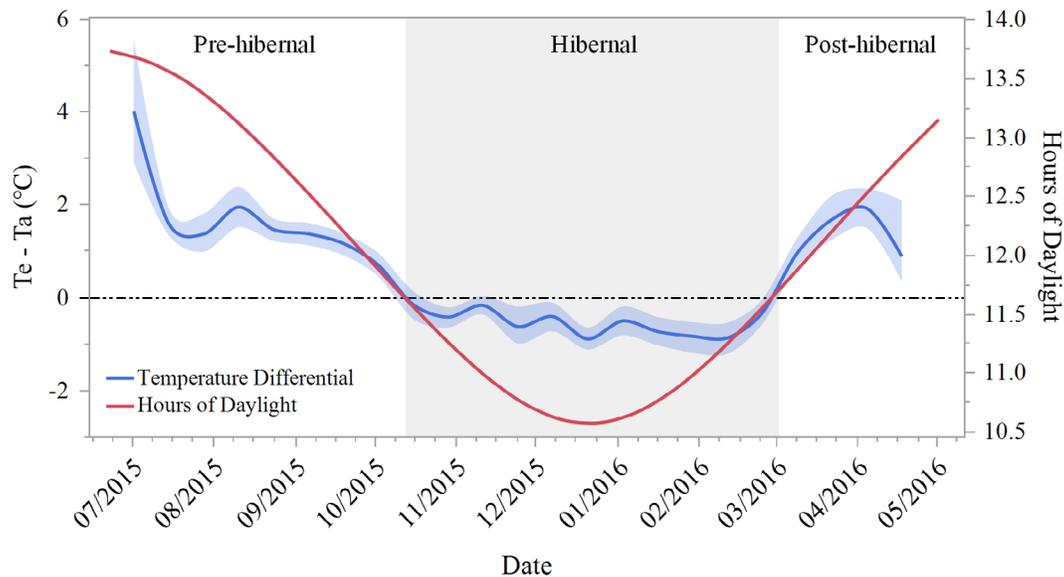


Fig. 2. Temperature ( $^{\circ}\text{C}$ ) differential between median sun-exposed soil ( $T_e$ ) and ambient ( $T_a$ ; blue line with 95% confidence of fit buffer, left axis) and duration of daylight (red line, right axis) by date. The dashed line at zero represents the lower threshold when there is no longer a positive differential in available thermal environments (i.e., basking could not increase body temperature above ambient). Gray section between mid-October 2015 and early March 2016 represents general *Salvator merianae* hibernal timing from this study. Daylength data for the region were downloaded from timeanddate.com, and thermal data were collected from temperature data-loggers deployed over approximately 46 weeks in 2015–2016 in the Greater Everglades ecosystem, Florida, USA.

previous studies described tegus as thermal conformers during nighttime hours or periods of dormancy within their native range (Andrade et al. 2004, Sanders et al. 2015). Unfortunately, we had no way of determining how deep or cavernous the hibernacula were or how deeply the animals could have gone to possibly find warmer subsurface temperatures. However, water tables are high in the region, presumably limiting available usable depth of burrows, and published soil temperatures during winter months are lower than those of the available subsurface temperatures we recorded (Mount and Brannon, 2007).

This is the first study to record  $T_b$  of free-ranging *S. merianae*, and we found that tegus did not appear to thermally conform to subsurface/hibernaculum temperatures during hibernation in southern Florida. We found that minimum  $T_b$  across all seasons is higher than all other temperature minima (Appendix S2: Table S1). However, because Andrade et al. (2004) found that the rate of overnight heat loss in a 3.5 kg tegu was approximately  $0.44^{\circ}\text{C}/\text{h}$  and Cecchetto and Narretto (2015) found that the heating rate by SVL in

this species is relatively quick ( $0.22\text{--}0.33^{\circ}\text{C}/\text{min}$ ), the coarseness of our data prevents a fine-scale description of changes due to thermal inertia. Recent work suggests that gut microbes could also have some impact on heat production in endotherms (Kohl and Carey 2016, Rosenberg and Zilber-Rosenberg 2016), but directed research in this area and for ectotherms is underdeveloped. However, Tattersall et al. (2016) demonstrated that captive *S. merianae* were capable of not only seasonally regulating body temperature metabolically during the reproductive period but could generate temperature differentials in thermally neutral conditions over several days of testing. The maintenance of body temperatures above those available at subsurface/hibernaculum that we found suggests that the animals either found stable and higher subsurface temperatures at deeper depths, emerged from hibernation to find suitable basking sites, or exhibited facultative endothermy.

Soil depth is an important consideration because deep soil can have a stabilizing effect on internal burrow temperatures relative to the external

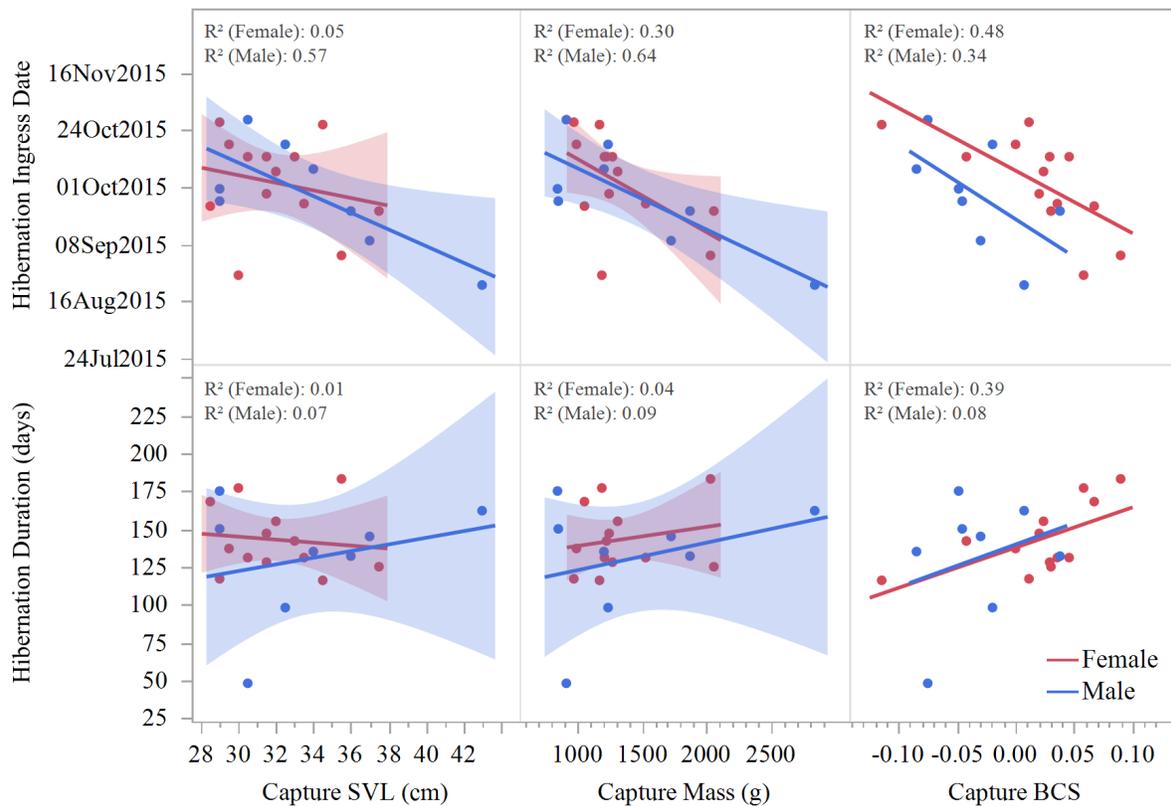


Fig. 3. Hibernation ingress date and duration as a function of mass (g), snout-vent length (SVL; cm), and body condition score (BCS; residuals from regression of log-log-transformed SVLs and mass where 0 represents the mean) at first capture for female and male *Salvator merianae* ( $n = 21$ ) in the Greater Everglades ecosystem of southern Florida, USA. Shaded areas are 95% confidence intervals. Confidence intervals are not shown on Capture BCS to improve clarity. Sexes are not statistically different but displayed as separate colors for interpretive use.

environment. However, because the southern tip of Florida has a shallow subsurface layer of limestone bedrock meeting high water tables, tegus invading the Everglades region are likely more depth-limited in hibernacula compared with their native range. We did not excavate and measure the depth or dimensions of our study animals' hibernaculum due to limited accessibility, development/structures, rock entrances, and landownership issues. Consequently, our subsurface/hibernacula temperature measurements likely do not represent the immediate temperature surrounding the hibernating study animals, but instead characterize average soil temperatures available. However, Mount and Brannon (2007) investigated soil temperatures in southern Florida and found that the shallow soil layer over limestone bedrock in our study area was

isohyperthermic, meaning that they vary little over the seasons ( $\leq 6^{\circ}\text{C}$ ), peaking in late summer/early fall ( $\sim 27^{\circ}\text{C}$ ) and averaging  $20.0\text{--}21.9^{\circ}\text{C}$  during the winter months. Those temperatures are somewhat lower than our shallower subsurface/hibernacula average temperature ( $22.9^{\circ}\text{C}$ ). Considering this, it is unlikely that tegus could have found warmer temperatures in deeper soil, and arguably not high enough to reach what would be required to raise and maintain their hibernation-period  $T_b$  to the temperatures we detected ( $24.5^{\circ}\text{C}$ ) if they were simply thermally conforming.

Interestingly, weekly  $T_b$  was typically warmer than all other environmental temperatures, including during the hibernation period when behavioral thermoregulation would be limited to basking events. Yet, basking events were rarely observed (24 basking events by 13 individuals

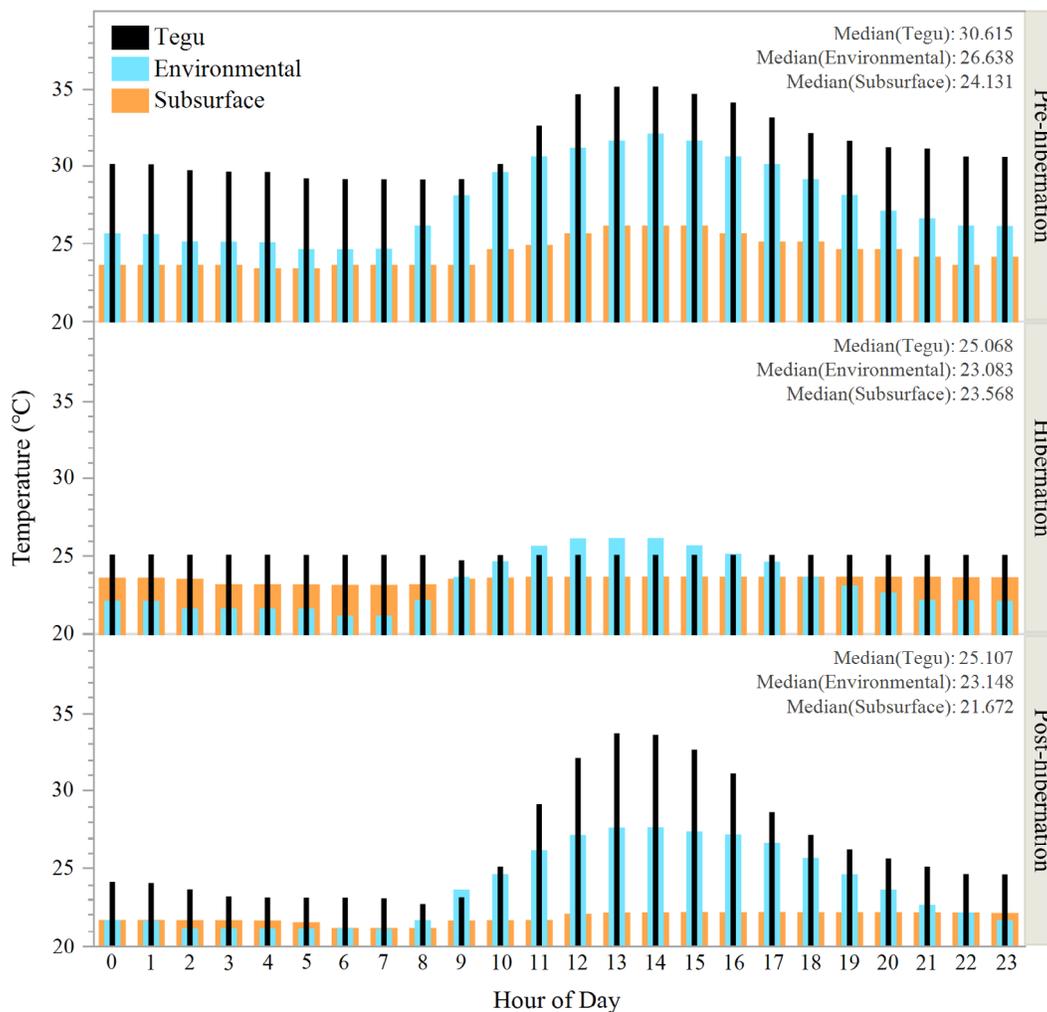


Fig. 4. Median hourly temperatures for *Salvator merianae* (tegu), subsurface/hibernaculum, and combined environmental ( $T_a$ ,  $T_e$  and  $T_s$ ) dataloggers during days when animals were in pre-hibernation, hibernation, and post-hibernation, Greater Everglades ecosystem, Florida, USA. Median  $T_b$  and environmental temperatures are displayed per period in the upper right corner of each panel.

over the more than 2900 potential basking days during hibernation). During basking events, the variation in  $T_b$  increased over other inactive hibernation days, averaging a  $10.7^\circ\text{C}$  change during basking days vs.  $0.5^\circ\text{C}$  during hibernation, despite there being reduced change in subsurface/hibernaculum temperatures during these two periods ( $1.2^\circ\text{C}$  vs.  $1.4^\circ\text{C}$ , respectively). This positive  $\Delta T_b$  is expected when an animal behaviorally thermoregulates as these did (as supported by trail camera images). Throughout the remaining inactive periods, variation in  $T_b$  was

about a third of that seen in  $T_{h_v}$ , despite the animals having not moved out of their burrows. Additionally, when we investigated hibernation  $T_b$  in the hours just before sunrise (when no basking opportunities would have been recently available), we found that tegus maintained stable temperatures averaging  $2\text{--}5^\circ\text{C}$  above those found in available thermal habitats. Thermal inertia cannot account for the tegus' ability to maintain hourly  $T_b$  above other thermal habitats available for the entire 138-d hibernation duration in dark and cold conditions (Seebacher and

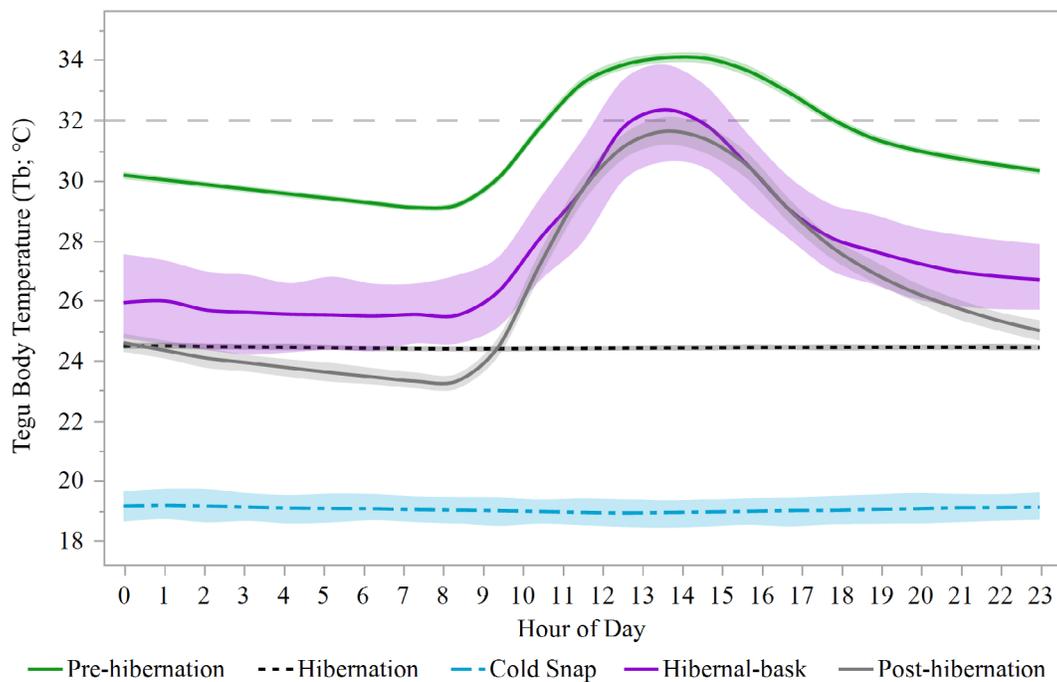


Fig. 5. Mean *Salpator merianae* (tegu)  $T_b$  by hour of day and biologically significant time period (each line is buffered with the confidence of fit) in the Greater Everglades ecosystem, Florida, USA. The number of individual tegu  $T_b$  by time period represented in the figure is as follows: per-hibernation,  $n = 21$ ; hibernation,  $n = 21$ ; cold snap,  $n = 19$ ; hibernation bask,  $n = 13$ ; and post-hibernation,  $n = 19$ . The upper dashed line at 32°C represents the purported lower behaviorally maintained temperature for this species in the native wild (Andrade et al. 2004).

Shine 2004, Milsom et al. 2012). The animals in our study either did not or rarely exhibited behavioral thermoregulation (basking) during hibernation, yet exhibited consistently higher body temperatures than were available in thermal habitats. Indeed, the departure between  $T_b$  and the temperature in associated subsurface/hibernaculum is in alignment with the recent discovery of facultative endothermy in this species (Tattersall et al. 2016) and suggests that *S. merianae* may also undergo metabolic thermogenesis while in hibernation, but this is the first study to document these type of data in the wild, and directed study should be undertaken.

We found little to no sex difference in any of the  $T_b$  data except for three widely spaced weeks, two weeks when female  $T_b$  exceeded males' (September and late March), and one week when male  $T_b$  was higher (late January/early February). Although we detected no sex difference in ingress or egress hibernation dates, we did note that females tended to ingress

about a week later and egress about two weeks later than males; these dates are in line with the sex differences we detected in  $T_b$  timing. Fifty percent of males ingressed by 28 September 2015 and likely began to more closely thermally align to the lower but stable subsurface temperatures. By 1 February 2016, 50% of males egressed and their higher  $T_b$  was likely due to behavioral thermoregulation (Winck et al. 2011); however, increased male  $T_b$  has also recently been correlated with a ramping up of testosterone in preparation for the breeding season (Zena et al. 2020). Endocrinology and activity patterns may also help explain the increase in female  $T_b$  we found in late March; Zena et al. (2020) found that progesterone increased female activity associated with nesting. The sexually dimorphic hibernation phenology trend we noted is consistent with previous observations of *S. merianae* in their native range where males emerge from hibernation before females (Winck and Cechin 2008, Chamut et al. 2012).

Tegus hibernated for an average of 138 d, which was remarkably consistent with the 137 d observed by McEachern et al. (2015) for other individuals in this invasive population. There was some notable variation, however, and individuals with a relatively higher BCS at capture entered hibernation sooner and remained hibernating longer. These findings agree with studies on lizard assemblages in the native range where larger individuals disappeared from trap arrays earlier in the hibernal season than smaller individuals (Fitzgerald et al. 1999). Further, we found that lower BCS corresponded to inconsistent or shorter hibernation periods. However, we found that those individuals with higher capture BCSs also had higher fat mass at the study's conclusion. There is evidence that hibernal fat metabolism is morphologically allometric (de Souza et al. 2004), and a higher fat mass may have allowed these larger individuals to hibernate for a longer and more consistent time period. Though we would expect that activity expenditures will be lower in lizards resting in burrows as opposed to those that are active (Bennett and Nagy 1977, Christian et al. 1995), the relatively new finding that tegus can exhibit facultative endothermy (as our findings of maintained high hibernation  $T_b$  in the wild also support) raises the question as to how these animals retain higher levels of fat mass without replenishing stores through foraging (i.e., while hibernating). In a study comparing two sympatric *Eremias*, Nagy et al. (1984) found that though the more vagile species spent more energy foraging, its change in mass and growth rate was nearly twice that of the sedentary species. Although we could not detect a similar significant correlation in the growth of more active animals within our study population over winter, we did see a trend ( $P = 0.0585$ ); two of the three study animals with the greatest mass gain (all males) included the individual with the shortest hibernation period (48 d) and the individual that did not hibernate at all. A larger sample size might confirm that those animals that do not possess adequate fat stores to metabolically endure winter months are indeed those animals that remain active, or shorten hibernation, to acquire energy stores.

This type of behavioral plasticity (skipping hibernation and basking during winter) in tegus is relatively unknown (Andrade et al. 2004,

McEachern et al. 2015) and may be facultatively isolated to males. Studies in the native range indicate that female reproductive output (as expressed by intense vitellogenesis) may be almost exclusively dependent on available body reserves proximal to hibernation timing (Manes et al. 2007). This is because there is asynchrony in tegu seasonal gonadal development as males that emerge from hibernation gain earlier access to resources while undergoing spermatogenesis prior to female emergence but mate soon after female emergence when females are still previtellogenic (Fitzgerald et al. 1993, Noriega et al. 2002, Manes et al. 2007, Winck and Cechin 2008). This would indicate that males get a head start on identifying key reproductive resources and females with higher fat stores are more fecund when the time comes to direct those resources to egg development. Whatever the reason for skipping hibernation, or why retained fat stores correlated with extended hibernation time, the plasticity exhibited within our study population confirms the adaptability of the species that may aid population expansion to invade new areas.

The onset of hibernation in wild tegus has been unclear despite receiving research efforts over more than three decades (Abe 1983, Fitzgerald et al. 1999, Andrade et al. 2004, Sanders et al. 2015). Work with captive *S. merianae* has suggested that mechanisms triggering dormancy appear to be changes in light and temperature initiated by a behavioral decision (Milsom et al. 2008, Toledo et al. 2008, Tattersall et al. 2016), but no work has been done to monitor this relationship in free-ranging individuals. We found that the best environmental predictor of the hibernal time frame was negative weekly median temperature differentials between the ambient air temperature and exposed substrate temperatures (i.e., below zero). In weeks with positive differences, tegus generally remained active above ground. Once the differences were no longer positive, the study animals generally went into hibernation not to emerge again until  $\Delta T_e - T_a$  were again above zero (Fig. 2). Though the change is gradual, the temperature variation also coincided with the time of the year when southern Florida experiences daylengths of less than 11.7 h, further justifying the purported link between hibernal timing and the environmental factors of light and temperature seen in captive

studies. Concordantly, the variation in *S. meriana* activity across Brazil appears to be correlated with latitude, which in turn influences daylength and light intensity (Srbek-Araujo 2020). Our study indeed agrees with previous *S. meriana* studies, conducted in their native range, that a combination of daylength and temperature differentials affects seasonal activity, including triggering the ingress into and egress from hibernation. Additionally, these findings can be used by managers to help identify activity periods to improve tegu removal efforts. For instance, male tegus establishing mating ranges and female tegus establishing nesting sites post-hibernation (Winck and Cechin 2008) actively range more widely than those whose resources are established. Thus, each is more likely to encounter a trap during this period of time. Being able to effectively predict when tegus will egress from hibernation could allow managers to mobilize trapping operations to maximize the removal of reproductive individuals.

We found that active-season hourly  $T_b$  patterns in our invasive population aligned with local thermal habitat regimes, as has been documented in other ectotherms (Currylow et al. 2012), and with the idealized daily  $T_b$  profile for a thermoregulating lizard (Adolph and Porter 1993; Fig. 5). Diel activity patterns in tegu's native range can be unimodal and track the hottest period of the day, matching our unimodal temperature distributions (Van Sluys and Rocha 1999). We observed mean active-period tegu  $T_{b(max)}$  between 33.3°C and 36.5°C (Appendix S2: Table S1 and Appendix S3: Fig. S1), concordant with previously reported preferred  $T_b$  of 32–38°C (Andrade et al. 2004, Cecchetto and Naretto 2015). However, we recorded annual mean temperatures somewhat higher than those reported by Noriega et al. (2002) from the native range (24°C vs. 19°C). Zerebecki and Sorte (2011) found that many invasive species often exhibit a broader temperature tolerance than native species, permitting them to disproportionately affect the ecosystem. Indeed, the active period for tegus in our population is somewhat extended compared with areas in their native range where they may hibernate for 6 months (Andrade et al. 2004). In southern Florida, tegus have also demonstrated the ability to modulate both  $T_{b(max)}$  and  $T_{b(min)}$ , even during temperature

extremes, and have now been shown to tolerate colder winters in Alabama (Goetz et al. 2021; present study; Appendix S3: Figs. S1, S2). This ability to phenotypically adjust when interacting with the available local conditions suggests that *S. meriana* exhibit great behavioral plasticity for survival across habitats.

## CONCLUSIONS

Invasive species are one of the largest threats to native biodiversity worldwide. Understanding the thermal ecology of species that are vagile, adaptable, and prolific is fundamental in predicting the extent and consequences of biological invasions. The Argentine giant tegu is increasingly revealing such adaptations through plasticity in behavior and thermal tolerance. It has become a pest near its native range in Brazil and in its non-native range in southern Florida, and there is evidence that it can readily establish in areas where it is introduced (Krysko et al. 2011, Abrahão et al. 2019, Haro et al. 2020). We show that *S. meriana* hibernation timing correlates with microclimate and photoperiod, but during winter inactivity, they can maintain body temperatures greater than those available in thermal habitats, suggesting that adverse climatic conditions are not likely to restrict the species from establishing well outside of their current range in southern Florida.

## ACKNOWLEDGMENTS

We thank Erin Crandall, Jillian Josimovich, Molly Richard, and Sarah Staton for their assistance in the field. Lea' Bonewell provided administrative and logistical support. Funding and in-kind support was provided by U.S. Geological Survey (USGS) Greater Everglades Priority Ecosystem Science Program, National Park Service, USGS Invasive Species Program, University of Florida, and Miami-Dade County. This work was conducted in coordination with the South Florida Water Management District, in accordance with Florida Fish and Wildlife Conservation Commission permits # EXOT 16-14 and EXOT 15-12b, and under the USGS Institutional Animal Care and Use Committee protocol #2014-13 and amendments. Michelle Collier and Robert Reed designed the study and acquired funding and permissions; Michelle Collier led fieldwork and managed data collection; Emma Hanslowe, Sarah Moy, and Alejandro Grajal-Puche

conducted fieldwork; Bryan Falk, Amy Yackel Adams, and Robert Reed assisted with study implementation; Brian Cade assisted with analyses; Frank Ridgley conducted surgeries and directed animal care; Andrea Currylow compiled and analyzed data and led production of the manuscript; all authors contributed to and edited the final manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## LITERATURE CITED

- Abe, A. S. 1983. Observations on dormancy in tegu lizard, *Tupinambis teguixin* (Reptilia, Teiidae). *Naturalia* 8:135–139.
- Abe, A. S. 1995. Estivation in South American amphibians and reptiles. *Brazilian Journal of Medical & Biological Research* 28:1241–1247.
- Abrahão, C., J. Russell, J. Silva, F. Ferreira, and R. Dias. 2019. Population assessment of a novel island invasive: tegu (*Salvator merianae*) of Fernando de Noronha. Pages 317–325 in C. R. Veitch, M. N. Clout, A. R. Martin, J. C. Russell, and C. J. West, editors. *Island Invasives 2017 Conference*. IUCN Species Survival Commission (SSC), Gland, Switzerland; Dundee, UK.
- Adolph, S. C., and W. P. Porter. 1993. Temperature, activity, and lizard life histories. *American Naturalist* 142:273–295.
- Andrade, D. V., C. Sanders, W. K. Milsom, and A. S. Abe. 2004. Overwintering in tegu lizards. Pages 339–348 in B. Barnes and H. Carey, editors. *Life in the cold: Evolution, mechanisms, adaptation, and application*. Twelfth International Hibernation Symposium. University of Alaska, Fairbanks, Alaska, USA.
- Barraco, L. A. 2015. Risk assessment of the nonnative Argentine black and white tegu, *Salvator merianae*, in south Florida. Thesis. Florida Atlantic University, Boca Raton, Florida, USA.
- Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697–700.
- Cecchetto, N. R., and S. Naretto. 2015. Do sex, body size, and reproductive condition influence the thermal preferences of a large lizard? A study in *Tupinambis merianae*. *Journal of Thermal Biology* 53:198–204.
- Chamut, S., G. A. Jahn, O. E. Arce, and M. E. Manes. 2012. Testosterone and reproductive activity in the male tegu lizard, *Tupinambis merianae*. *Herpetological Conservation & Biology* 7:299–305.
- Chiarello, A., A. Srebek-Araujo, H. Del-Duque Jr., E. de Coelho, and C. Rocha. 2010. Abundance of tegu lizards (*Tupinambis merianae*) in a remnant of the Brazilian Atlantic forest. *Amphibia-Reptilia* 31:563–570.
- Christian, K. A., L. Corbett, B. Green, and B. W. Weavers. 1995. Seasonal activity and energetics of two species of varanid lizards in tropical Australia. *Oecologia* 103:349–357.
- Currylow, A. F., B. J. MacGowan, and R. N. Williams. 2012. Short-term forest management effects on a long-lived ectotherm. *PLOS ONE* 7:e40473.
- Currylow, A. F., B. J. MacGowan, and R. N. Williams. 2013. Hibernation thermal ecology of eastern box turtles within a managed forest landscape. *Journal of Wildlife Management* 77:326–335.
- de Souza, S. C. R., J. E. de Carvalho, A. S. Abe, J. E. P. W. Bicudo, and M. S. C. Bianconcini. 2004. Seasonal metabolic depression, substrate utilisation and changes in scaling patterns during the first year cycle of tegu lizards (*Tupinambis merianae*). *Journal of Experimental Biology* 207:307–318.
- Dorcas, M. E., et al. 2012. Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences USA* 109:2418–2422.
- Duever, M., J. Meeder, L. Meeder, and J. McCollom. 1994. The climate of south Florida and its role in shaping the Everglades ecosystem. Pages 225–248 in S. M. Davis and J. C. Ogden, editors. *Everglades: The ecosystem and its restoration*. St. Lucie Press, Delray Beach, Florida, USA.
- Enge, K., B. Kaiser, and R. Dickerson. 2006. Another large exotic lizard in Florida, the Argentine black and white tegu. Pages 26–29 in *The 28th Annual Gopher Tortoise Council Meeting*. The Gopher Tortoise Council, Valdosta, Georgia, USA.
- Falk, B. G., R. W. Snow, and R. N. Reed. 2017. A validation of 11 body-condition indices in a giant snake species that exhibits positive allometry. *PLOS ONE* 12:e0180791.
- Ferreguetti, Á. C., J. Pereira-Ribeiro, H. G. Bergallo, and C. F. D. Rocha. 2018. Abundance, density, and activity of *Salvator merianae* (Reptilia: Teiidae) and the effect of poaching on the site occupancy by the lizard in an Atlantic forest reserve, Brazil. *Austral Ecology* 43:663–671.
- Fitzgerald, L. A. 1994. *Tupinambis* lizards and people: a sustainable use approach to conservation and development. *Conservation Biology* 8:12–15.
- Fitzgerald, L. A., J. Chani, and O. Donadio. 1991. *Tupinambis* lizards in Argentina: implementing management of a traditionally exploited resource. Pages 303–316 in J. Robinson and K. Redford, editors. *Neotropical wildlife: Use & conservation*. University of Chicago Press, Chicago, Illinois, USA.

- Fitzgerald, L. A., F. B. Cruz, and G. Perotti. 1993. The reproductive cycle and the size at maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the Dry Chaco of Argentina. *Journal of Herpetology* 27:70–78.
- Fitzgerald, L. A., F. B. Cruz, and G. Perotti. 1999. Phenology of a lizard assemblage in the dry Chaco of Argentina. *Journal of Herpetology* 33:526–535.
- Goetz, S. M., D. A. Steen, M. A. Miller, C. Guyer, J. Kottwitz, J. Roberts, E. Blankenship, P. Pearson, D. Warner, and R. N. Reed. 2021. Argentine black and white tegu (*Salvator merianae*) can survive the winter under semi-natural conditions well beyond their current invasive range. *PLOS ONE* 16: e0245877.
- Hanslowe, E., J. Duquesnel, R. Snow, B. Falk, A. Yackel Adams, E. Metzger, M. Collier, and R. Reed. 2018. Exotic predators may threaten another island ecosystem: a comprehensive assessment of python and boa reports from the Florida Keys. *Management of Biological Invasions* 9:369–377.
- Haro, D., L. D. McBrayer, J. B. Jensen, J. M. Gillis, L. R. Bonewell, M. G. Nafus, S. E. Greiman, R. N. Reed, and A. A. Yackel Adams. 2020. Evidence for an established population of tegu lizards (*Salvator merianae*) in southeastern Georgia, USA. *Southeastern Naturalist* 19:649–662.
- Hela, I. 1952. Remarks on the climate of southern Florida. *Bulletin of Marine Science* 2:438–447.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Animal Behaviour* 30:676–679.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–91 in C. Gans and F. H. Pough, editors. *Biology of the reptilia*, Vol. 12. Physiology. Academic Press, New York, New York, USA.
- Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4:131–135.
- Jarnevich, C. S., M. A. Hayes, L. A. Fitzgerald, A. A. Yackel Adams, B. G. Falk, M. A. M. Collier, L. R. Bonewell, P. E. Klug, S. Naretto, and R. N. Reed. 2018. Modeling the distributions of tegu lizards in native and potential invasive ranges. *Scientific Reports* 8:10193.
- Jimenez-Valverde, A., and J. M. Lobo. 2011. Tolerance limits, animal. Pages 661–663 in D. Simberloff and M. Rejmanek, editors. *Encyclopedia of biological invasions*. University of California Press, Berkeley & Los Angeles, California, USA.
- Klug, P. E., R. N. Reed, F. J. Mazzotti, M. A. McEachern, J. J. Vinci, K. K. Craven, and A. A. Yackel Adams. 2015. The influence of disturbed habitat on the spatial ecology of Argentine black and white tegu (*Tupinambis merianae*), a recent invader in the Everglades ecosystem (Florida, USA). *Biological Invasions* 17:1785–1797.
- Kohl, K. D., and H. V. Carey. 2016. A place for host-microbe symbiosis in the comparative physiologist's toolbox. *Journal of Experimental Biology* 219:3496–3504.
- Kraus, F. 2009. *Alien reptiles and amphibians: a scientific compendium and analysis*. Springer Science & Business Media, Dordrecht, The Netherlands.
- Krysko, K. I., et al. 2011. Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: outlining the invasion process and identifying invasion pathways and stages. *Zootaxa* 3028:1–64.
- Krysko, K. L., R. Reed, M. R. Rochford, L. P. Nunez, and K. M. Enge. 2019. *Python bivittatus* Kuhl 1820, Burmese python, nonnative. Pages 454–458 in K. L. Krysko, K. M. Enge, and P. E. Moler, editors. *Amphibians & reptiles of Florida*. University Press of Florida, Gainesville, Florida, USA.
- Krysko, K., L. Somma, D. Smith, C. Gillette, D. Cueva, J. Wasilewski, K. Enge, S. Johnson, T. Campbell, and J. Edwards. 2016. New verified nonindigenous amphibians and reptiles in Florida through 2015, with a summary of over 152 years of introductions. *Reptiles & Amphibians* 23:110–143.
- Lanfri, S., V. D. Cola, S. Naretto, M. Chiaraviglio, and G. Cardozo. 2013. Understanding the ecological niche to elucidate spatial strategies of the southernmost *Tupinambis* lizards. *Amphibia-Reptilia* 34:551–565.
- Manes, M. E., T. Noriega, F. Campos Casal, and S. Apichela. 2007. Ovarian changes during the reproductive cycle of the *Tupinambis merianae* lizard raised in a temperate environment. *Cuadernos de Herpetología* 21:21–29.
- Mazzotti, F. J., M. McEachern, M. Rochford, R. N. Reed, J. K. Eckles, J. Vinci, J. Edwards, and J. Wasilewski. 2015. *Tupinambis merianae* as nest predators of crocodylians and turtles in Florida, USA. *Biological Invasions* 17:47–50.
- McEachern, M. A., A. A. Yackel Adams, P. E. Klug, L. A. Fitzgerald, and R. N. Reed. 2015. Brumation of introduced black and white tegus, *Tupinambis merianae* (Squamata: Teiidae), in southern Florida. *Southeastern Naturalist* 14:319–328.
- Meshaka, W. E. J., F. J. Mazzotti, and M. R. Rochford. 2019. Ecological plasticity and the future of the Argentine giant tegu (*Salvator merianae* Dumeril, 1839) in the southeastern U.S. *Southeastern Naturalist* 18:659–676.
- Milsom, W. K., D. V. Andrade, S. P. Brito, L. F. Toledo, T. Wang, and A. S. Abe. 2008. Seasonal changes in daily metabolic patterns of tegu lizards (*Tupinambis*

- merianae*) placed in the cold (17°C) and dark. *Physiological & Biochemical Zoology* 81:165–175.
- Milsom, W. K., C. Sanders, C. Leite, A. S. Abe, D. V. Andrade, and G. Tattersall. 2012. Seasonal changes in thermoregulatory strategies of tegu lizards. Pages 317–324 in T. Ruf, W. Arnold, E. Millesi, and C. Bieber, editors. *Living in a seasonal world: Thermoregulatory and metabolic adaptations*. Springer Berlin Heidelberg, New York, New York, USA.
- Mohan, M., and B. Kariyanna. 2018. Chapter 16 – Shifting equilibrium of pest and diseases in agriculture. Pages 459–485 in C. Sivaperuman, A. Velmurugan, A. K. Singh, and I. Jaisankar, editors. *Biodiversity and climate change adaptation in tropical islands*. Academic Press, Elsevier Inc., San Diego, California, USA.
- Mount, H. R., and G. R. Brannon. 2007. The isohyperthermic soil temperature boundary in southern Florida. *Soil Horizons* 48:39–42.
- Nagy, K. A., R. B. Huey, and A. F. Bennett. 1984. Field energetics and foraging mode of Kalahari *Lacertid* lizards. *Ecology* 65:588–596.
- Noriega, T., M. A. Ibáñez, E. Bru, and M. E. Manes. 2002. The testicular cycle of captive *Tupinambis merianae* lizards in a temperate environment. *Cuadernos de Herpetología* 16:119–127.
- Pernas, T., D. J. Giardina, A. McKinley, A. Parns, and F. J. Mazzotti. 2012. First observations of nesting by the Argentine black and white tegu, *Tupinambis merianae*, in south Florida. *Southeastern Naturalist* 11:765–770.
- Pike, D. A., J. K. Webb, and R. Shine. 2011. Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21:274–280.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Pirhalla, D. E., S. C. Sheridan, V. Ransibrahmanakul, and C. C. Lee. 2015. Assessing cold-snap and mortality events in south Florida coastal ecosystems: development of a biological cold stress index using satellite SST and weather pattern forcing. *Estuaries & Coasts* 38:2310–2322.
- Pringle, R., J. Webb, and R. Shine. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- Rosenberg, E., and I. Zilber-Rosenberg. 2016. Do microbiotas warm their hosts? *Gut Microbes* 7:283–285.
- Sanders, C. E., G. J. Tattersall, M. Reichert, D. V. Andrade, A. S. Abe, and W. K. Milsom. 2015. Daily and annual cycles in thermoregulatory behaviour and cardio-respiratory physiology of black and white tegu lizards. *Journal of Comparative Physiology B* 185:905–915.
- Seebacher, F., and R. Shine. 2004. Evaluating thermoregulation in reptiles: the fallacy of the inappropriately applied method. *Physiological & Biochemical Zoology* 77:688–695.
- Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? *Trends in Ecology & Evolution* 14:186–189.
- Simberloff, D., et al. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28:58–66.
- Snow, R., K. Krysko, K. Enge, L. Oberhofer, A. Ludwicka-Bradley, and L. Wilkins. 2007. Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. Pages 418–438 in R. W. Henderson and R. Powell, editors. *Biology of the boas and pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- Srbek-Araujo, A. C. 2020. Activity pattern of the black-and-white tegu, *Salvator merianae* (Squamata, Teiidae), in an Atlantic forest remnant in southeastern Brazil. *Herpetology Notes* 13:93–99.
- Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences USA* 111:5610–5615.
- Tattersall, G. J., C. A. C. Leite, C. E. Sanders, V. Cadena, D. V. Andrade, A. S. Abe, and W. K. Milsom. 2016. Seasonal reproductive endothermy in tegu lizards. *Science Advances* 2:e1500951.
- Taylor, E. N., et al. 2020. The thermal ecology and physiology of reptiles and amphibians: a user's guide. *Journal of Experimental Zoology A* 2020:1–32.
- Toledo, L. F., S. P. Brito, W. K. Milsom, A. S. Abe, and D. V. Andrade. 2008. Effects of season, temperature, and body mass on the standard metabolic rate of tegu lizards (*Tupinambis merianae*). *Physiological & Biochemical Zoology* 81:158–164.
- USGS. 2020. USGS groundwater data for USA. National Water Information System: Web Interface. <https://nwis.waterdata.usgs.gov/nwis/gw>
- Van Sluys, M., and C. Rocha. 1999. *Tupinambis merianae* (common tegu): activity. *Herpetological Review* 30:42–43.
- Viets, B. E., M. A. Ewert, L. G. Talent, and C. E. Nelson. 1994. Sex-determining mechanisms in squamate reptiles. *Journal of Experimental Zoology* 270:45–56.
- Webb, J. K., and R. Shine. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biological Conservation* 86:233–242.

- Winck, G. R., C. C. Blanco, and S. Z. Cechin. 2011. Population ecology of *Tupinambis merianae* (Squamata, Teiidae): home-range, activity and space use. *Animal Biology* 61:493–510.
- Winck, G. R., and S. Z. Cechin. 2008. Hibernation and emergence pattern of *Tupinambis merianae* (Squamata: Teiidae) in the Taim Ecological Station, southern Brazil. *Journal of Natural History* 42:239–247.
- Zena, L. A., D. Dillon, K. E. Hunt, C. A. Navas, C. L. Buck, and K. C. Bicego. 2020. Hormonal correlates of the annual cycle of activity and body temperature in the South-American tegu lizard (*Salvator merianae*). *General & Comparative Endocrinology* 285:113295.
- Zerebecki, R. A., and C. J. B. Sorte. 2011. Temperature tolerance and stress proteins as mechanisms of invasive species success. *PLOS ONE* 6:e14806.

### DATA AVAILABILITY

Data are available from the U.S. Geological Survey: <https://doi.org/10.5066/P9QCSKRR>.

### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3579/full>