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LIVING IN HOT SAND: THE THERMAL BIOLOGY OF *SCINCUS SCINCUS*, THE SANDFISH SKINK

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ABSTRACT

Little is known about the natural history of Sandfish Skinks (*Scincus scincus*), despite a range spanning two continents. In arid and hot environments across North Africa and the Arabian Peninsula, these lizards are uniquely adapted to a sand dune environment. However, much about the basic biology of this species remains unknown, especially concerning adaptations to its thermal environment. With this study, we compiled a robust suite of thermal biology parameters to assess within-individual trait covariation in Sandfish Skinks (*n* = 8). We found one of the highest recorded critical thermal maxima for a vertebrate ectotherm (mean: 48.2 °C), suggesting a large thermal safety margin. We quantified thermal preferences and documented use of sand horizons to thermoregulate. We monitored individual body temperatures day and night for one week and found significant differences in active and inactive thermoregulation. Additionally, we quantified thermal dependence of performance by recording sprinting speed and diving speed, important for prey capture and predator avoidance, across a range of temperatures. Finally, we measured the critical thermal minimum (CT_{MIN}) and maximum (CT_{MAX}), allowing us to build a complete thermal performance curve (TPC) for two behaviors, which we used to estimate optimal temperatures for performance. We then tested the relationship between thermal preferences and performance, finding no support for the thermal coadaptation hypothesis in the context of hunting or predator avoidance. Overall, these data provide understanding of how this unique ectotherm survives in the extreme thermal conditions of a hot desert.

The importance of thermal biology for herpetofauna generally, and for squamates in particular, has been appreciated and well-studied for many decades due to its effect on every aspect of their lives (Angilletta, 2009; Bodensteiner et al., 2021; Stevenson et al., 1985). For many years we have understood how temperature affects squamates, whereby increasing body temperature increases relative performance of a myriad of physiological processes and behaviors, until a peak is reached followed by rapid decline at high temperatures (i.e., a thermal performance curve; Angilletta, 2009; Huey & Kingsolver, 1989; Taylor et al., 2021). Nonetheless, in many taxa, we often lack understanding of how thermoregulatory behaviors and thermal dependence of physiological processes may interact to shape an organism's ecology and trait evolution. For instance, we could expect a positive relationship between preferred body temperature (T_{PREF}), average body temperature achieved via thermoregulation, and optimal body temperature (T_{OPT}), the body temperature at which peak performance occurs (Huey & Kingsolver, 1989; Taylor et al., 2021). Correlated selection on selected body temperatures and optimal temperatures for performance, known as the thermal coadaptation hypothesis, has been studied at both intra- and interspecific levels (Huey & Bennett, 1987; Michelangeli et al., 2018). The central idea of the coadaptation hypothesis is that one would expect evolution to favor individuals whose T_{PREF} and T_{OPT} align. Operating at maximum possible performance should facilitate outcompeting conspecifics, for example, in allowing a lizard to run and catch a prey item faster than a conspecific who cannot run as fast. Despite what we may expect from an evolutionary perspective, however, a pattern of positive correlation between these traits is often the opposite of what is observed. For most species, T_{PREF} is, with very few exceptions, lower than T_{OPT}, a pattern that is found in a variety of squamate clades from Iguania to Gekkonidae (Aparicio Ramirez et al., 2021; Crowley, 1985; Dematteis et al., 2022). One clade that is mostly absent in existing literature on thermal coadaptation is Scincidae. Despite making up approximately 23% of all lizard species (Uetz, 2023), to our knowledge only one study tests the coadaptation hypothesis in skinks (Huey & Bennett, 1987). The gap in knowledge regarding thermal coadaptation in skinks is an especially important gap to fill, given the broad geographic range and diverse niches Scincidae inhabit across the globe.

Organisms inhabiting desert environments face high temperatures and extreme temperature variation at both short and long timescales (Araya-Donoso et al., 2022; Bradshaw, 1988; Lillywhite, 2016). Additionally, desert organisms often face challenges in other abiotic factors that can make thermoregulation difficult, such as reduced water availability and a challenging structural habitat (Araya-Donoso et al., 2022; Bradshaw, 1988; Lillywhite, 2016). Environmental conditions of deserts have produced species uniquely adapted to these extreme environments, such as Namib Desert Dune Lizards (*Meroles anchietae*) which lift their legs to reduce conducting heat from the sand, Panther Chameleons (*Furcifer pardalis*) which vary their level of UV

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absorption via shifting subcutaneous crystals, and multiple other desert lizard species that have higher levels of heat shock proteins (Robinson & Barrows, 2013; Teyssier et al., 2015; Zatsepina et al., 2000).

One of the more iconic and ubiquitous groups from the Sahara region are members of the genus *Scincus*, desert specialists with a variety of adaptations allowing them to inhabit barren sand dunes, often without access to water (Šmíd et al., 2021). The Sahara reaches daytime surface temperatures up to 48 °C and nighttime surface temperatures as low as 0 °C (NOAA, 2021) making thermoregulation challenging both day and night. High thermal inertia of sand allows it to act as a buffer against extreme temperature fluctuation throughout the day. Even at the hottest points, just a few centimeters below the surface is 10 to 15 °C cooler, with this dynamic being switched at night, remaining warmer underground than the chilled surface (Louge et al., 2013). While mechanisms for thermoregulation are unknown in the majority of semifossorial psammophiles, one possibility for such organisms may involve moving between sand horizons, but there may be other nonexclusive thermoregulatory strategies.

Sandfish Skinks (*Scincus scincus* Linnaeus, 1758) are medium-sized (mean snout-vent length of our lab colony: 95.4 mm) skinks originating from northeastern Saharan Africa (Šmíd et al., 2021). The species has evolved several adaptations to aid in hunting and the challenges of sand dwelling. For example, scales are resistant to sand abrasion while remaining low in friction (Allam et al., 2019; Baumgartner et al., 2007; Staudt et al., 2012; Vihar et al., 2016; Wu et al., 2018), specialized airways prevent fine sand particles from entering their lungs (Stadler et al., 2016; Vihar, 2015), and they can detect minute surface vibrations while below the surface (Hetherington, 1989, 1992). A well-studied adaptation of Sandfish Skinks is their ability to “dive” and “swim” below the sand, giving the nominal species *S. scincus* its common name “Sandfish.” Members of the genus can propel themselves beneath the surface of sand without using their limbs, by undulating their body like a fish (Baumgartner et al., 2008; Maladen et al., 2009), allowing them to avoid predator detection and extreme heat (E. N. Arnold, 1995; Attum et al., 2007). Despite our understanding of these intriguing adaptations, we still lack knowledge of many basic aspects of natural history, such as diet, reproductive behavior, and activity period. One aspect of this species’ natural history of foremost importance is its thermal biology, especially relevant as climate change rapidly alters thermal qualities of a variety of environments, including the already-hot desert landscape (Mirzabaev et al., 2022). Given our lack of knowledge of *S. scincus* thermal biology, it is currently unknown how they cope with the desert’s range of temperatures or how fluctuation in body temperature affects physiology and performance.

Our study serves both to provide essential natural history information about this lizard species and to test hypotheses about the relationship between thermoregulatory behavior and measures of ecologically relevant performance, including sprinting and diving. By quantifying an extensive range of parameters related to the thermal biology of *S. scincus*, including diurnal and nocturnal thermal preferences, activity patterns, and thermal limits, we provide essential data to understand how these organisms interact with their environment. We then leverage these data to test two primary hypotheses. We first hypothesize that diving will be relatively thermally insensitive due to the need for animals to quickly dive at any temperature to avoid predation. Specifically, we predict a lower T_{OPT} and a wider thermal performance breadth (B_{80}) for diving time when compared to sprinting speed. Our second hypothesis is for coadaptation between T_{PREF} and T_{OPT} for sprinting, which would indicate that animals select temperatures to optimize this important hunting behavior. Taken together, testing these hypotheses demonstrates how selective pressures on different performance traits may shape the degree of thermal coadaption between physiology and thermoregulatory behavior and how these patterns may be context dependent.

MATERIALS AND METHODS

Animal Acquisition and Husbandry.—Wild-caught animals from Egypt were acquired from a commercial supplier (Underground Reptiles, Deerfield Beach, Florida, USA) on 9 November 2021 (*n* = 4) and 13 May 2022 (*n* = 4). We are unaware of any current methodology to confidently identify sex of individual *S. scincus* based on external characteristics, so we are unable to report sex (though we note current work in the lab is directed toward this goal). Individuals were marked with visible implant elastomer on the ventral surface between osteoderms and epidermis (Penney et al., 2001; Schmidt & Schwarzkopf, 2010). Animals were kept in two plastic bins (38 × 54 × 33 cm) filled to a depth of 14 cm with all-purpose sand (Mastercraft, Eau Claire, Wisconsin, USA). Water was provided *ad libitum* in a small water dish and boxes were occasionally misted (less than once per week). Ambient light was provided on a 12:12 schedule (08:00–20:00) and skinks were provided UVB via UVB bulbs (10.0, Reptisun, Germany) from 08:00–20:00. Ambient room temperature was maintained at 19.3 ± 2.0 °C (mean ± SD) for the duration of the experiment and ceramic heat bulbs (100-watt, 17 cm from sand surface), were on from 08:30–16:00 and provided a surface temperature gradient of 20–50 °C. Skinks were fed five crickets per skink three times per week, with vitamin and calcium dusting occurring once every week. Handling of skinks was kept to once per week to conduct experiments and health monitoring and weighing. We measured snout-vent length to the nearest 0.01 mm with digital calipers (mean: 95.43 mm, range: 87.3–111.15 mm; model: CD-6, Mitutoyo, Japan). To monitor animal health, we measured mass to the nearest 0.01 g weekly throughout the experiment (pre-experiment mean: 20.06 g, range: 13.52–27.70 g; SF-400D, JiangYin SuoFei Electronic Technology, Jiangyin City, China).

Thermal Preference Methods.—We utilized a temperature sensor/transmitter to record skink body temperature continuously for one week. We adhered a CubiSens data logger (0.5 g; CubiSens TS100; CubeWorks, Ann Arbor, Michigan, USA) with cyanoacrylate (Gorilla Super Glue Gel, Cincinnati, Ohio, USA) to the dorsal scales just posterior to the scapulae after first cleaning the skin with 70% isopropyl alcohol (see Fig. 1 for example). In separate measurements, we validated the glue-on sensor/transmitter approach dur-

FIG. 1. Sandfish Skink (*Scincus scincus*) with a wireless CubiSens temperature data logger on its back. The temperature logger (CubiSens TS100; CubeWorks, Ann Arbor, Michigan, USA) adhered to the dorsum measures 7.5 × 9.4 × 4.2 mm.

ing a period which mimicked morning warming, whereby lizards were initially in a cool environment and then provided the opportunity to thermoregulate for four hours, with temperature recorded every five minutes. During this time, temperatures recorded with the dorsally attached logger closely matched those of a thermocouple probe (Omega Engineering Type T thermocouple, 36 gauge, connected to a digital temperature logger: HH806AU, Omega Engineering, Norwalk, Connecticut, USA) inserted into the cloaca ($R^2 = 0.99$; $P < 0.0001$, slope ± SD: 1.05 ± 0.003; Fig. S1). For thermal preference trials, animals were placed into a plastic tub (50 cm wide × 84 cm long) filled to a depth of 15 cm with sand. A 100-watt ceramic heating bulb, 17 cm above the surface, provided a continuous and stable gradient of approximately 18 to 48 °C. We recorded substrate temperatures using a PACE data logger system (XR5-SE-20 mV, Boone, North Carolina, USA), which recorded temperatures in eight locations every 30 seconds. Probes were located at depths of 15 cm, 8 cm, 1 cm, and on the surface, both under the heat bulb and at the cool end of the bin. Animals were left undisturbed for seven consecutive days, without prey and with water provided *ad libitum* in a small dish in the cool end of the bin. The CubiSens data logger attached to the dorsum transmitted temperature every 10 minutes for the duration of the trial. The ambient light cycle was identical to that in normal husbandry conditions (see above). We removed data from the first day to allow acclimation to the experimental gradient after handling and relocating. Additionally, due to logger failure we lost 4 days of data out of 48 total days (see Fig. S2). Thermal preference was measured from 16 September 2022 to 11 November 2022.

Diving Measures.—Sand diving is a behavior performed by *S. scincus* in their natural habitat to escape predation attempts (Attum et al., 2007). Diving trials were conducted at seven temperatures, with lizards split into two groups and each group experiencing temperatures in a random order, with the exception that performance at the highest temperature was measured last. Performance trials at the highest body temperature were conducted last, due to possible negative health consequences for the animal following the trial (though none were observed). A plastic bin (27 × 38 × 17 cm) was filled with 5 cm of sand and kept in the incubator overnight at the trial temperature. A minimum of one hour before each trial, animals were placed into separate individual cups partially filled with sand pre-warmed to target body temperature, and moved to the incubator. Target body temperatures (T_b) for performance trials were 15, 20, 25, 30, 35, 40, and 45 °C, spanning the observed activity range of this species. For target body temperatures of 35, 40, or 45 °C, incubators were set 2 °C higher to achieve the T_b. Once removed from the incubator and their cups, we immediately measured T_b via a thermocouple (Type K, Omega Engineering) inserted ~0.5 cm into the cloaca. The bin of diving sand was removed from the incubator immediately before each trial. We then released skinks from ~5 cm above the surface of the sand, providing an identical starting point for each measure of diving. Once the skinks were fully in contact with the sand, they were then given a predator stimulus in the form of a human hand hovering or waving over them. Trials were recorded with a high-speed camera (120 fps; AG-AC30, Panasonic, Kadoma, Osaka, Japan) positioned above the diving bin until skinks fully submerged themselves in sand or movement ceased for 10 seconds, because not all animals fully concealed themselves. The process was repeated three times at each temperature for each animal. If skinks did not perform any diving behavior after 10 seconds, it was recorded as a "no dive." We analyzed video with the software BORIS (v. 7.13, University of Torino, Italy). We marked the start of dives when the animal's nose began to penetrate the sand, and the end of dives once the animal was completely submerged or animals remained stationary for 10 seconds. Additionally, dives were ranked on a five-point scale as to "quality" of dives (five: skink completely submerged with no visible body part; four: skink submerged except a small section of the tail [< 10% of dorsal surface area visible]; three: ~ 50% of dorsal surface visible on sand surface; two: skink submerged only head [most of the body exposed]; one: skink did not dive). For analyses and creation of thermal performance curves (see below), we only included diving times for dives that achieved a quality score of four or five. Diving trials were conducted from 15 September 2022 to 10 February 2023.

Sprinting Measures.—A lizard's sprint speed is a traditional measure often used to quantify thermal performance at a variety of temperatures (Huey & Kingsolver, 1989; Telemeco et al., 2022). In *S. scincus*, sprinting is used as a hunting behavior, rather than as a predator avoidance behavior as in most squamate species (Attum et al., 2007; Miles, 2004). By measuring the effects of temperature on both diving and sprinting, we were able to compare thermal performance curves (TPC) for both predator avoidance and hunting. We followed the same protocol described in the diving methodology to set skink body temperature. After being in the incubator for a minimum of one hour, we removed skinks and recorded cloacal temperature. Animals were then placed at one end of a racetrack (200 cm length × 18 cm width) outfitted with infrared movement sensors (Trackmate Racing, Surrey, British Columbia, Canada) every 25 cm, and a thin layer (0.5 cm) of sand on the floor. Skinks were spurred to move with a paintbrush or finger lightly touching the base of the tail. Lizards were allowed to sprint the entire distance of the track and then re-run for a total of three sprint trials. For analysis, we used the top speed recorded across a 25-cm interval at each temperature. Sprint trials were conducted from 4 November 2022 to 27 January 2023.

Critical Thermal Limits.—Critical thermal minimum ($\mathrm{CT_{MIN}}$) and critical thermal maximum ($\mathrm{CT_{MAX}}$) are vital components of an animal's natural history, because they represent limits of organismal function. $\mathrm{CT_{MIN}}$ and $\mathrm{CT_{MAX}}$ trials followed similar procedures to one another, with temperatures gradually decreasing and increasing, respectively. Prior to being placed into an incubator, skinks had a thermocouple (Type T, 36 gauge) placed ~0.5 cm into their cloaca, secured with a small drop of superglue and tape just posterior to the cloaca. Then, as with performance trials described above, skinks were placed into an incubator for one hour in cups filled with sand (15 °C for $\mathrm{CT_{MIN}}$ and 40 °C for $\mathrm{CT_{MAX}}$). After one hour, skinks were removed one at a time, and we recorded cloacal body temperature as the starting temperature. For $\mathrm{CT_{MIN}}$ trials, animals were placed into a plastic container (13 × 19 × 10 cm) which was placed in a cooler filled with ice. We adjusted placement of the container in the ice to achieve a cooling rate of 1 °C/min. For $\mathrm{CT_{MAX}}$ trials, animals were placed into the same plastic container under a 100-watt incandescent heat bulb. We adjusted position under the bulb to achieve a heating rate of 1 °C/min. For $\mathrm{CT_{MIN}}$ trials, once body temperature reached 15 °C, animals were flipped onto their backs every 1 °C decrease in temperature until 12 °C, then were flipped every 0.5 °C decrease. For $\mathrm{CT_{MAX}}$, once body temperature reached 40 °C, animals were flipped onto their backs every 1 °C increase in temperature until 45 °C, then were flipped every 0.5 °C increase. The temperature where righting was no longer completed after 15 seconds of prodding at the tail base and legs was recorded as the $\mathrm{CT_{MIN}}$ or $\mathrm{CT_{MAX}}$ (Taylor et al., 2021). Following the recording of $\mathrm{CT_{MIN}}$ or $\mathrm{CT_{MAX}}$, we removed the probe from the cloaca using acetone to dissolve the superglue and tape adhesive. Critical thermal limits were measured from 19 December 2022 to 17 February 2023.

Statistics: Thermal Preferences.—We conducted all analyses in the Programming Language R (R Core Team, 2022) and created data plots using the *ggplot2* package (Wickham, 2016). Based on body temperature data traces, one researcher (EHL) characterized body temperature into periods of activity and inactivity (example trace presented in Fig. 2; traces for all animals presented in Fig. S2). Lizard body temperature data indicate that animals exhibited discrete and regular patterns of activity and inactivity, and based on this observation, we analyzed thermal preference separately for active and inactive periods. From continuously recorded body temperature data, we extracted five parameters describing thermal preferences for active and inactive periods, following Taylor et al. (2021; see thermal parameters and definitions in Table 1). We assessed differences in these parameters between active and inactive periods using a paired *t*-test. We then calculated repeatability and 95% confidence interval, and the associated *p*-value (likelihood ratio test) for each trait using the *rptR* package (Stoffel et al., 2017).

Statistics: Thermal Performance Curves for Sprinting and Diving.—To describe thermal dependence of sprint and dive performance, we created thermal performance curves using the "beta function", an approach first developed to describe thermal dependence of plant growth rates (Yan & Hunt, 1999), and since shown to be effective for modeling performance traits in ectotherms, including lizards (Telemeco et al., 2022; Tomlinson, 2019). The beta function is advantageous in that estimated parameters are readily interpretable biologically:

$$\text{Performance} = W_f \times \left(\frac{CT_{MAX} - T_b}{CT_{MAX} - T_{OPT}}\right) \times \left(\frac{T_b}{T_{OPT}}\right)^{\frac{T_{OPT}}{CT_{MAX} - T_{OPT}}} \qquad (1)$$

where T_b is body temperature, W_f is peak performance, T_{OPT} is the temperature at which W_f is achieved, and CT_{MAX} is the high temperature where performance equals zero (all temperatures in Kelvin). Following Telemeco et al. (2022), we used the *nls* function in R to fit a performance curve for each individual, using body temperature measured with a thermocouple before each trial as T_b and the measured value of $\mathrm{CT_{MAX}}$ for each individual. We were unable to measure $\mathrm{CT_{MAX}}$ for one individual, so we used the mean value for other skinks (48.2 °C). In addition to the data for performance measured at seven temperatures, we incorporated the $\mathrm{CT_{MIN}}$ for each individual skink by setting performance to zero (for sprinting) or infinite (for diving) at this temperature. We were unable to measure $\mathrm{CT_{MIN}}$ for three indi-

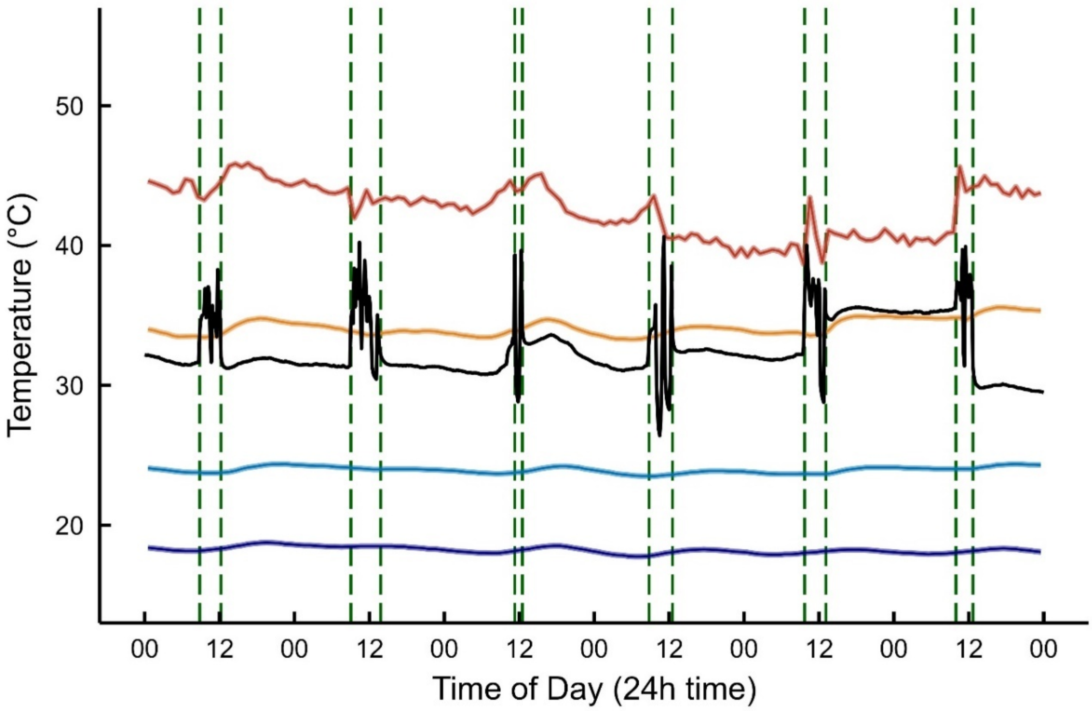

FIG. 2. Example plot of selected body temperature over the course of one week for wild-caught adult Sandfish Skinks (*Scincus scincus*). The black line indicates body temperature of the individual animal. Colored lines represent temperature of the sand horizons at various depths and locations, demonstrating the full range of available temperatures. Deep probes were placed at a depth of 15 cm (dark blue line), medium probes at a depth of 8 cm (light blue line), shallow probes were placed at a depth of 1 cm below the surface of the sand (yellow line), and surface probes placed on the sand surface (red line). Green dashed vertical lines show the start and end of activity on a given day. See Fig. S2 for plots of all animals.

viduals, so we used the mean value for other skinks (10.6 °C). We elected to use values of CT_{MIN} and CT_{MAX} as the TPC endpoints because the loss of righting response represents the extreme limit of potential locomotion. Because faster diving performance is represented by lower values, we fit performance curves using the inverse of dive time. After fitting TPCs for each individual skink, we extracted estimates of W_f and T_{OPT} for each individual and used model-predicted values to estimate the temperature range across which 80% of maximum performance is achieved (B_{80}). We assessed model fit by calculating the root-mean-square error (RMSE) for each performance curve (sprinting mean ± SD RMSE = 0.183 ± 0.065 ms^{-1}; diving mean ± SD RMSE = 0.127 ± 0.054 s^{-1}). Plots showing raw data with fitted performance curves further demonstrate the fit of models (Fig. S3, S4).

Statistics: Hypothesis Testing.—We conducted paired *t*-tests (two-tailed) on Sprint T_{OPT} vs. Dive T_{OPT} and Sprint B_{80} vs. Dive B_{80} to test the hypotheses that thermal performance curves for sprinting and diving exhibited different shapes, including a Bonferroni correction of α for multiple comparison of parameters derived from thermal performance curves. Our data were normally distributed, so we used parametric correlations (Pearson correlations) to test for patterns of among-individual variation in T_{OPT}, B_{80}, and W_f between performance traits, again employing a Bonferroni correction. To test the thermal coadaptation hypothesis, we utilized paired *t*-tests and Pearson correlation tests to assess the relationship between optimal temperatures for performance (Sprint T_{OPT} and Dive T_{OPT}) and T_{PREF}. Finally, we tested for among-individual correlations in activity time and maximum performance (fastest sprint speed and lowest diving time) with a Pearson correlation test.

RESULTS

Thermal Preferences.—Lizards displayed a matutinal behavioral pattern with discrete activity periods, whereby they began their activity on average at 08:05 h each morning and remained active for approximately four hours (Fig. 2; Table 1). Once lizards stopped actively thermoregulating, they did not move until the following morning. Lizards thermoregulated during active times to a mean of 34.5 °C and during inactive times to a mean of 32.4 °C. VT_{MAX}, Upper T_{SEL}, and T_{PREF} were significantly higher during active periods compared to inactive periods. We present full results of thermoregulatory measures and comparisons in Table 1 and Fig. 2 (patterns for all individuals are in Fig. S2). Our repeatability estimates demonstrated evidence for consistent among-individual variation in upper and lower limits of selected temperatures (Upper T_{SEL} and Lower T_{SEL}) and mean selected temperature (T_{PREF}). Additionally, we found evidence that activity start time and duration of activity period were repeatable (Table 2). No other thermoregulatory traits during active or inactive periods were repeatable.

TABLE 1. Definition, abbreviation, summary statistics, and *t*-test results comparing active and inactive measures for seven thermoregulatory behavior values of wild-caught adult Sandfish Skinks (*Scincus scincus*) measured during active and inactive periods. Definitions from Taylor et al. (2021). Significant differences shown in bold, with one ($P < 0.05$), two ($P < 0.01$), or three ($P < 0.001$) asterisks.

			Value ± SD (Range)		
Term	Abbreviation	Definition	Active	Inactive	*t*-test results
Voluntary thermal minimum	$\mathrm{VT}_{\mathrm{MIN}}$	The lowest single body temperature selected during a period of time	28.22 ± 2.18 °C (23.78–30.40 °C)	29.30 ± 1.46 °C (27.50–30.98 °C)	t_7 = -0.96 P = 0.3678
Voluntary thermal maximum	$\mathrm{VT}_{\mathrm{MAX}}$	The highest single body temperature selected during a period of time	41.01 ± 0.75 °C (39.94–42.25 °C)	35.64 ± 1.98 °C (31.94–38.40 °C)	**t_7 = 6.72** **P = 0.00027*** **
Lower selected temperature	Lower $\mathrm{T}_{\mathrm{SEL}}$	Lower limit of interquartile range (25th percentile) of selected temperatures during a period of time	33.03 ± 1.11 °C (30.95–34.56 °C)	32.00 ± 1.57 °C (28.91–33.73 °C)	t_7 = 1.28 P = 0.2395
Upper selected temperature	Upper $\mathrm{T}_{\mathrm{SEL}}$	Upper limit of interquartile range (75th percentile) of selected temperatures during a period of time	36.05 ± 0.75 °C (34.79–36.99 °C)	32.81 ± 1.47 °C (29.47–34.14 °C)	**t_7 = 4.83** **P = 0.0019** **
Preferred temperature	$\mathrm{T}_{\mathrm{PREF}}$	The average of the interquartile range of selected temperatures during a period of time	34.49 ± 0.86 °C (32.97–35.46 °C)	32.36 ± 1.48 °C (29.16–33.87 °C)	**t_7 = 2.98** **P = 0.020* **
Time active	$\mathrm{Act}_{\mathrm{Time}}$	Time spent moving in thermal gradient	4.12 ± 1.15 h (2.88–5.99 h)	–	–
Start time of activity	$\mathrm{Act}_{\mathrm{Start}}$	Average time past midnight at which activity started	8.09 ± 0.94 h (7.01–9.59 h)	–	–

TABLE 2. Repeatability estimates and 95% bootstrapped confidence intervals for seven thermoregulatory behavior values of wild-caught adult Sandfish Skinks (*Scincus scincus*). Significant estimates shown in bold, with one ($P < 0.05$) or two ($P < 0.01$) asterisks, as determined by likelihood ratio tests.

	Repeatability [95% CI]	
Abbreviation	Active	Inactive
$\mathrm{VT}_{\mathrm{MIN}}$	R = 0.014 [0, 0.210] P > 0.999	R = 0.137 [0, 0.440] P = 0.28
$\mathrm{VT}_{\mathrm{MAX}}$	R = 0.102 [0, 0.386] P = 0.248	R = 0.140 [0, 0.469] P = 0.266
Lower $\mathrm{T}_{\mathrm{SEL}}$	**R= 0.271 [0, 0.565]** **P = 0.0239* **	R = 0.171 [0, 0.499] P = 0.209
Upper $\mathrm{T}_{\mathrm{SEL}}$	**R = 0.279 [0, 0.577]** **P = 0.0201* **	R = 0.169 [0, 0.507] P = 0.213
$\mathrm{T}_{\mathrm{PREF}}$	**R = 0.336 [0, 0.618]** **P = 0.00676** **	R = 0.154 [0, 0.484] P = 0.24
$\mathrm{Act}_{\mathrm{Time}}$	**R = 0.271 [0, 0.564]** **P = 0.0431* **	–
$\mathrm{Act}_{\mathrm{Start}}$	**R = 0.339 [0, 0.628]** **P = 0.00674** **	–

Thermal Performance Curves for Sprinting and Diving.—Both sprinting and diving performance were thermally sensitive, with performance curves demonstrating a classical shape with gradual increases to an optimum tempera-

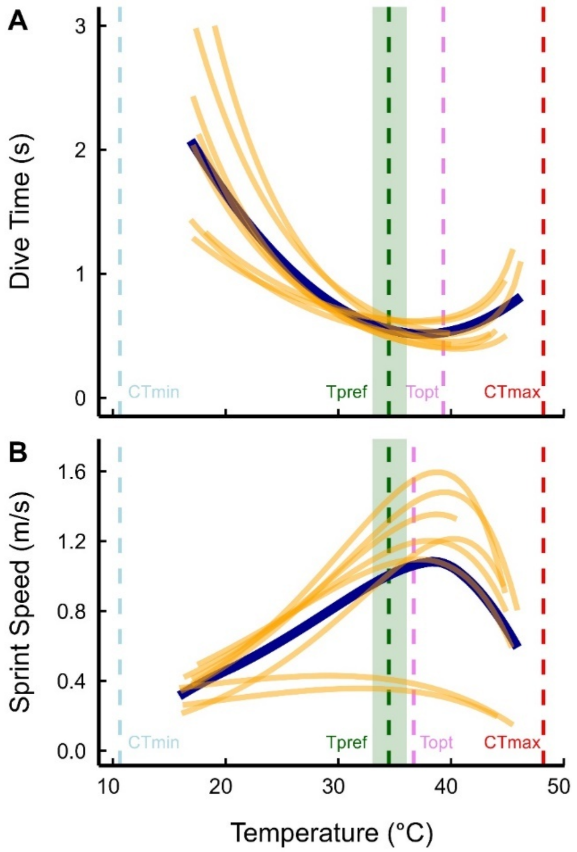

FIG. 3. Thermal performance curves for diving time (A) and sprint speed (B) measured on wild-caught adult Sandfish Skinks (*Scincus scincus*). Yellow lines indicate thermal performance curves for individual animals, whereas the dark blue line represents the mean. Thermal performance curves were created using the beta function (see text for statistical details). Vertical lines show population mean values for critical thermal minimum (CT_{MIN}), critical thermal maximum (CT_{MAX}), optimal temperature for performance (T_{OPT}), and preferred body temperature (T_{PREF}). Shading around the T_{PREF} line indicates interquartile range of selected body temperatures.

ture, then rapid decreases at temperatures above optimum (Fig. 3; see Fig. S3 and Fig. S4 for raw data plotted with each fitted thermal performance curve). A summary of measured CT_{MAX} and CT_{MIN} values and all parameter estimates from thermal performance curves is presented in Table 3.

Hypothesis Tests of Among-individual Correlations.—T_{OPT} for sprinting was significantly cooler than that for diving (mean: 37.8 vs. 39.6 °C, $t_{df=7} = -3.63$, $P = 0.0084$, Bonferroni-corrected $\alpha = 0.025$) and B_{80} for sprinting was significantly larger than that for diving (mean: 12.6 vs. 9.5 °C, $t_{df=7} = 3.49$, $P = 0.010$, Bonferroni-corrected $\alpha = 0.025$). T_{OPT} for sprinting and diving was positively correlated among individuals (T_{OPT}: $r = 0.89$, $t_{df=6} = 4.74$, $P = 0.0032$, Bonferroni-corrected $\alpha = 0.017$) and B_{80} trended in that direction, though was not significant after correction for multiple comparisons (B_{80}: $r = 0.77$, $t_{df=6} = 2.97$, $P = 0.025$, Bonferroni-corrected $\alpha = 0.017$), indicating similar among-individual patterns of thermal dependence in the two performance measures. Further, W_f was negatively correlated among individuals (W_f $r = -0.88$, $t_{df=6} = -4.65$, $P = 0.0035$, Bonferroni-corrected $\alpha = 0.017$), indicating that fast-sprinting individuals were also fast divers (lower dive times indicate faster performance). We did not find support for the thermal coadaptation hypothesis using either sprint or dive performance. Both Sprint T_{OPT} and Dive T_{OPT} were higher than active T_{PREF} (mean active T_{PREF}: 34.5 °C; Sprint *t*-test: $t_{df=7} = 3.41$, $P = 0.011$; Sprint correlation: $r = -0.12$, $t_{df=6} = -0.31$, $P = 0.77$; Dive *t*-test: $t_{df=7} = 9.05$, $P < 0.0001$; Dive correlation: $r = 0.19$, $t_{df=6} = 0.47$, P = 0.66). Finally, we found no evidence that skinks spending more time active were better at sprinting or diving performance (Sprint correlation: $r = -0.50$, $t_{df=6} = -1.41$, $P = 0.21$; Dive correlation: $r = 0.24$, $t_{df=6} = 0.60$, $P = 0.57$).

DISCUSSION

Our results reveal key aspects in the natural history of the semifossorial desert specialist *S. scincus*, specifically in how both physiological and behavioral traits allow this species to deal with extreme temperatures faced by desert organisms. *S. scincus* has evolved one of the highest published critical thermal maxima for a squamate (mean: 48.2 °C), allowing it to survive daily temperature spikes. To our knowledge there are only four published studies on species in the families Agamidae, Teiidae, and Liolamidae, reporting a higher CT_{MAX}, making this the highest reported CT_{MAX} for a member of Scincomorpha (Diele-Viegas et al., 2018; Heatwole, 1970; Mitchell, 1973; Paulissen, 1988). The large range between active preferred body temperature and critical thermal maximum (average difference of 13.7 °C) provides a large thermal safety margin for the species, which may protect *S. scincus* from continuing increases in temperature (Sunday et al., 2014). A high physiological tolerance suggests that lizards cannot always behaviorally avoid extreme temperatures of their environment. Not only has the species evolved a physiological tolerance of extreme temperatures, but they have also concentrated their periods of activity in early morning. The morning activity period takes place from around 08:00–12:00 h, thus allowing any hunting or necessary surface behaviors to occur before encountering peak daily temperatures. Furthermore, the period for which an animal was active and the temperature they selected during that period of activity were consistently different among individuals. The significant repeatability of active period duration and thermal preferences during activity suggests among-individual variation in thermoregulatory behaviors and setpoints, which may be tied to other aspects of thermal physiology (Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, et al., 2017).

Using a novel method of wireless body temperature tracking, we recorded skink body temperatures continuously over a week and precisely differentiated an animal's daily active and inactive periods. The technique also allowed us to ascertain that selected body temperatures differed between periods of activity above ground versus inactivity below ground. Our method of tracking body temperature above and below ground, using miniature sensor-transmitters, which provide real-time data monitoring, opens the door to quantify thermal biology of other species

TABLE 3. Summary statistics for eight thermal performance values of wild-caught adult Sandfish Skinks (*Scincus scincus*).

Abbreviation	Term	Definition	Value ± SD (Range)
CT_{MIN}	Critical thermal maximum	Maximum body temperature where righting response can occur	10.64 ±1.57 °C (8.50–12.90 °C)
CT_{MAX}	Critical thermal minimum	Minimum body temperature where righting response can occur	48.19 ± 0.45 °C (47.10–48.50 °C)
Sprint T_{OPT}	Sprinting optimal temperature	Optimal body temperature to sprint	37.80 ± 2.51 °C (33.20–40.38 °C)
Sprint W_f	Sprinting maximum performance	Fastest sprint speed recorded	1.10 ± 0.47 ms^{-1} (0.36–1.60 ms^{-1})
Sprint B_{80}	Sprinting performance breadth	Temperature range over which 80% of maximum performance can be obtained for sprinting	12.59 ± 3.89 °C (8.53–19.63 °C)
Dive T_{OPT}	Diving optimal temperature	Optimal body temperature to dive	39.56 ± 1.50 °C (37.19–41.47 °C)
Dive W_f	Diving maximum performance	Fastest time to submerge beneath the surface recorded	0.49 ± 0.09 s (0.39–0.62 s)
Dive B_{80}	Diving performance breadth	Temperature range over which 80% of maximum performance can be obtained for diving	9.45 ± 3.62 °C (3.60–13.59 °C)

in a variety of contexts. This method is especially useful for small organisms, whose body size may preclude larger sensors (e.g., iButtons, radiotelemetry) or whose behavior prohibits wired body temperature monitoring in a natural environment. The findings from this novel method also highlight the importance of examining thermal preferences during an organism's inactive period, as they can significantly differ from preferences during their active period (Rutschmann et al., 2024). In desert environments, the horizons of sand offer organisms a thermal gradient and potential refuge from extreme surface temperatures (Louge et al., 2013). *S. scincus* are able to exploit spatial thermal heterogeneity to effectively regulate body temperature, theoretically via both horizontal and vertical movements. Importantly, thermal heterogeneity below ground can allow lizards to select effectively a position where they can remain inactive but also maintain preferred body temperatures. We clearly demonstrated that even during inactive periods, lizards select temperatures within a narrow range. Below-ground thermoregulation provides the benefit of simultaneously preventing exposure to harmful temperatures and predators on the surface.

We observed a large discrepancy between preferred body temperatures and thermal limits, providing a large thermal safety margin. This high CT_{MAX} is notable because thermoregulatory behaviors often act to forestall evolution of physiological tolerances (Bodensteiner et al., 2021; Muñoz, 2022). The extremely high CT_{MAX} we observed here suggests that skinks are not always able to avoid high temperatures behaviorally, and that there has been selection on physiological capacity to withstand such temperatures. While the relatively high CT_{MIN} additionally suggests that skinks can either physiologically tolerate cold temperatures in a safe refuge (e.g., under the sand) or avoid these temperatures by effectively thermoregulating to warmer depths during cool periods (e.g., nighttime). Despite this extraordinary tolerance of high temperatures, future work should be directed toward quantifying depth limits of diving and subsurface locomotion, which may limit thermoregulation in this environment and explain the evolution of physiological tolerance to high temperatures.

The thermal coadaptation hypothesis postulates that optimal body temperature for traits closely linked to fitness should also be the body temperature to which animals thermoregulate when possible. The premise for the thermal coadaptation hypothesis stems from the idea that an individual's fitness will be higher if they are able to perform those fitness-linked traits to their optimum. The thermal coadaptation hypothesis was first proposed by Huey and colleagues and was largely tested from an interspecific perspective, with support for a general trend that if a species has a higher optimal temperature for performance its preferred temperature was more likely to be high as well (Angilletta, 2009; Bodensteiner et al., 2021; Huey & Bennett, 1987; Huey & Kingsolver, 1989). However, overlap of preferred body temperature and optimal temperature was largely overlooked within species; recent work has found mixed to no support for the hypothesis at the intraspecific level (Aparicio Ramirez et al., 2021; Lailvaux & Irschick, 2007; Neel et al., 2020). One potential explanation for the lack of correlation at the intraspecific level is a "tipping point hypothesis": often, there is a rapid decline in performance followed by death beyond the optimal performance temperature (Gangloff & Telemeco, 2018; Huey & Kingsolver, 1989). To avoid these sudden decreases in performance or even death due to small increases in body temperature, animals may thermoregulate significantly below that point, providing a behavioral buffer from physiological failure (Aparicio Ramirez et al., 2021; Huey & Bennett, 1987; Martin & Huey, 2008). *S. scincus* offers an interesting study organism to test this explanation, due to the large gap between optimal body temperature and critical thermal maximum (average individual thermal safety margin of 13.7 °C). Given this large safety margin and lack of risk of overheating at temperatures slightly above optima, we expected to find a pattern of thermal coadaptation. Contrary to our expectation, we found a large and significant gap and lack of among-individual correlation between preferred temperatures and optimal temperatures for sprinting and diving performance. Our findings are also contrary to the "tipping point hypothesis": even in *S. scincus*, a species with a large gap between optimal temperatures and upper thermal limits, we observed no evidence of coadaptation. The lack of thermal coadaptation might be best explained by the "optimality hypothesis" (Aparicio Ramirez et al., 2021; Martin & Huey, 2008), which explains that the benefits of thermoregulating to higher temperatures diminish as the slope of a thermal performance curve decreases at temperatures approaching the optimum.

An alternative explanation is that thermal coadaptation only manifests with physiological processes and exposure occurring over a longer timescale (Carlo et al., 2018; Gangloff & Telemeco, 2018). Exposure to high suboptimal but sublethal temperatures for longer periods of time may disrupt essential homeostatic systems, such as those related to metabolism or water balance (Telemeco & Gangloff, 2021). One would assume that the species has evolved to be physiologically resistant to short-term temperature spikes, due to the environment they live in presenting a constant threat of deadly exposure to acute extreme temperatures. If so, it would not be readily apparent from our performance trials, which never lasted more than two hours, because failure to uptake more energy than expended or desiccation would only begin to present as a health issue in exposure over a longer period. *S. scincus* presents an excellent organism to continue exploring patterns of coadaptation at the intraspecific level, for example, if the "tipping point hypothesis" only applies over longer periods of exposure to high temperatures above the optimum.

Interestingly, we observed different patterns of among-individual variation in the effects of temperature on diving and sprinting ability of *S. scincus*. Specifically, we observed little heterogeneity among thermal performance curves for diving, such that all individuals followed similar patterns (Fig. 3A). In contrast, we documented relatively high among-individual variation in sprinting performance. It appears that there are two distinct patterns of thermal dependence of sprint speed (Fig. 3B), whereby most lizards follow traditional patterns of thermal dependence, while others are insensitive, but slower overall. We conducted a suite of correlation tests to ascertain a link between dive or sprint speed and other thermal preference parameters but found no correlations. One possibility is that observed variation in sprint speed is linked with individual variation in morphology (S. J. Arnold, 1983). We plan to direct a future research project to conduct a comprehensive suite of morphological measures and test for relationships between these and performance of ecologically relevant tasks. One possible nonexclusive explanation for the wide variation we see in sprinting and the minimal variation we see in diving could be explained by the "life-dinner principle": traits which allow individuals to escape predation events will experience higher selective pressures, and therefore less variation among individuals, compared to traits less closely linked to survival (Dawkins et al., 1997). In the context of this study, for *S. scincus,* diving is a predator escape mechanism, whereas sprinting is a hunting mechanism (Attum et al., 2007). Thus, the predator escape mechanism of diving has low variation, as there will usually be another chance at a meal, but not another chance to escape a predation event.

Overall, *S. scincus* are excellent and novel model organisms for testing hypotheses of how ectotherms survive in structurally and thermally challenging environments. We identified a suite of behavioral and physiological adaptations to deal with environmental pressures, including a limited activity period of four hours in the morning and an extremely high critical thermal maximum. Additionally, we found no support for intraspecific thermal coadaptation, which has seldom been tested in species of the family Scincidae. Whereas thermoregulatory behaviors and thermal dependence of performance traits were not correlated, individuals were consistently different in their selected body temperature and activity periods. To obtain these results, we utilized a novel method of wireless body temperature logging, which can permit similar tests and observations in other species inhabiting extreme or below-ground environments. For the long-term survival of the species, we posit that *S. scincus* are likely able to handle increasing warming of the climate via their high critical thermal maximum; however, limits in diving depths could constrain thermoregulatory behaviors and need further investigation. Nonetheless, there are still many unknown aspects of the natural history of this species, despite being widespread geographically and easily obtained in the pet trade. We hope to promote further investigations of the species' natural history, such as reproduction and thermal biology of early life-history stages, which are essential in predicting responses to future environmental changes.

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DATA AVAILABILITY

Data and analysis code are archived with Mendeley Data (doi: 10.17632/6xyn387yct.1).

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online alongside the manuscript.

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SUPPLEMENTARY MATERIALS

Supplementary Data

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