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Sexual Dimorphism of Thermal Preference in Florida Scrub Lizards (Sceloporus woodi) and Predicting Response to Climate Change in Two Rare Habitats

Sidney E. Anderson

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SEXUAL DIMORPHISM OF THERMAL PREFERENCE IN FLORIDA SCRUB LIZARDS (SCELOPORUS WOODI) AND PREDICTING THE RESPONSE TO CLIMATE CHANGE IN TWO RARE HABITATS

by

SIDNEY ANDERSON

(Under the Direction of Lance McBrayer)

ABSTRACT

The Florida Scrub Lizard *(Sceloporus woodi)* is endemic to Florida, where it inhabits fragments of xeric sandhill uplands including endangered long-leaf pine and sand pine scrub habitats. Lizards depend on a predictable range of temperatures to maximize their growth and productivity, and to do so, they shuttle among various thermal micro-environments. Thus, the spatial distribution of temperatures in the habitat is important. Habitats dominated by either high or low extremes of an organism's preference are energetically costly and dangerous (less optimal), especially to gravid females. This study examines thermal preference of a near-threatened species that also inhabits increasingly rare habitats. I incorporate data on both sexes into a biophysical model that uses environmental and organismal data to estimate daily activity times under current and 3°C warming climate conditions. Male *S. woodi* preferred a temperature 2°C higher than that of females, whereas females had a wider thermal tolerance than males, which could facilitate adjustments to environmental change. Under a 3°C warming scenario, females are predicted to have activity times shifted later in the day while males are predicted to experience longer activity times. These results have implications for conservationists, habitat managers, and broader considerations on the mixed effects of climate change. With variable responses to climate change, males and females are predicted to alter activity time differently in order to survive. Management decisions on the timing and types of habitat disturbance are likely to have differential effects on sexes, thus managers are encouraged to apply techniques that benefit both sexes.

INDEX WORDS: Thermoregulation, Lizard, Herpetology, Climate change, Thermal biology

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SIDNEY ANDERSON

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COLLEGE OF SCIENCE AND MATHEMATICS

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SIDNEY ANDERSON

Major Professor:	Lance McBrayer
Committee:	Johanne Lewis
	Elizabeth Hunter

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TABLE OF CONTENTS

ACKNOWLEDGMENTS 2

LIST OF TABLES 4

LIST OF FIGURES 5

CHAPTER 1 6

INTRODUCTION 6

CHAPTER II 11

METHODS 11
Study Species 11
Study Area 11
Field Collection and Husbandry 12
Thermal Preference 12
Critical and Voluntary Thermal Indices 13
Operative Temperature 14
Modeling climate warming using NicheMapR 15
Microclimate Model in NicheMapR 15
Ectotherm Model in NicheMapR 16

CHAPTER III 17

RESULTS 17
Thermal Preference 17
Critical Minima and Maxima; Voluntary Maxima 17
Thermal Opportunity and Quality of Habitats 18
Activity Time 18

CHAPTER IV 27

DISCUSSION 27
Conclusion 31

REFERENCES 32

LIST OF TABLES

Page

Table 1: Thermal characteristic definitions …..……..20
Table 2: Thermal biology summary data…..21
Table 3: Habitat quality summary data..22

LIST OF FIGURES

Page

Figure 1: Current and future operative temperatures..23
Figure 2: Capture times by predicted activity times...24
Figure 3: Current and future predicted activity times...25
Figure 4: Empirical and predicted thermal preference and operative temperature data.............26

CHAPTER 1

INTRODUCTION

As global climate change continues, the impact is likely to be seen first on endemic species, and or those with reduced ranges (Sinervo, 2010). Three of the five warming scenarios currently modeled by the International Panel on Climate Change predict global land temperatures to warm by 3°C or more in the next 60-80 years (Lee et al., 2021). Small ectotherms are especially susceptible to climate shifts and extinctions are likely due to decreases in activity time impacting long-term survival(Sinervo et al., 2010). Furthermore, species that occupy unique or rare habitats will be particularly prone to increased competition by species with broader thermal tolerance and range shifts that may occur in response to changing climates are already being seen (Sinervo et al., 2010, Enge et al., 2021).

Small ectotherms depend on predictable temperature regimens that allow them to survive in thermally variable environments (Huey and Kingsolver, 1989). Daily or seasonal variation in temperature can be mitigated via behavioral mechanisms (Huey and Stevenson, 1979; Hutchinson and Maness; 1979), but not all temperature changes are equal. Ectotherms, by definition, rely on the temperature of the environment to maintain physiological processes and fall into one of two categories: thermoconforming, assuming the ambient temperature of their surroundings, or thermoregulating, maintaining a body temperature within a certain range or around a certain value via behavioral mechanisms. Shuttling efficiently among temperatures depends on the spatial distribution of the temperatures within the habitat where temperatures at the extremes of an organism's range require more shuttling than a habitat with a mosaic of temperatures within the organism's range. The former makes behavioral thermoregulation more costly to the organism in both energy expenditure and exposure to predators (Buckley et al., 2015). Ectotherms can afford to imprecisely thermoregulate at lower temperatures (Blouin-Demers et al., 2002). However, they spend more energy on thermoregulation and survival than other processes at extreme temperatures and may have to be more precise in doing so (Huey and Slatkin, 1976; Neel and McBrayer, 2018).

Every habitat contains a specific set of temperatures in which ectotherms must perform daily activities. Operative temperatures (T_e; Table 1) are all ambient temperatures (e.g. air, ground, solar, etc.) for all aspects of the habitat affecting heat retention at the scale of the organism (Dzialowski, 2005). The organism persists in a habitat because it can maintain a body temperature within its critical thermal limits, i. e. temperatures at either extreme that result in loss of function and, during prolonged exposure, death., yet organism's may experience temperatures above these limits for short durations with no adverse effects (Cowles and Bogert, 1944; Lutterschmidt and Hutchison, 1997).

However, survival or persistence within a given range of operative temperatures does not mean that organisms may not prefer, or benefit from, opportunities to choose a different range of operative temperatures. An organism's preferred temperatures, or set-point range (T_{set}; Table 1), is the range of ideal temperatures that an organism would select when presented with a gradient of options independent of its natural environment (Hertz et al., 1991).

Habitats of different qualities have different energetic requirements for their constituent residents, as do habitats of different size and with different spatial distribution of microclimates (Huey and Raymond, 1991; McCoy and Mushinsky, 1999; Hokit and Branch, 2003; Buckley et al., 2015; Sears and Angilletta, 2015; Sears et al., 2016). The distribution and frequency of microhabitats (i. e. thermal heterogeneity) provides differences in both protection from and exposure to predators as well as availability and access to necessary temperatures (Sears et al., 2016). A high-quality habitat provides the smallest difference between the organism's preferred temperatures and the provided operative temperatures; a low-quality habitat has a large difference between the available temperatures and those preferred by the organism (Hertz et al., 1991). Low quality habitats at higher temperatures require more effort dedicated to precise thermoregulation than at lower temperatures, or any habitat of high quality (Blouin-Demers and Nadeau, 2005; Neel and McBrayer, 2018). Habitat quality changes throughout the day limits activity time available and the intensity with which the organism can complete various life history processes (e.g. foraging and reproduction; Grant and Dunham, 1988; Grant, 1990; Gunderson and Leal, 2015).

Decreasing energy expenditure and predator exposure is crucial to gravid females as the reproductive season consists of a series of trade-offs in resource allocation among reproduction, foraging, and thermoregulation (Zera and Harshman, 2001). The increased movement required for shuttling between temperatures will not only increase the female's exposure to predators, but also use energetic resources (Huey and Slatkin, 1976). Alternatively, should she not increase her shuttling behavior, the female may choose to remain in a thermally stressful microclimate to avoid increasing energy expenditure and predator exposure. This may result in increased metabolic rates and/or physiological stress for the organism and similarly affect her ability to produce successful offspring while overcoming the stress of her environment. The Florida Scrub Lizard (*Sceloporus woodi*) produces 2 or 3 clutches per year (Jackson and Telford, 1975), yet offspring have low vagility and disperse only up to 1 km (Heath et al., 2012). Survival of hatchling *S. woodi* decreases in smaller forest patches (Hokit and Branch, 2003), and these patches are also likely to be warmer than large patches due to their large edge-to-interior ratio (Tuff et al., 2016). Thus, the impacts of thermal environment on gravid females will provide information on potential impacts on population growth in warming temperatures (Hokit and Branch, 2003; McCoy et al., 2004).

Female lizards are responsible for the production of offspring to maintain populations, thus their ability to produce successful clutches depends on their ability to respond to the stress of reproduction while persisting in the environment they experience (Niewarowski and Dunham, 1994). Habitats with temperatures on either extreme end of T_{set} will require a female to spend more time thermoregulating, therefore spending energy and resources she might have allocated to her offspring (Buckley et al., 2015, Neel and McBrayer, 2018). A female that allocates more energy to reproduction reduces her likelihood of survival by reducing her ability to forage and escape predators as a result of decreased mobility (Shine, 1980), but a female allocating more energy to survival reduces her lifetime reproductive output (Shine, 1980; Niewarowski and Dunham, 1994). Certain habitat characteristics can have different effects on males and females, and even on gravid and non-gravid females (Hokit and Branch, 2003). Reproductive females may have different thermal preferences than non-gravid female or male reptiles of the same species (Grant, 1990; Braña, 1993; Charland and Gregory, 1995; Mathies and Andrews, 1997; Blouin-Demers et al., 2002; Juri et al., 2018); gravid females can even have changing preferences depending on their reproductive stage (Grant, 1990; Juri et al., 2018).

This study compares the thermal preference of gravid and non-gravid females, females from different habitat types, and sexes. If gravid and nongravid females differ in thermal preference, then habitat quality and efficiency of thermoregulation should also be different for each group. If male and female thermal preference differ, then habitat quality and efficiency of thermoregulation should also differ for each group. This has implications for habitat management because this species occupies two of the imperiled habitat types in North America.

As global temperatures warm, informed decisions on management practices and how they affect their constituent thermal environments are needed. I expect NicheMapR models to predict a shift and reduction of activity times for males and females in each habitat type, with stronger effects under greater warming scenarios.

CHAPTER II

METHODS

Study Species

Sceloporus woodi is a sexually dimorphic lizard that matures quickly and frequents sunny, sandy areas for basking in central and south Florida, USA (Jackson and Telford, 1974; Enge and Branch, 2019). *Sceloporus woodi* is a rare endemic to most of Florida, with large populations still occupying fragmented habitats in the Ocala National Forest (ONF). Previous research on this species has found that management can influence access to suitable temperatures as well as impact risk aversion behavior (Neel and McBrayer, 2018, McBrayer and Parker, 2020 The *S. woodi* populations in the ONF have been found to more densely occupy recently burned longleaf pine habitat and frequent microclimates along roads (Kaunert and McBrayer. 2015). However, female-specific thermoregulation, the impacts of gravidity, and how it relates to what is already known about the thermal structure of the habitat types remains unstudied.

Study Area

This study examines lizards from long-leaf pine (LLP) and sand pine scrub (SPS habitats) in ONF. LLP is a highly endangered habitat dominated by longleaf pine trees and wiregrass species that currently only occupies 3-5% of it's historic range (Brockway et al., 2005; Clark et al., 2018). It is not only one of the most species rich habitats outside the tropics, but it is also valuable for timber production (Brockway et al., 2005; Clark et al., 2018). SPS is also a highly endangered habitat dominated by shrubs and currently managed for the support of the Florida scrub Jay (Hinchee and Garcia, 2017; Donald and Marion, 2020). Both site types in the ONF are managed through burning or roller chopping, with differential effects on the populations in either (Kaunert and McBrayer, 2015).

Field Collection and Husbandry

I captured males and females from long leaf pine and sand pine scrub habitats in the Ocala National Forest between May and July 2021. Only lizards caught within 0-60 seconds of initial observation were used to minimize potential for internal body temperature changes due to movement and stress. Immediately after capture, cloacal body temperature was measured by inserting a Schultheis thermometer into the cloaca. Females were determined to be gravid by palpating the abdomen on both sides to feel for the presence of eggs. Lizards were stored in cloth bags in a cool environment and transported back to the Georgia Southern University for housing. Lizards were housed individually in tanks with 1-2 inches of sand. Each was provided with a 100W bulb for heat at one end of the tank and a retreat site at the other end of the tank. Lizards were watered immediately upon entering the tank and were not fed or watered again until after testing in the thermal gradient. This was to ensure that all lizards were at the same state of digestion at the time of testing. Lizards acclimated to the lab at a room temperature of 25°C for 24 hours before testing. Lizards were not tested for thermal preference if they had been held for more than 72 hours. Individuals were returned to the site from which they were captured within 1 week.

Thermal Preference

Only females were tested for thermal preference during this season. All male Tset and critical thermal data was provided by Neel and McBrayer (2018). To determine individual $T_{set,}$ each individual was placed in one of six lanes (15 cm W X 2 m long) in a thermal gradient ranging from 24º-50º C (Hertz et al., 1991; Camacho and Rusch, 2017; Neel and McBrayer, 2018). After a one-hour acclimation period, a probe was inserted into the cloaca and taped to the subject's ventrum to monitor body temperature continuously for two hours (Paranjape et al., 2012; Juri et al., 2018, Neel and McBrayer, 2018). This is known to be reliable and safe method for gravid females (Paranjape et al., 2012). I chose to continuously monitor T_b to reduce handling stress experienced by the animal while in the laboratory setting. Thermal preference was determined by taking the mean of the central 80% of temperatures experienced by the lizard in the thermal gradient (Neel and McBrayer, 2018).

Critical and Voluntary Thermal Indices

Subsets of lizards from each habitat and sex were tested for critical thermal minimum and maximum (CTmin; CTmax) and voluntary thermal maximum (VTmax) with at least 1 day having passed since testing in the thermal gradient. No lizard was used for both critical and voluntary thermal testing. Critical thermal and voluntary thermal testing were conducted on the same days following capture each week. CTmax was determined by placing individuals in an opaque bucket under a 200 W heat lamp that gradually increased in temperature. A thermocouple continuously monitoring temperature was taped to their ventral side. Lizards were tested for righting response every minute. When an individual could no longer right themselves, the last recorded temperature was taken as CTmax. CTmin was determined by placing individuals on top of an ice pack. A thermocouple continuously monitoring temperature was taped to their ventral side. Lizards were tested for righting response; when an individual could no longer right themselves, the last recorded temperature was taken as CTmin. Voluntary thermal max is defined as the maximum temperature an organism will let themselves experience before they seek shade (Logan et al., 2021). In this experiment, VTmax was determined by placing organisms into an opaque bucket under a heat lamp. A thermocouple continuously monitoring body temperature was taped to the ventral size of the organism. Individuals were monitored for shade seeking behavior, defined as continuous effort to escape the chamber. This type of behavior is noticeably different from exploratory movement (Logan et al., 2021). At the time when individuals exhibited shade-seeking behavior, the last recorded temperature was taken as VTmax.

Operative Temperature

Sixteen PVC isoforms sized to match female snout-vent length were placed in LLP and SPS habitats each week. Four sets of four isoforms were placed at full sun and full shade in the sand and full sun and full shade in the leaf litter to determine the T_e for those locations throughout the summer (Shine and Kearney, 2001). Four additional isoforms were placed on perch sites (tree trunks in LLP) to represent the additional microclimate available in that habitat. Isoform models mimic the size and habitat use of the study organism, providing data on the predicted body temperature at that location if the organism were not actively thermoregulating. IButton data loggers inside the isoforms recorded temperature every 10 minutes over the course of one 24-hour day each week for the duration of the summer. Using this data in combination with the field active body temperatures recorded at capture and preferred temperatures determined in the lab, we estimated thermal quality of each habitat type for gravid females using the equation for effectiveness of thermoregulation (E; $E = 1- (d_b/d_e)$; Table 1; Hertz et al., 1993).

As technology in ecological studies evolves and becomes more accessible, different methods of measuring environmental parameters become available. While isoforms are the historic method of recording operative temperature (Hertz and Huey, 1991), methods like thermal imagery are becoming more prevalent in ecological studies. As a secondary measure of operative temperature, I used a FLIR E40 thermal camera to take imagery of the isoforms while deployed to compare the accuracy and effectiveness of each method in determining T_e of a habitat. Using the FLIR, thermal images were taken at chest height of the observer (~1 meter from the ground) at a 90° angle above the isoform deployed in each environment. If vegetation altered the camera's ability to capture the isoform, the angle was altered but remained as close to 90° as possible. The average temperature of the isoform recorded in the image was compared to the average recorded temperature of the Ibutton dataloggers inside the isoforms on the same substrate type at the time the image was captured.

Modeling climate warming using NicheMapR

NicheMapR is a deductive modelling package that applies available environmental and organismal data to estimate thermal constraints, daily or seasonal activity times, and energy budgeting under different conditions (Cavallo et al., 2014; Walker et al., 2014, Maino et al., 2016; Kearney and Maino, 2019; Kearney and Porter, 2019). The model estimates the current constraints on an organism in a given location and models warming of the estimated daily temperatures to estimate the species' response to climate change, such as having reduced daily activity time, forcing individuals to spend more time thermoregulating instead of mating, foraging, or producing young (Shine, 1980).

Microclimate Model in NicheMapR

The microclimate model draws its information from the monthly global climate data gathered from dataloggers in an approximately 10x10 km grid nearest to the geographic location selected (Kearney and Porter, 2016). All manipulatable values were left at the default for the package except shade values, soil type, and warming scenario. The shade values we used were obtained from Williams (2010) calculations of average canopy cover in each habitat. We ran the model at a high shade value (SPS = 23, LLP = 89) and a low shade value (SPS = 0, LLP = 44) in each habitat and averaged the probability of activity prediction from each. Soil type was set to sand. Warming scenario was affected at 3° C.

Ectotherm Model in NicheMapR

Using the climate conditions generated by the microclimate model under the parameters that we set, the ectotherm model used physiological and morphological parameters to generate predicted activity times at each hour of the day over the course of the year. We adjusted the following parameters to the values determined by our empirical data: Tset, CTmin, CTmax, VTmax, weight. Shape was set to lizard, ability to burrow and climb were enabled at the relevant height and depth for *S. woodi,* and photoperiod was set to diurnal.

CHAPTER III

RESULTS

Thermal Preference

The mean T_{set} of gravid and non-gravid females did not differ (gravid n = 47, nongravid n = 35; ANOVA; $F_{1, 80} = 0.53$, p = 0.737; Table 2). Based on this result, gravid and non-gravid females were pooled for subsequent analyses. The mean T_{set} of females in LLP and SPS habitats did not differ (LLP n = 32, SPS n = 50; ANOVA; $F_{1, 80} = 0.24$, p = 0.882; Table 2). The mean T_{set} of males (37.01 ± 0.16) was 2.02° C higher than that of females (34.9 ± 0.14; male n = 68, female n = 82; ANOVA; $F_{1, 148} < 0.0001$, $p < 0.0001$; Table 2). Male T_{set} was significantly greater than female T_{set}, after controlling for body size (ANCOVA; $F_{1, 118} = 463.03$, $p < 0.0001$).

Critical Minima and Maxima; Voluntary Maxima

Female CTmax did not differ between SPS and LLP (LLP n = 6, SPS n = 16; ANOVA; $F_{1, 19} = 1.708$, p = 0.21; Table 2), nor did female CTmin (LLP n = 6, SPS n = 14; ANOVA; $F_{1, 18} = 0.0029$, p = 0.958; Table 2). The CTmax of females (42.13 ± 0.43) was 1.2° C higher than that of males (40.93 ± 0.16; female n = 22, male n = 56; nonparametric Wilcoxon, $\chi^2 = 5.35$, p = 0.021, Table 2). The CTmin of males (19.67 ± 0.23) was 2.89° C higher than the females' (16.78 ± 0.96; male n = 56, female n = 20; nonparametric Wilcoxon, $\chi^2 = 9.38$, p = 0.0022; Table 2). Female VTmax did not differ between LLP and SPS (LLP n = 13, SPS n = 18; nonparametric Wilcoxon, $\chi^2 = 3.62$, p = 0.057; Table 2), nor did the VTmax of males (LLP n = 11, SPS n = 17; ANOVA; $F_{1, 26} = 3.71$, p = 0.065; Table 2). VTmax did not differ between males and females (male n = 28, female n = 31; ANOVA; $F_{1, 57} = 0.235$, p = 0.63; Table 2).

Thermal Opportunity and Quality of Habitats

The field-active T_b of females (35.83 ± 0.36) in LLP was 1.3° C warmer than females in SPS (34.51 ± 0.29; LLP n = 29, SPS n = 44; ANOVA; $F_{1, 71} = 0.0064$, p = 0.0032; Table 2). On average, SPS was 1° C hotter than LLP (nonparametric Wilcoxon, $\chi^2 = 9.24$, p = 0.0024). There is no significant difference between the values recorded by the iButton dataloggers and those recorded by the thermal imaging camera (nonparametric Wilcoxon; $\chi^2 = 2.4$, p = 0.121, Figure 1a). Subsequent results were calculated using the data recorded by the iButton dataloggers. The thermal quality of habitat (d_e) did not differ between LLP and SPS habitats (LLP n = 14, SPS n = 16; nonparametric Wilcoxon; $\chi^2 = 1.66$, p = 0.197; Table 3). The accuracy of thermoregulation (d_b) did not differ between females in each habitat (LLP n = 14, SPS n = 16; nonparametric Wilcoxon; $\chi^2 = 0.667$, p = 0.79; Table 3). The efficiency of thermoregulation (E) did not differ between habitats (nonparametric Wilcoxon; $\chi^2 = 0.44$, p = 0.62). The accuracy of thermoregulation did not differ between males and females (male n = 67, female n = 30; nonparametric Wilcoxon; $\chi^2 = 2.4$, p = 0.1213; Table 3).

Activity Time

NicheMapR's predicted activity time for females in each habitat aligns closely with the times individuals were captured during this study (Figure 2). Similar activity times are predicted between habitats, though females in LLP were caught within a shorter time range than females in SPS. Under a 3° C warming scenario, females in both habitat types are predicted to have activity times of similar length to present day, but these activity times will be shifted later in the day (Figure 3). Males are predicted to have longer activity times under a 3° C warming scenario (Figure 3). Currently, no habitat except scrub reaches the critical thermal limit for either sex

(Figure 4). Under future predicted conditions, both habitat types are expected to reach critical thermal limits for both sexes (Figure 1b).

Table 1: Thermal biology and habitat quality terms and definitions.

Abbreviation	**Definition**
T_e	Operative Temperature - Ambient temperatures available to an organism in a habitat at a given time
T_{set}	Set point range/ Preferred Temperature - The range of body temperatures the organism prefers to operate within; measured in the lab using a thermal gradient; the central 80% of values collected over a predetermined amount of time
T_b	Field active body temperature - Body temperature measured at time of capture in the field.
d_b	The difference between T_b and T_{set}; $d_b = 0$ if within T_{set} range; $d_b = T_b - T_{set}$ upper if T_b is greater than T_{set}; $d_b = T_b - T_{set}$ lower if T_b is less than T_{set}
d_e	The difference between T_e and T_{set}; $d_e = 0$ if within T_{set} range; $d_e = T_e - T_{set}$ upper if T_e is greater than T_{set}; $d_e = T_e - T_{set}$ lower if T_e is less than T_{set}
E	Effectiveness of thermoregulation; $E = 1 - (\overline{db}/\overline{de})$
CTmax/CTmin	Critical thermal maximum and minimum; temperatures at either end of an organism's thermal tolerance that result in loss of function and, eventually, death
VTmax	The maximum body temperature an animal will experience before it seeks shade or refuge

Table 2: Thermal preference, field active body temperature, critical thermal minimum and maximum, and voluntary thermal maximum of *Sceloporus woodi* by gravidity, habitat type, and sex (mean ± 1 SE). Sample sizes are enclosed in parentheses. Shared pairs of letters indicate significant difference ($p \leq 0.05$) between comparisons. All male values were provided in of Neel and McBrayer (2018) (with permission), except VTmax which was measured in this study.

		All	**Gravid**	**Nongravid**	**LLP**	**SPS**
F	**T_b**	35.03±0.24 (73)	34.9±2.28 (41)	35.2±1.74 (32)	35.83±0.36^{d} (29)	34.51±0.29^{d} (44)
	T_{set}	34.9 ±0.14^{a} (82)	34.2±0.16 (47)	34.7±0.19 (35)	34.8±0.19 (32)	35.1±0.15 (50)
	CTMax	42.13±0.43^{b} (22)	—	—	43.00±0.79 (6)	41.78±0.49 (16)
	CTMin	16.78±0.96^{c} (20)	—	—	16.69±1.8 (6)	16.81±1.17 (14)
	VTMax	39.43±0.29 (31)	—	—	39.92±0.45 (13)	39.08±0.38 (18)
M	**T_b**	33.6±0.2 (147)	—	—	33.7±2.37 (103)	33.5±2.73 (44)
	T_{set}	37.01±0.16^{a} (68)	—	—	37.04±1.60 (47)	39.97±1.38 (22)
	CTMax	40.93±0.16^{b} (67)	—	—	40.37±0.18 (34)	41.17±0.23 (22)
	CTMin	19.67±0.23^{c} (67)	—	—	18.9±0.32 (34)	19.9±0.38 (22)
	VTMax	39.64±0.31(28)	—	—	40.3±0.45 (11)	39.1±0.37 (17)

Table 3: Thermal quality of habitat; accuracy of thermoregulation, and efficiency of thermoregulation (mean ± 1 SE) between habitats and sexes. Sample sizes enclosed in parentheses. Data for males provided by Neel and McBrayer (2018) with permission.

	F		**M**	
	LLP	**SPS**	**LLP**	**SPS**
d_e	-1.156±0.82 (14)	-1.92±0.64 (16)	5.68±0.75 (43)	4.65±0.47 (24)
d_b	-0.124±0.26 (14)	-0.175±0.16 (16)	3.57±0.53 (43)	3.05±028 (24)
E	0.76±0.48 (14)	0.91±0.25 (16)	0.45±0.05 (43)	0.6±0.04 (24)

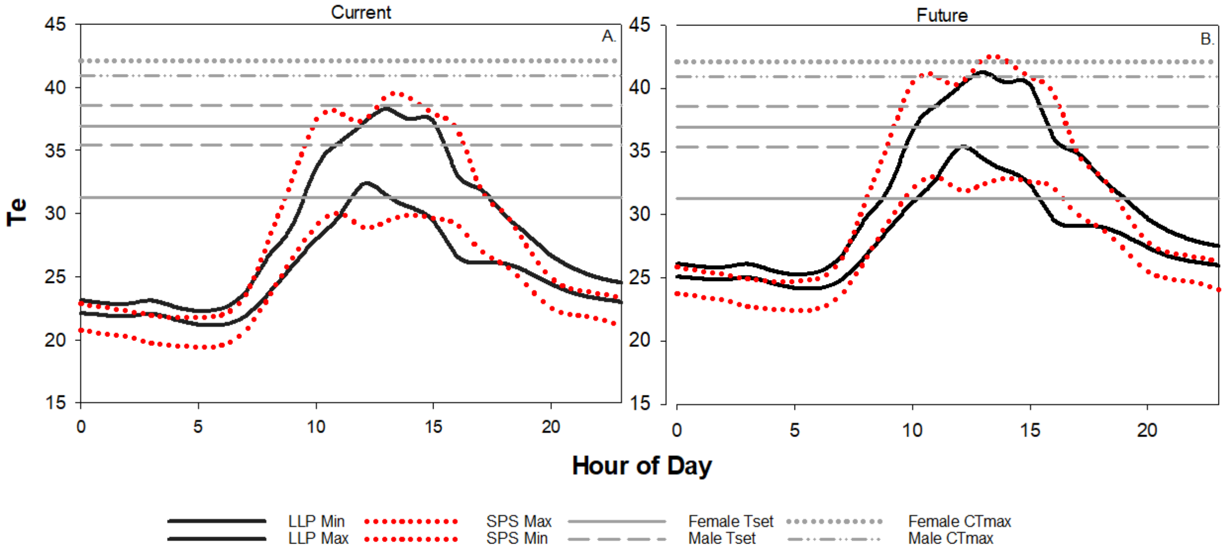

Figure 1: A. Average range of operative temperatures available in each habitat for a 24-hour period from May to July calculated from isoform data. Females are exposed to more temperatures within their preferred thermal range than males in both habitats. B. Present operative temperature data warmed 3° C to simulate potential temperatures expected 60-80 years in the future. Males are exposed to more operative temperatures within their thermal range, but both habitats more frequently reach operative temperatures at or above their critical limits than under present conditions.

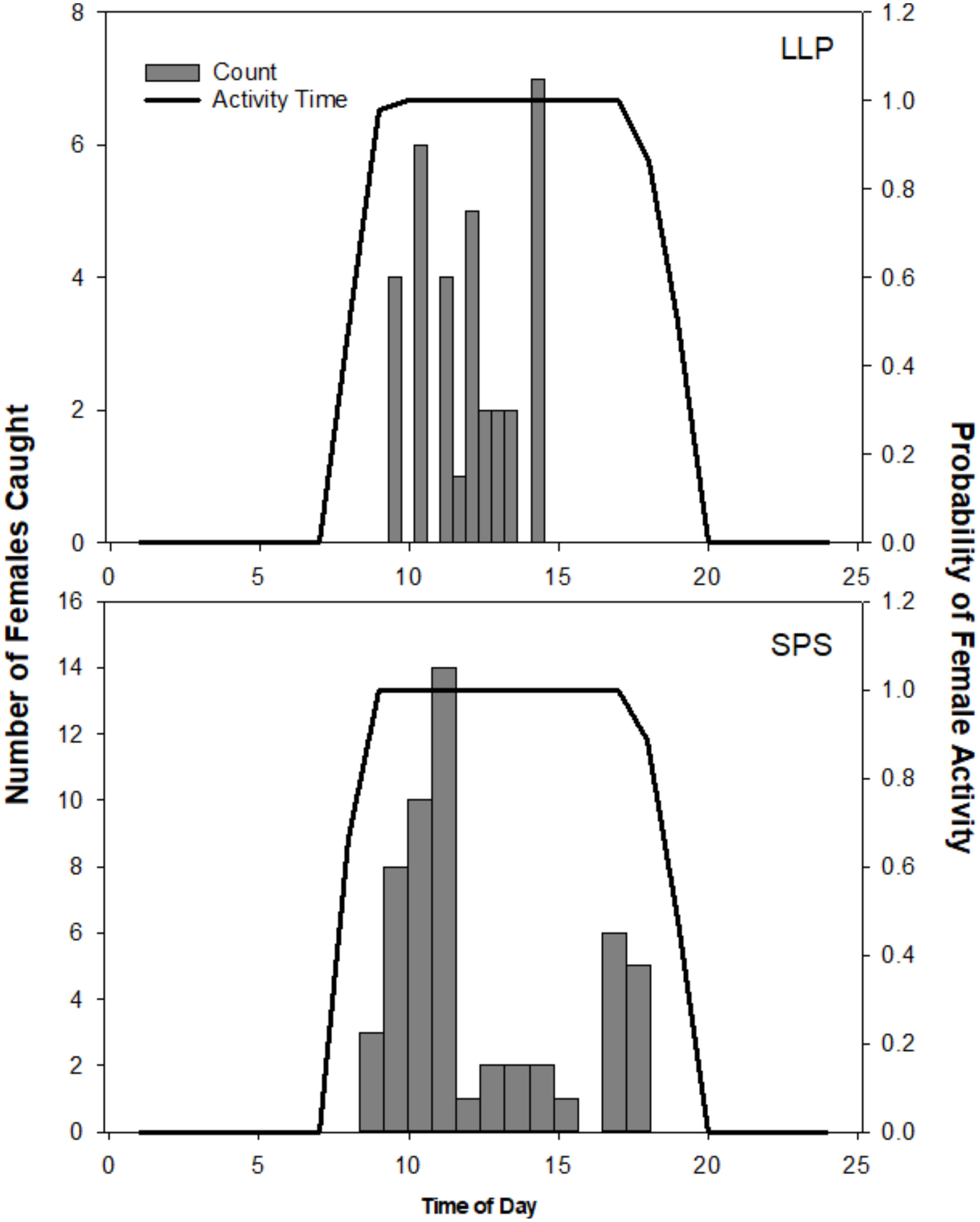

Figure 2: Female activity time estimated by NicheMapR by number of females caught in each habitat during each hour throughout the summer. Similar activity times are predicted in LLP and SPS.

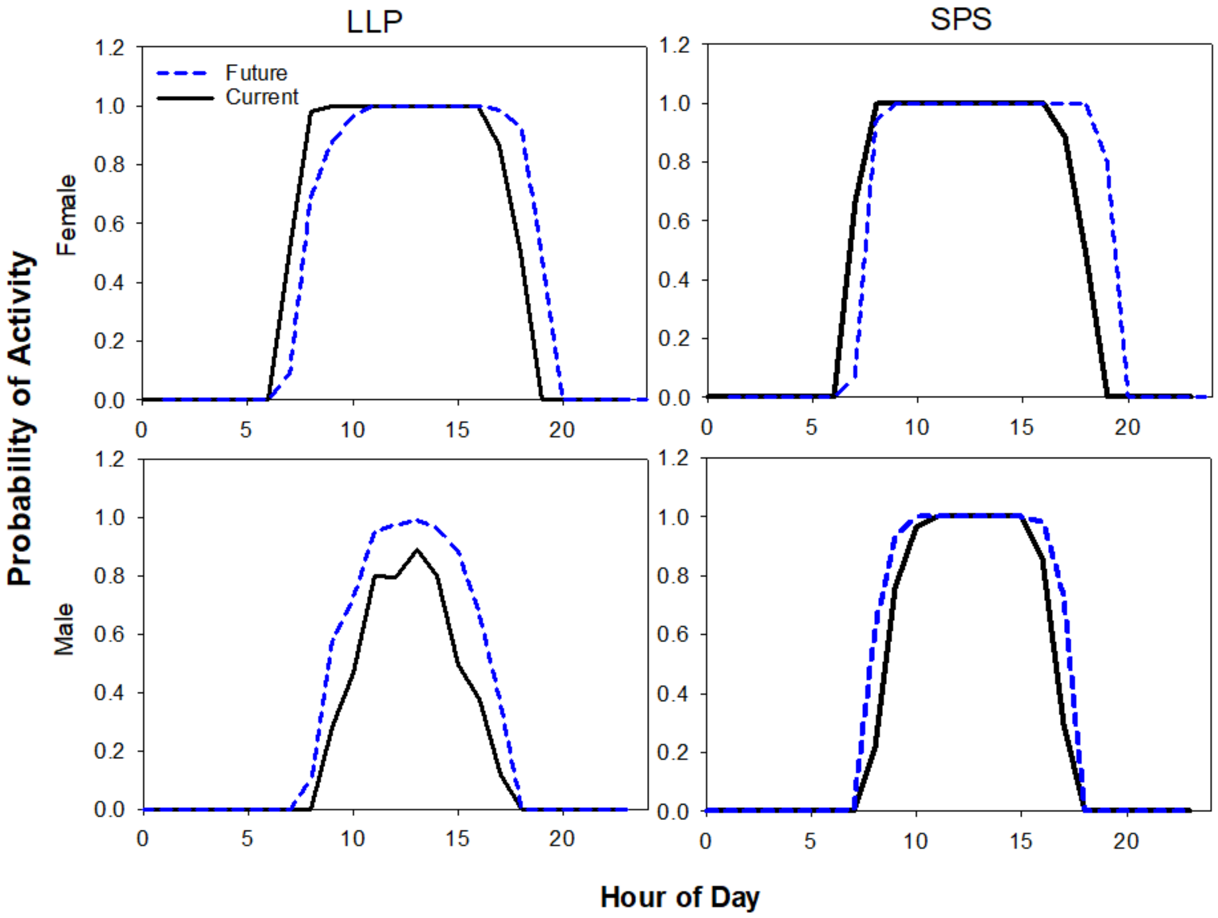

Figure 3: Current and future NicheMapR predicted activity times for each sex in each habitat. Future activity times generated under a 3° C warming scenario within the microclimate model. Females are predicted to experience a shift in activity time to later in the day in both habitats, while males are predicted to experience an increase in activity time in both habitats.

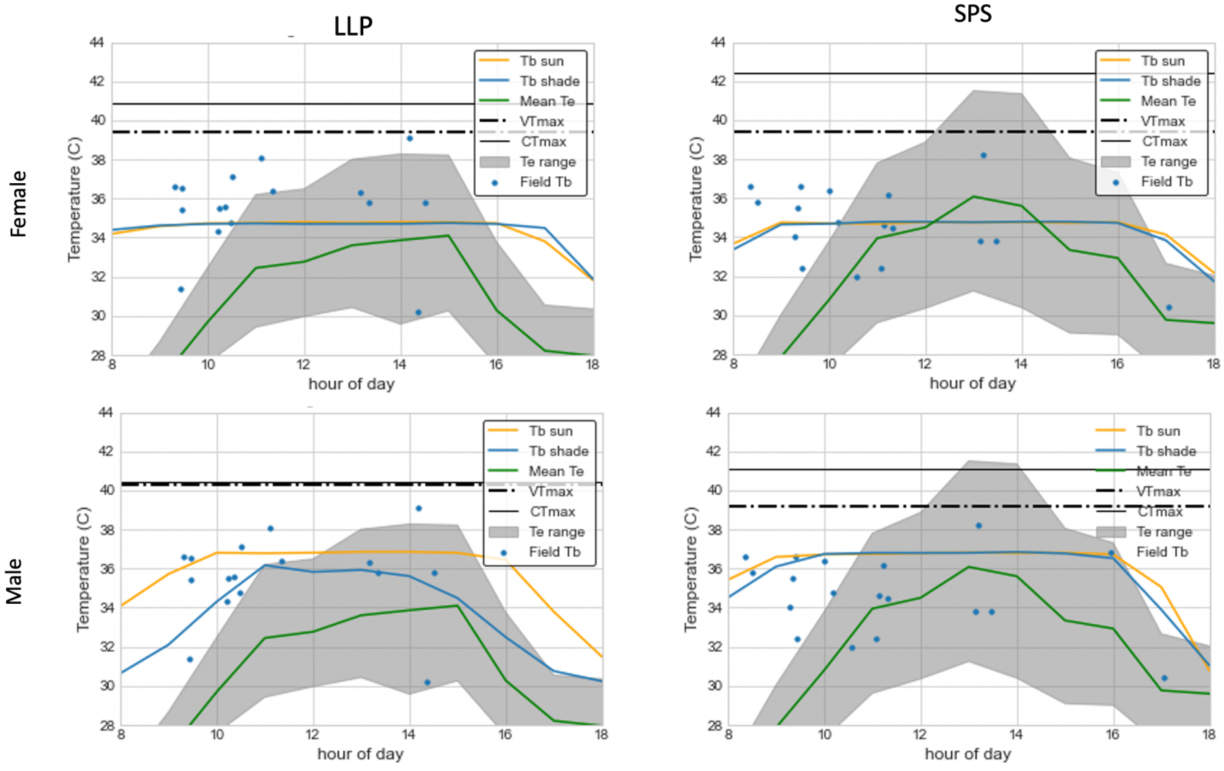

Figure 4: Top left and top right panels depict female data in LLP and SPS habitats respectively. Bottom left and right panels depict male data in LLP and SPS respectively. Solid and dotted black lines and blue dots depict empirical thermal preference data; shaded gray area depicts operative temperature range recorded by iButton dataloggers; blue and yellow lines depict NicheMapR predicted body temperatures in sunny and shady environments. Recorded operative temperatures do not reach CTmax for any sex except males in SPS habitats. NicheMapR predicted body temperatures fall within empirical field-active Tb range for females; empirical male field active Tb tended to be lower than NicheMapR predicted body temperature.

CHAPTER IV

DISCUSSION

We found sexual dimorphism in *S. woodi* thermal preference (Table 2; Figure 2). This contrasts with another recent study on *Sceloporus woodi* at a SPS site farther south that found no difference between sex and differences between gravid and non-gravid females (Gainsbury, 2020). This may be due to a difference in sample size, as our study examined three times the number of individuals as the previous. Dimorphism in thermal preference was noted to be uncommon in reptiles (Huey and Pianka, 2007), yet several studies suggest that an underlying mechanism may exist (Grant, 1990; Braña, 1993; Charland and Gregory, 1995; Mathies and Andrews, 1997; Brown and Weatherhead, 2000; Blouin-Demers et al., 2002; Woolrich-Peña et al., 2012; Beal et al., 2014; Juri et al., 2018, Logan et al., 2021). The cause of this dimorphism, when it occurs, is likely due to body size (Woolrich-Peña et al. 2012; Beal et al., 2014). In our case, we found that while body size plays a role in T_{set} dimorphism, it is not the only source of this difference. This suggests that there is some other mechanism driving thermal preference between sexes. In studies where T_{set} is linked to body size of sexually dimorphic species, the smaller sex has the higher thermal preference, as seen in males of this study (Beal et al., 2014**;** Table 2).

Field-active T_b may be higher in females in LLP because it is less risky to remain in sunny areas. Orton and McBrayer (2018) showed that *S. woodi* has lower rates of predation and are more cryptically colored in LLP. Also, LLP has more leaf litter and tree perches available than in SPS, thus LLP offers better locations for cryptic perching and reduces the risk of predation (Orton et al., 2018). Additionally, females in LLP are exposed to temperatures above their T_{set} range for a shorter portion of the day than females in SPS (Figure 2), allowing them to utilize open, sunny substrates for a longer portion of the day. Thus, the added retreat sites and enhanced crypsis in LLP may allow females to remain active at warmer temperatures. While female field-active T_b is higher than mean T_{set} in LLP, field-active body temperature is still within the T_{set} range selected by females (Figure 2). Females also exhibit a wider range of thermal tolerance than males (Table 2), which may suggest better acclimation to climate change, although both sexes are likely to experience variable environmental temperatures (Pottier et al., 2021).

Male VTmax is similar to CTmax, indicating they are willing to risk exposure to extremely unfavorable temperatures (Table 2, Figure 4). However, if male plasticity is lower and they acclimate to climate change more slowly than females, it could result in a disparity in survival between sexes, thereby generating future life history issues if fewer males survive (Pottier et al., 2021). Additionally, if males spend more time thermoregulating as they acclimate to new T_e, they will have less time for foraging, mating, etc.

NicheMapR predicts shifted activity times under a 3° C warming scenario (Figure 3), whereby female activity time is shifted an hour later in the day. Females in LLP are predicted to have a shortened activity time; however, females in SPS are predicted to have a similar activity time to present conditions. Similar activity time with higher temperatures is perhaps a limitation of the NicheMapR software, as it cannot account for the spatial distribution of microclimates in each habitat type that possess useable temperatures. Additionally, NicheMapR assumes that the lizards have access to retreat sites (or perches) which may not necessarily be the case if the habitat has been recently managed via clear cutting, as is very often the case in SPS. Sand pine scrub sites already achieve higher temperatures than LLP sites. Recently clear cut SPS sites are unlikely to provide the necessary retreat sites or perches for effective thermoregulation. In LLP, perch sites are available and vary throughout the day, so access to perches best suited for the temperatures experienced at particular temperatures is key to continuing to thermoregulate accurately (Neel and McBrayer 2018). In both LLP and SPS, lizards shift to perches as opposed to other microhabitats as the day warms, as they are cooler than terrestrial habitats (Adolph, 1990; Porter et al., 1973; Neel and McBrayer, 2018). An animal's ability to use a habitat is impacted by the distribution and accessibility of microhabitats within the habitat; if too much of a habitat is composed of unfavorably warm microclimates, this limits the space an animal can use within the habitat (Sears and Angilletta, 2015; Sears et al., 2016). Warmer microhabitats like sunny leaf litter, woody debris, or even sand currently used by *S. woodi* may become unfavorable for females in a warming climate for large periods of the day in SPS, limiting the accessibility of areas within the habitat (Rangel-Patiño et al., 2020). Females in both habitats display use of all of these substrates early in the day under current conditions. If these substrates become unfavorable earlier in the day, females will move to cooler tree perches sooner in the day than they currently do, which could have an impact their social interactions and foraging opportunities.

Predicted field-active T_b for females in both sun and shade fall within the range of empirical field active T_b in both habitats but predicted T_b for males is greater than most field active T_b at capture (Figure 4). No habitats reach the critical thermal limits of either sex, except for males in SPS (Figure 4). Interestingly, male activity time is predicted to be extended in both habitats, as they will be exposed more frequently to temperatures within their thermal preference range (Figure 3). However, the increase in temperature predicted by warming scenarios results in more of the day at or above the critical thermal temperature for both sexes. Currently, individuals of both sexes are, on average, infrequently exposed to operative temperatures at or above their critical thermal limits, resulting in unimpeded activity time on most days. The increased risk of intolerable temperatures more frequently, for longer periods of the day will result in guaranteed reduced activity times on the days where those temperatures are reached.

The risk of frequent intolerable temperatures could result in an interesting dynamic between the sexes, as females are exposed to less tolerable temperatures, while males will be better able to tolerate the higher temperatures. Previous research has shown that ectotherms cannot afford to imprecisely thermoregulate at high temperatures (Neel and McBrayer, 2018), so should females in the future be exposed to more unfavorably high temperatures, they will be forced to spend more time thermoregulating, even as males may be able to spend less time thermoregulating and devote more energy to foraging, social interactions, etc. The tradeoffs for reproduction under this condition certainly warrant further investigation, as they may not favor population persistence in certain SPS sites.

The females in ONF in both LLP and SPS display an efficiency of thermoregulation 30 percent greater than that of males in the same habitat (Table 3). Some studies have attributed more efficient thermoregulation to reproductive state, so more research is necessary to more accurately determine the reproductive status of females and what effects that may have on female thermoregulation (Mathies and Andrews, 1997; Woolrich-Peña et al., 2015).

In addition to effects between the sexes, future studies should consider the habitat requirements for egg development–it is likely that terrestrial habitats may become too hot for proper egg development, despite the adult ability to survive and reproduce (Sun et al., 2021). Since offspring survival is linked to size at hatching and temperatures experienced during development influence speed of development and offspring size, more research is required into the thermal requirements and tolerance of *S. woodi* embryos to determine the reproductive effects that these warming climates may have based on temperatures experienced pre- and postoviposition (Sinervo, 1990; Damme et al., 1992; Booth, 2006; Radder et al., 2008; Lorioux et al., 2013; Dayananda et al., 2017).

Conclusion

This study found that while predicted activity times may not decrease, both sexes will face increased risk of reaching critical thermal temperatures in both habitats. These results have implications for how we consider ectothermic organisms' responses to climate change—variable responses to the same changes in a habitat could result in differential survival between sexes, or even shifts in activity time that could impact species reproduction as physiological demands between sexes are altered. These implications are especially relevant for species with small ranges or those that live in threatened habitats since they not only have to compete with wide-spread species, but also have less habitat in general in which to respond to environmental changes. These implications extend beyond ectothermic species to any rare species that also live in rare habitats. When implementing management practices for these habitats and species, this study demonstrates the likely interplay between climate change and the impacts of management decisions.

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