Integrating Spatial Constraints and Biotic Interactions to Assess the Costs of Thermoregulation by Lizards

by

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ABSTRACT

Many animals thermoregulate to maximize performance. However, interactions with other animals, such as competitors or predators, limit access to preferred microclimates. For instance, an animal may thermoregulate poorly when fighting rivals or avoiding predators. However, the distribution of thermal resources should influence how animals perceive and respond to risk. When thermal resources are concentrated in space, individuals compete for access, which presumably reduces the thermoregulatory performance while making their location more predictable to predators. Conversely, when thermal resources are dispersed, several individuals can thermoregulate effectively without occupying the same area. Nevertheless, interactions with competitors or predators impose a potent stress, often resulting in both behavioral and physiological changes that influence thermoregulation. To assess the costs of intraspecific competition and predation risk during thermoregulation, I measured thermoregulation, movement, and hormones of male lizards (*Sceloporus jarrovi*) in experiment landscapes, with clumped to patchy distributions of microclimates. I found lizards aggressively competed for access to microclimates, with larger males gaining priority access when thermal resources were aggregated. Competition reduced thermoregulatory performance, increased movements, and elevated plasma corticosterone in large and small males. However, the magnitude of these responses decreased as the patchiness of the thermal environment increased. Similarly, under simulated predation risk, lizards reduced thermoregulatory performance, decreased movements, and elevated plasma corticosterone. Again, with the magnitude of these responses decreased with increasing thermal patchiness. Interestingly, even without competitors or predators, lizards in clumped arenas moved greater distances and circulated more corticosterone than did lizards in patchy arenas, indicating the thermal quality of the thermal landscape affected the energetic demands on lizards. Thus, biologists should consider species interactions and spatial structure when modeling impacts of climate change on thermoregulation.

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CHAPTER ONE:

Introduction

Thermoregulation is an adaptation adopted by nearly all organisms to optimize various performance traits (Bogert 1949, Seebacher 2005, Angilletta 2009). Not surprisingly, scientists have studied the impacts of temperature for over half a century (Weese 1917, Smith 1929, Cole 1943, Cowles and Bogert 1944). However, standard methods for quantifying costs and predicting patterns of thermoregulation are still quite limited. For instance, many thermal biologists rely on the indice of d_e to describe the thermal quality of a habitat, which equals the difference between the mean of operative environmental temperatures and an animal's preferred temperature (Hertz et al. 1993). Although this indice captures a frequency distributions of operative temperatures, using either mathematical or physical models (Porter et al. 1973, Bakken and Gates 1975, Dzialowski 2005, Denny and Harley 2006), it fails to account for the spatial distribution of operative temperatures (Angilletta 2009, Sears and Angilletta 2015). In fact, there can be many spatial distributions for any frequency distribution that all result in the same value of d_e! Thus, it is not surprising that use of d_e to assess thermoregulatory costs in natural environments produces inconsistent results (Christian and Weavers 1996, Blouin-Demers and Nadeau 2005, Herczeg et al. 2006), which likely lead to erroneous measures of energetics (Sears 2006, Sears and Angilletta 2015).

A similar but more sophisticated method of predicting costs of thermoregulation is through mechanistic modeling. With these models, researchers link environmental conditions such as temperature to biological processes (Kearney and Porter 2004, Buckley 2008, Kearney and Porter 2009, Buckley et al. 2010, Maino et al. 2016), which then define thermal constraints on activity, survivorship, or fecundity (Adolph and Porter 1993, Bowler et al. 2017, Levy et al. 2017). However, a general assumption of existing mechanistic models is that if favorable microclimates exist, animals will access them at no cost (Buckley 2008, Kearney and Porter 2009, Buckley 2010, Elith et al. 2010, Leroux et al. 2013). In reality, however, many factors impose a cost of thermoregulation (Huey and Slatkin 1976b, Angilletta 2009). In general, lizards thermoregulate more effectively when thermal resources are patchily distributed compared to when they are clumped (Sears et al. 2016, Basson et al. 2017), which likely affects energetic costs (Sears and Angilletta 2015, Basson et al. 2017). And the presence of competitors or predators may limit access to desired microclimates. For instance, mate guarding or predator avoidance may prevent individuals from shuttling between sun and shade patches needed for effective thermoregulation (Skelly 1994, Polo et al. 2005, Webb and Whiting 2005, Ancona et al. 2010). Thus, biologists should consider species interactions and spatial structure when modeling costs of thermoregulation.

To further complicate matters, the distribution of thermal resources should influence how animals perceive and respond to risk. When thermal resources are concentrated in space, individuals compete for access (Regal 1971, Magnuson et al. 1979, Rusch and Angilletta 2017), which presumably reduces the thermoregulatory performance and makes their location more predictable to predators (Mitchell and Lima 2002). Conversely, when thermal resources are dispersed, several individuals can thermoregulate effectively without occupying the same area. Nevertheless, interactions with competitors or predators impose a potent stress, often resulting in both behavioral and physiological changes that likely influence thermoregulation (Greenberg and Crews 1990, Summers 2002, Polo et al. 2005, Preest and Cree 2008).

Study Species

Yarrow's spiny lizards (*Sceloporus jarrovi*) are a montane species located in southeast Arizona, southwest New Mexico, and north central Mexico. The lizards used in these studies were from the Chiricahua Mountains in southeast Arizona (~ 1500-2500 m) and ranged in size from 12-37 g. These lizards exhibit a strong thermal preference (~ 34.0 ± 1.4 °C) when isolated in a thermal gradient (Schuler et al. 2011, Sears et al. 2016, Rusch and Angilletta 2017) and do not show adverse thermoregulatory effects of implanted temperature logger (Sears et al., 2016; Rusch et al., 2017). Males are highly territorial and aggressive towards conspecifics during breeding season (Ruby 1978) and avoid predators by hiding in refuges (Cooper 2008, Cooper and Avalos 2010). Thus, these lizards make an ideal study organism when examining how abiotic and biotic factors influence thermoregulation.

Dissertation Summary

The aim of my dissertation was to assess the thermoregulatory costs of intraspecific competition and predation risk. I measured thermoregulation, movement, and hormones of male lizards (*Sceloporus jarrovi*) in experimental landscapes with clumped and patchy distributions of microclimates.

In chapter 2, I examined whether the presence or size of a conspecific affected thermoregulation and hormones of lizards in laboratory arenas with a single heat source. I measured body temperatures, movements, corticosterone, and testosterone of lizards both when in isolation and when paired with a conspecific.

In Chapter 3, I examined whether the presence or size of a conspecific interacted with the distribution of thermal resources to affect movements, aggression, and hormones of lizards. To manipulate the thermal environment, I used large, outdoor arenas (400 m^2) with three distinct distributions of shade; 1 large patch (12 x 12 m), 4 medium patches (6 x 6 m), or 16 small patches (3 x 3 m). I then exposed lizards to one thermal treatment both when isolated and paired with a conspecific. I recorded spatial positions, scored aggression, and measured corticosterone and testosterone of lizards both when in isolation and when paired with a conspecific.

In chapter 4, I examined how a simulated predation risk interacted with the distribution of thermal resources to affect movements, thermoregulation, and glucocorticoids of lizards. I exposed isolated lizards either to control treatments (no risk) or predation treatments in the same arenas used in chapter 3 (described above). However, lizards only experienced one of two thermal environments; 1-patch and 4-patch designs. I recorded spatial positions, body temperatures, and plasma corticosterone of lizards.

CHAPTER TWO:

Competition during thermoregulation altered the body temperatures and hormone levels of lizards

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Abstract

Every organism must thermoregulate to maximize its performance, but competing organisms limit access to preferred microclimates. Such competition often creates hierarchies in which dominant individuals have more access to limited resources than subordinate individuals. To assess the costs of competition during thermoregulation, I measured thermoregulation, movement, and hormones of male lizards (*Sceloporus jarrovi*) when alone and when paired with a smaller or larger conspecific. Large males were 31% closer to the heat source when paired than when alone, resulting in a higher mean body temperature (35.7°C vs. 33.9°C). Conversely, small males were 40% farther from the heat source when paired, resulting in lower mean body temperature (32.1°C vs. 33.6°C). When paired, large and small males to circulate 26% and 44% more corticosterone, respectively. Conversely, large males circulated 26% more testosterone when paired, while small males circulated 26% less testosterone. Both dominant and subordinate males incurred costs when paired, including poorer thermoregulation, more movement, and greater physiological stress. Thus, competition for thermal resources should feature more prominently in ecological and evolutionary models of thermoregulation.

Introduction

In many species of animals, individuals compete aggressively to secure access to limited resources (Trivers 1976, Chase et al. 2002, Sapolsky 2005, Wilson et al. 2007). Winning competitive interactions enhances growth, survival or reproduction, but also costs energy and imposes risk (Maynard Smith and Harper 2003). Thus, when competition persists, individuals establish dominance hierarchies that minimize the need for costly aggression (Barnard and Burk 1979, Chase et al. 2002, Tattersall et al. 2012). Within a dominance hierarchy, an individual's position depends on phenotypes (e.g., size, speed, or color) that presumably signal its ability to compete (Garland Jr et al. 1990, Maynard Smith and Harper 2003, Senar 2006). In turn, social rank alters behavior and physiology, especially in subordinates (Leshner 1975, Greenberg and Wingfield 1987, Sapolsky 2002), because higher ranking individuals gain greater access to resources (Barnard and Burk 1979, Downes and Shine 1998, Sapolsky 2005). In this way, social dominance enhances growth, survival, or reproduction (Emlen and Oring 1977, Petren and Case 1996, Ybarrondo and Heinrich 1996), ultimately conferring greater fitness to dominant individuals (Defries and McClearn 1970, Schuett 1997, Koenig 2002).

Although competition for food or mates has received the most attention (Schoener 1982, Andersson 1994, Wiley and Poston 1996, Wong and Candolin 2005), animals also compete for microclimates needed to regulate temperature and hydration (Magnuson et al. 1979, Schoener 1983a, Valeix et al. 2008). In cold environments, rare sources of heat enable individuals to elevate their temperature and improve performance (Donkoh 1989, Angilletta 2001, Rojas et al. 2012). In hot environments, rare sources of shade enable individuals to stay cool and conserve water (Kearney et al. 2009, Sears and Angilletta 2015, Sears et al. 2016). Since preferred microclimates occur heterogeneously in space, dominant individuals can exclude others from desirable microclimates (Magnuson et al. 1979, Downes and Shine 1998, Žagar et al. 2015). Connell's (1961) classic study of barnacles illustrates the advantage of monopolizing certain microclimates; the dominant species occupied cooler and wetter sites, forcing the subordinate species to occupy sites that reduced growth, reproduction, and survival. Alternatively, some species of ants leave their nests only during hot periods of the day to avoid aggression from dominant species during cooler periods of the day. Activity during hot periods may reduce locomotor performance but enhances foraging and survival (Cerda et al. 1998, Albrecht and Gotelli 2001). Within a species, competition for microclimates leads to territoriality, whereby dominants exclude subordinates from their territories. Consequently, subordinates thermoregulate less effectively and exhibit more stress when territoriality prevents them from accessing preferred microclimates (Beitinger and Magnuson 1975, Downes and Shine 1998, Summers 2002).

To quantify costs of competition for thermal resources, I studied male spiny lizards (*Sceloporus jarrovi*) when paired with a larger or smaller conspecific. These lizards shuttle between sun and shade to regulate body temperature in artificial and natural settings (Mathies and Andrews 1997, Schuler et al. 2011, Sears et al. 2016). During the breeding season, large males exclude small males from their territories, ensuring exclusive access to more space and thus more resources (Simon 1975, Ruby 1978, Moore 1987). As territorial behavior of males increases throughout the season, so do circulating levels of corticosterone and testosterone (Moore 1986). These hormones influence a variety of behaviors, but typically have opposing effects. For example, testosterone often increases aggression and activity, while corticosterone reduces these behaviors (Moore 1988, DeNardo and Sinervo 1994, Schuett et al. 1996, Haenel et al. 2003). In some experiments, artificially elevated levels of corticosterone caused lizards to bask more frequently and prefer higher temperatures compared to controls (Belliure and Clobert 2004, Preest and Cree 2008). By measuring the movements, temperatures, and hormones of males in artificial thermal arenas, I tested hypotheses about the costs and benefits of dominance when thermal resources were rare. When lizards were paired, I expected the larger individual to access thermal resources more frequently and thermoregulate more accurately and more precisely compared to small lizards. I also expected the smaller individual to experience greater physiological stress during competition compared to large lizards, reflected by lowered testosterone and elevated corticosterone circulating in plasma (Greenberg and Crews 1990, Schuett et al. 1996).

Methods

Collection and husbandry of animals

In August of 2012, I collected 24 adult males of *Sceloporus jarrovi* in the Chiricahua Mountains of Arizona (1500-2500 m). After capture, lizards were transported to the

Sevilleta Field Station in New Mexico. Upon arrival, lizards were weighed (mean ± SD = 26.2 ± 4.0 g) and toe-clipped for identification (Perry et al. 2011).

Lizards were housed individually in plastic terraria (30 x 26 x 13 cm) lined with paper towels. Terraria were heated from below at one end to create a thermal gradient, thus allowing lizards to freely thermoregulate. The operative environmental temperatures along this gradient ranged from 23° to 42°C, as determined by hollow copper models of a lizard (Bakken and Gates 1975). Cardboard was placed between each terrarium to prevent lizards from viewing each other. Every other day, lizards were provided water and fed adult crickets (*Acheta domestica*) and larval beetles (*Tenebrio morio*) coated with a powder of vitamins and calcium (Rep-Cal, Los Gatos, CA, USA). Animals were maintained this way for two weeks before our experiment. Four lizards that refused to eat regularly were excluded from the study.

Preferred body temperatures

I measured the preferred body temperatures of lizards in artificial thermal gradients following the methods of Schuler and colleagues (2011). These measurements enabled me to establish that lizards would thermoregulate in our arenas and determine the temperatures that they prefer. Thermal gradients were created in plastic containers (112 x 35 x 30 cm) with a substrate of sand (~1 cm deep). These containers were kept in a room at 20 °C and uniformly illuminated from above by fluorescent lights. A 150-W infrared lamp (Exo-Terra, Mansfield, MA, USA), suspended above one end of each container, created a range of operative temperatures from 22° to 44°C. This type of gradient works well for lizards that thermoregulate by basking under natural conditions and forces the lizard to periodically retreat from the infrared lamp to avoid overheating (Angilletta 2009, Schuler et al. 2011).

Each lizard was placed in a thermal gradient at 2000 h, when infrared and fluorescent lights were off. The following morning, fluorescent and the infrared lights were turned on at 0600 and 0700 h, respectively, and were turned off at 2000 and 1700 h, respectively. On this day, lizards explored the thermal gradient undisturbed. On the next day, the bulbs were activated for the same periods, and body temperatures were recorded every 2 h between 0800 and 1600 h. To measure body temperature, each lizard was captured by hand and a quick-reading thermometer (T-4000, Miller & Weber, Inc., Queens, NY) was inserted in its cloaca. During the 44 h that each lizard spent in a thermal gradient (36 h of habituation and 8 h of measurements) no food or water was provided. Based on a previous study, we do not expect that preferred body temperatures of *S. jarrovi* would have differed if food and water were provided (Schuler et al. 2011). After these measurements, each lizard was returned to its terrarium, during which food and water were offered every other day.

Implantation of temperature loggers

Five days after measuring preferred body temperatures, I surgically implanted a miniature temperature logger (1.43 ± 0.05 g; Weedot, Alpha Mach, Inc., Qc, Canada) into the abdominal cavity of each lizard. Each logger was programmed to record temperature at a 10-minute interval for the duration of the experiment. To exclude fluids, loggers were coated first with a plastic sealant (Plasti Dip, Plasti Dip International, Blaine, Minnesota, USA) and then with paraffin wax (Gulf Wax, Kalton, Ohio, USA). Surgical procedures followed those of Sears and colleagues (2016). Two weeks after surgery, I re-measured preferred body temperatures, as described above, to see whether the surgery affected thermoregulation. The mean and standard deviations of preferred body temperature estimated from statistical modeling (see *Statistical analyses*) were virtually identical: 34.0 ± 1.4 °C before surgery and 34.0 ± 1.4 °C after surgery. Furthermore, no individual showed a large change in preferred body temperature (see Appendix; Fig. S2.1).

Experimental design and treatments

I recorded the body temperatures of male lizards when isolated and when paired with a larger or smaller conspecific. Observations were made in the same thermal gradients with the same diel cycles of fluorescent light and infrared light used to measure preferred body temperatures. Time-lapse cameras (Plant Cam, EBSCO Industries, Inc., Birmingham, Alabama, USA) were positioned 2 m above the gradients to capture the spatial positions of lizards every 5 min. A small plastic shelter, measuring 14 x 14 x 4 cm, was placed on the cooler side of the gradient to provide refuge from aggression.

I paired lizards according to mass, predicting that a large lizard would dominate thermal resources (i.e., heat lamp) when paired with a small lizard (Regal 1971, Ruby 1978, Downes and Shine 1998). Three weeks after surgeries, I weighed the lizards and divided them into two groups: the10 heaviest lizards (large) and the 10 lightest lizards (small). Mean masses of large and small lizards were 29.5 ± 2.1 g and 23.1 ± 2.6 g, respectively.

Then, lizards were paired according to their relative mass in each group; the heaviest lizard in the large group was paired with the heaviest lizard in the small group, and so on. The mean difference in mass between paired lizards was 6.4 ± 1.5 g.

Each pair was randomly assigned to one of two treatment orders: 1) isolation followed by competition, or 2) competition followed by isolation. Prior to experiments, lizards were given 48 h to habituate to a thermal gradient in isolation. After this period, half of the lizards were paired in a single gradient (competition treatment) and half were left alone (isolation treatment). Body temperatures and spatial positions were recorded from 0800 to 1700 h for the next two days. Because one lizard escaped from its arena, its pair was excluded from analyses.

Following the first treatment, I sampled blood from each lizard to measure circulating levels of corticosterone and testosterone. This sample was taken on the morning after the first treatment (0900-0930 h). Each lizard was captured by hand and ~50 µL of blood was collected in a capillary tube by rupturing the orbital sinus. Once filled, each tube was sealed with Critoseal (Fisher Scientific, Pittsburgh, Pennsylvania, USA) and stored on ice. Blood samples were centrifuged within 1 h to separate red blood cells from plasma. Once separated, plasma was stored at -80 °C until assayed (see below). Blood samples were collected within 2 min of capture to minimize effects of handling stress on circulating corticosterone (Langkilde and Shine 2006). After bleeding, lizards were returned to terraria with food and water for 7 days. Following this period, the entire procedure was repeated, except that lizards in the competition treatment were switched to the isolation treatment, and vice versa (see Appendix; Table S2.1 for a diagram of events). At the end of the experiment, I had body temperatures, spatial positions, and blood samples for each lizard in isolation and in competition.

Video analysis

I analyzed the time-lapse photos to estimate the mean distance from the heat lamp and the total movement by each lizard throughout the experiment. For each photo, a Cartesian coordinate system was applied with computer software (Tracker, version 4.90, Douglas Brown). Then, I used triangulation to measure the distance between the lizard’s body, at the base of neck between the shoulder blades, and the center of the heat lamp. Similarly, the distances between successive positions were summed to estimate the total distance moved. Positions were analyzed between 0800 and 1700 h, as were recorded body temperatures (see *Statistical analyses* below).

Hormone assays

For each blood sample, I quantified total plasma concentrations (both free and bound fractions) of corticosterone and testosterone. Hormones were measured using commercial enzyme-linked immunoassay kits (Enzo Life Sciences, Farmingdale, NY). Samples were analyzed in duplicate on the same day, following instructions supplied with the kit. The assays were validated with standard curves, constructed from separate serial dilutions for corticosterone and testosterone (Fokidis et al. 2009). There were no differences between the slopes of a curve produced by serial plasma dilution for corticosterone (4- to 64-fold) or testosterone (8- to 200-fold) and a standard curve for each hormone. This approach enabled us to determine the appropriate dilutions for testing our samples, which was 32-fold for corticosterone and 128-fold for testosterone. Diluted samples were distributed randomly within a 96-well plate for each hormone. The sensitivities of these assays were 32.02 pg ml^{-1} for corticosterone and 7.81 pg ml^{-1} for testosterone. Mean coefficients of variation within assays were 5.04% for corticosterone and 8.80% for testosterone (n = 2 plates with 36 samples each; one plate for corticosterone and one plate for testosterone).

Statistical analyses

I analyzed two types of statistical models. The first type was designed to see whether my method of surgically implanting a temperature logger altered the preferred body temperature of a lizard. The second type was designed to quantify effects of competition on variables of interest: body temperature, distance from heat lamp, total distance moved, and hormone concentrations.

Each analysis included a mixture of fixed, continuous, and random factors. When modeling preferred body temperature, we treated measurement period (pre-surgery or post-surgery) as a fixed effect, body mass (g) and time of day (h) as covariates, and the identity of the lizard as a random intercept. For the remaining analyses, I included three fixed factors: social rank (dominant or subordinate), treatment (isolation or competition), and treatment order (paired then alone, or alone then paired). Temporal block (1 or 2) and body mass (g) were covariates. The identity of the lizard was a random intercept. Because body temperature was measured multiple times within a treatment, I included day of trial (1 or 2) as an additional covariate. Finally, I included a correlation structure for time of day, which accounted for similarities between temperatures or positions recorded closely in time.

When testing hypotheses about competition, I considered the accuracy and the precision of thermoregulation. The accuracy of thermoregulation was estimated by comparing mean body temperatures during experiments to measures of preferred body temperatures taken before experiments. The precision of thermoregulation was estimated from the standard deviation of body temperature for each combination of competition treatment and social rank; a smaller standard deviation would imply that a specific rank of lizards thermoregulated more precisely in a given treatment.

Multimodel inference was used to estimate the most likely values of means and standard deviations. We used the full-average method, in which a parameter was considered zero when the factor did not appear in a model (Burnham and Anderson 2002). First, I used the procedure described by Zuur et al. (2009) to determine the most likely random component of the model. Then, I used the *nlme* library (Pinheiro et al. 2012) and the *MuMIn* library (Bartoń 2013) of the R Statistical Software (R-Core-Team 2015) to fit all possible models of fixed effects and to calculate the Akaike weight of each model (see Appendix; Tables S2.2-S2.6). The Akaike weight estimates the probability that a model describes the data better than other models. Finally, I used Akaike weights to calculate a weighted average of each parameter. The resulting values of parameters were used to calculate the most likely mean for each treatment level (see Appendix; Tables S2.7-S2.11). This approach eliminates the need to interpret *P* values, because all models (including the null model) contributed to the most likely value of each mean.

Results

When paired, both large males and small males used space differently and thermoregulated less accurately than when alone. As predicted, small males remained an average of 40% farther from the heat source (9.1 ± 6.8 cm; Fig. 2.1) when paired with large males. By contrast, large males were 31% closer, on average (8.9 ± 3.8 cm) when paired. Consequently, both large and small males thermoregulated less accurately (Fig. 2.2). Large males had a mean body temperature of 35.7°C, which exceeded the mean preferred temperature of 34.0 ± 1.4°C. Small males had a mean body temperature of 32.1°C, which fell below the preferred temperature (Fig 2.2). Surprisingly, only large males decreased their precision of thermoregulation, displaying a greater standard deviation of body temperatures during competition treatment (3.7°C vs. 3.2°C), whereas small males exhibited similar standard deviations during isolation and competition (2.5°C and 2.4°C, respectively). Despite these opposing shifts in body temperature, both large males and small males moved greater distances when paired than when alone (Fig. 2.3).

Both large males and small males experienced physiological responses to the presence of a conspecific male. The mean circulating concentration of corticosterone was greater after competition than after isolation for all lizards (Fig. 2.4), but this effect was almost twice as strong for small males than for large males (44% increase vs. 26% increase). Additionally, the competition treatment altered circulating concentrations of testosterone, but in opposite directions between ranks. Large, dominant males increased their mean circulating testosterone by 26%, while small, subordinate males decreased their mean circulating testosterone by 26% (Fig. 2.5). Because circulating testosterone varied considerably among individuals, the estimated magnitudes of these effects should be interpreted cautiously.

Discussion

Consistent with my theoretical perspective, male lizards competed for limited thermal resources, altering thermoregulatory performance according to social rank. Surprisingly, however, dominant males thermoregulated less accurately and less precisely than did subordinate males during competition, presumably by overexploiting limited thermal resources. On average, the larger male in a pair remained closer to the heat source and thus exceeded preferred temperatures more frequently (lower accuracy of thermoregulation), resulting in a broader range of body temperatures (lower precision of thermoregulation). In fact, dominant males often warmed well beyond their preferred range of temperatures (see Fig. 2.2), presumably while defending a heat source, sometimes approaching the mean critical thermal maximum for the species (41.0 ± 1.3 ºC; T. W. Rusch, unpublished). Thus, larger lizards pushed themselves to their thermal limits during competition. This result accords with an unreplicated observation by Regal (1971), who noticed that a male lizard fixated on a source of heat in the presence of another male, and then basked less after the intruder was removed. More recently, Downes and Shine (1998) reported that larger geckos occupied warm burrows in the evening, forcing smaller geckos to rest under cooler rocks or remain on the surface. Similar patterns have been documented for fish when competing for access to thermal resources in heterogeneous waters (Beitinger and Magnuson 1975, Beitinger and Fitzpatrick 1979, Magnuson et al. 1979). For example, small male bluegills were forced to occupy cooler or warmer water than preferred when paired with a large male (Beitinger and Magnuson 1975, Beitinger et al. 1975). Fish incur little risk of overheating through dominance, because water warms slowly throughout the day. However, terrestrial animals such as lizards experience rapid changes in environmental temperatures throughout the day, which creates a potential physiological cost of guarding a heat source.

For dominance to be adaptive during thermoregulation, the net benefit of high temperatures experienced by a dominant male must outweigh the net benefit of low temperatures experienced by a subordinate male. Although high temperatures increase energy expenditure and water loss (Congdon et al. 1979), they might simultaneously enhance sensory and locomotor performances (Huey 1982a, Angilletta et al. 2002). Access to thermal resources could help a male attract mates, which would explain why large lizards monopolized the heat source in the presence of a smaller conspecific. By contrast, subordinate males likely saved energy but might have captured prey or evaded predators less effectively (Bennett 1980, Angilletta 2001, Angilletta et al. 2002). However, small males likely endured a minimal loss of performance because rates of performance decline gradually when a lizard drops below its optimal temperature (Huey and Stevenson 1979, Martin and Huey 2008). And by giving up regular access to heat, a small male probably avoided aggression from a larger competitor, minimizing its loss of energy and risk of injury. Because dominant males periodically left the area under the infrared lamp, small males could attain preferred body temperatures some of the time (see Fig. 2.2).

Most males moved more in the presence of a competitor, likely because of aggressive interactions around the thermal resource. Although we did not quantify aggression, dominant males frequently paced and displayed to subordinates, occasionally leading to chasing and fighting. Such behaviors are expected when a lizard defends a resource from a competitor (Greenberg and Crews 1990, Žagar et al. 2015). Aggressive interactions over thermal resources have been documented in crocodiles (Seebacher and Grigg 2000). Small crocodiles emerged from cool waters to bask but were chased back into water by larger males. Consequently, small crocodiles could not warm to their preferred body temperature before fleeing, and returned to land less frequently afterward. Presumably, these ectotherms compete for thermal resources for the same reason that lizards in our study did: by preventing a subordinate from accessing a limited thermal resource a dominant male gains a physiological advantage that enables him to monopolize food, space, and mates. However, the small spatial scale of our thermal arenas might have exaggerated the impact of aggression, because a subordinate male could not escape the range of the dominant male. Indeed, small lizards spent time along the edges of the arenas, attempting to escape by jumping. This behavior surely affected the thermoregulatory performance of lizards, because they could not simultaneously thermoregulate and avoid aggressive interactions. Other studies in artificial environments revealed minimal effects of competition for thermal resources, even when a subordinate could not escape the presence of a dominant. For example, *Anolis bimaculatus* outcompeted *Anolis wattsi* for perch sites, forcing the *A. wattsi* to occupy hotter microclimates; however, *A. wattsi* did not grow slower, reproduce less, or eat different prey (Rummel and Roughgarden 1985). Similarly, large skinks excluded small ones from optimal microclimates, but the smaller skinks still maintained preferred temperatures by shuttling between other microclimates (Langkilde et al. 2005). Thus, the structure and complexity of the thermal landscape likely plays a role in thermoregulatory performance (Sears et al. 2016), with more complex environments potentially ameliorating the negative thermoregulatory effects of competition. Nonetheless, males of *S. jarrovi* in natural environments establish territories around the home ranges of females (Ruby 1978). Thus, territories of multiple males often overlap with that of a single female when she is receptive to mating. This spatial arrangement leads to regular aggressive interactions during the breeding season, especially in high density populations (Ball and Wingfield 1987, Marler and Moore 1988).

Competition for thermal resources should stress dominant and subordinate males disproportionally, as does competition for other resources (Greenberg and Crews 1990, Blanchard et al. 1995, Schuett et al. 1996). Compared to dominant males, subordinate males often circulate more corticosterone following aggressive interactions (Greenberg et al. 1984, Blanchard et al. 1993, Sapolsky 2002). This hormonal state can be beneficial, as elevated corticosterone mobilizes energy and has positive effects on metabolism (Sapolsky et al. 2000, Sapolsky 2002, Summers 2002). For instance, side-blotched lizards (*Uta stansburiana*) displayed greater stamina, slower resting metabolism, and faster recovery from anaerobic activity when corticosterone was elevated experimentally (Miles et al. 2007). If the same responses occur in *S. jarrovi*, elevated corticosterone during competition could enhance an individual's stamina for fighting or fleeing, as well as its recovery from this activity. Furthermore, a slower metabolism from elevated corticosterone would conserve energy and potentially enhance survival during the breeding season, a time when males patrol territories more frequently and forage less frequently (Simon 1975, Ruby 1978). Conversely, elevated levels of corticosterone can impose costs, such as reduced aggression or courtship. For example, Schuett and colleagues (1996) found that male copperheads (*Agkistrodon contortrix*) circulated more corticosterone after staged fights, with losers increasing more than winners. However, only losers ceased displaying to both rival males and receptive females, often retreating to a corner of the terrarium. Thus, submissive behaviors of subordinate male *S. jarrovi* possibly resulted from the circulating concentration of corticosterone reaching a threshold, which dominant males did not reach (Moore and Mason 2001). Given our experimental design, we cannot distinguish whether corticosterone levels increased because of competition for thermal resources or simply from the presence of a conspecific. Nonetheless, elevated concentrations of corticosterone could reduce the fitness of a male spiny lizard, which has a short window of opportunity for breeding each year (Ramírez-Bautista et al. 2002).

Multiple studies found direct effects of elevated corticosterone on thermoregulatory behavior (Belliure and Clobert 2004, Preest and Cree 2008, Cull et al. 2015). For instance, geckos basked more frequently and maintained higher temperatures when their levels of corticosterone were experimentally increased (Preest and Cree 2008). Thus, the elevated concentrations of corticosterone exhibited by dominant males of *S. jarrovi* might explain why they basked more frequently during competition in our experiment. If this were true, however, subordinate males should have also maintained higher temperatures during competition. Instead, subordinates were farther from the heat lamp and had lower temperatures during competition (see Figs. 2.1 and 2.2). Possibly, subordinate males tried to bask more frequently, as evidenced by their greater movement during competition, but were deterred from approaching the heat lamp by dominant males. A connection between corticosterone and thermoregulation would be important, because body temperature strongly affects biochemical reactions and organismal performance.

Following competition, most of the large males circulated more testosterone while most of the small males circulated less testosterone or remained at low baseline levels. This pattern seemingly contradicts a pattern reported by Moore (1987), who found no clear change in testosterone levels following a staged encounter between males. The discrepancy between these results could reflect differences in experimental design. We tested sampled the blood of each lizard before and after two days of interactions, whereas Moore (1987) only sampled lizards after a brief staged encounter. In Moore’s design, variation among individuals could obscure changes within individuals; changes within individual might have been detected had Moore also sampled blood before staged encounters. Moreover, the longer durations of interactions in our experiment enabled one male to establish dominance over the other, which correlates with shifts in testosterone (Greenberg and Crews 1990, Blanchard et al. 1993, Sapolsky 2005). Elevated testosterone causes animals to patrol, display, fight, and court more than usual, in the laboratory (Zielinski and Vandenbergh 1993, Klukowski et al. 2004, Mills et al. 2009) and the field (Marler and Moore 1988, Wingfield and Hahn 1994, John-Alder et al. 2009). Although these behaviors enhance access to resources, they can also deplete energy, cause injury, or attract predators (Marler and Moore 1988, Marler and Moore 1989, Wingfield et al. 1990). Therefore, elevated testosterone likely results in a tradeoff between the short-term costs of greater energy expenditure and reduced feeding with the long-term benefit of maintaining a territory during the breeding season (Goldberg 1972, Marler and Moore 1991, Marler et al. 1995). Again, this tradeoff makes sense in light of our results, because dominant males are already large and consequently benefit more from reproduction than from growth. Conversely, subordinates would benefit from either a low baseline or temporary reduction in testosterone, which discourages costly interactions with larger males (Marler and Moore 1988, Dufty 1989, Marler and Moore 1989, Summers 2002). If low testosterone suppresses aggression, a subordinate male would either become submissive to a dominant male (Greenberg and Crews 1990) or attempt to establish a territory elsewhere. Either behavior would reduce the risk of injury and loss of energy associated with high testosterone levels (Marler and Moore 1989, Wingfield et al. 1990), ultimately helping them become dominant in future breeding seasons. Further work with a larger sample would help to better understand these trends and reduce the observed variability.

In conclusion, I have shown that lizards compete for thermal resources in the way that earlier researchers have proposed (Magnuson et al. 1979). Thus, competition for a thermal resource can be viewed in the same way as competition for shelter, food, or mates, which could result in physiological stress. These considerations underscore the need to better understand how abiotic and biotic factors interact to determine an organism’s performance. If social hierarchies determine access to thermal resources, physiological performance will depend on the distribution of these resources in relation to the size of a territory (Huey and Slatkin 1976a, Sears and Angilletta 2015, Sears et al. 2016). Since territories of male lizards often overlap the ranges of several females (Ruby 1978, Haenel et al. 2003), subordinate males should have lower quality microclimates within their territories compared to dominant males and females, especially when thermal resources are rare. Furthermore, my results are important when assessing current and future threats of climate change, because climatologists predict continued warming on a global scale (Walther et al. 2002, Edenhofer et al. 2014). Such anthropogenic warming could limit the abundance of preferred microclimates (Sinervo et al. 2010a, Sears et al. 2016), exacerbating competition for space. Whether behavioral thermoregulation will enable animals to compensate for a warming climate will depend not only on the presence of thermal heterogeneity (Clusella-Trullas and Chown 2011, Sears et al. 2011, Buckley et al. 2015a) , but also on the ecological interactions within and among species.

Fig 2.1. When paired, large males and small males were closer to and farther from the heat source, respectively, than when alone. Black symbols and connecting lines represent the mean positions of each lizard in a treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

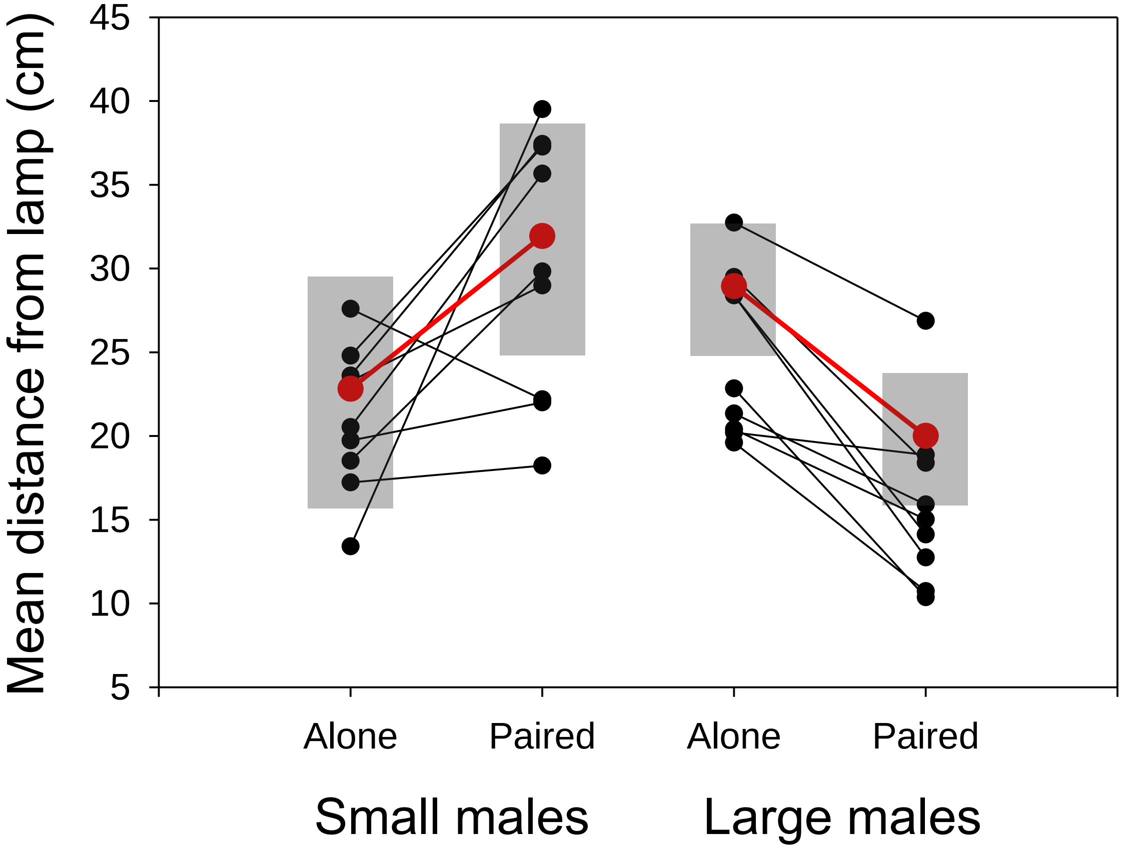


Fig 2.2. When paired, body temperatures of large males and small males were higher and lower, respectively, than when alone. Black symbols represent observed body temperatures of lizards in a treatment. Red symbols denote means and standard deviations computed by multimodel averaging. The gray bar and red bar depict the central 68% of preferred body temperatures (34.1 ± 1.4 ºC) and critical thermal maxima (41.0 ± 1.3 ºC; T. W. Rusch, unpublished data), respectively.

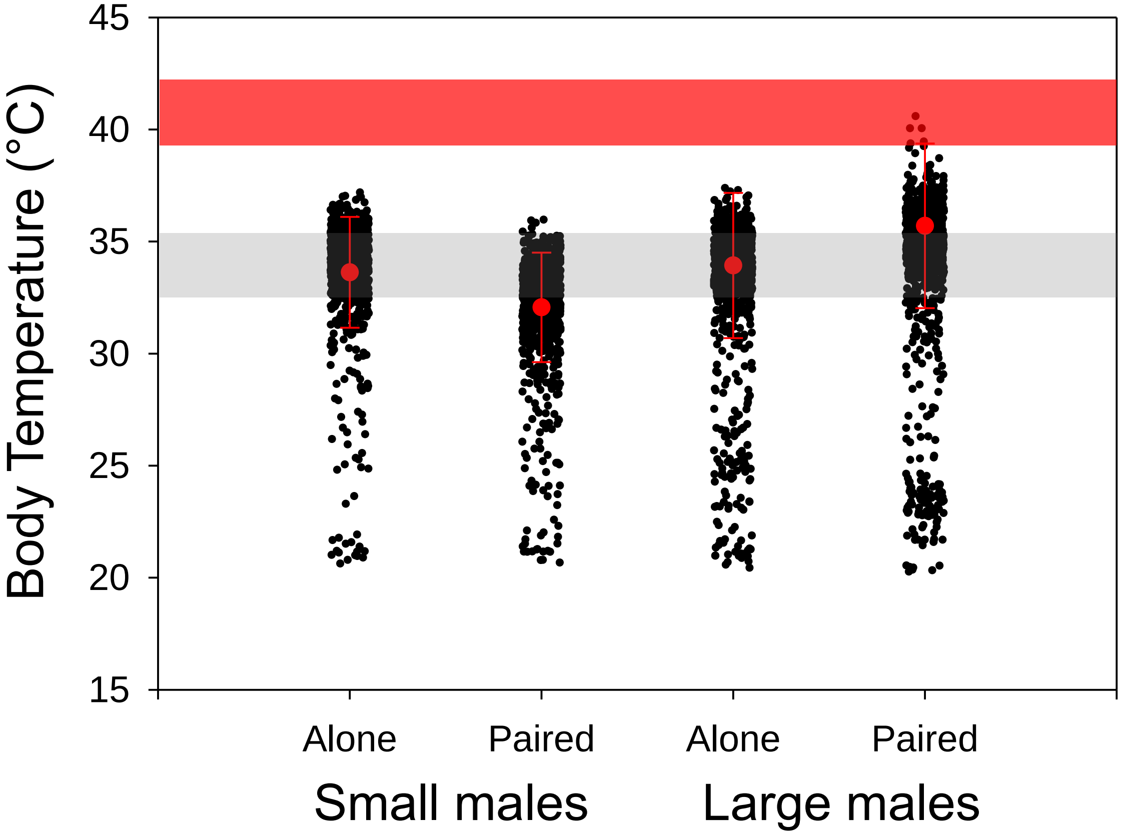


Fig 2.3. When paired, both large and small males moved greater distances than when alone. Black symbols and connecting lines represent the total distance moved by each lizard in a treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

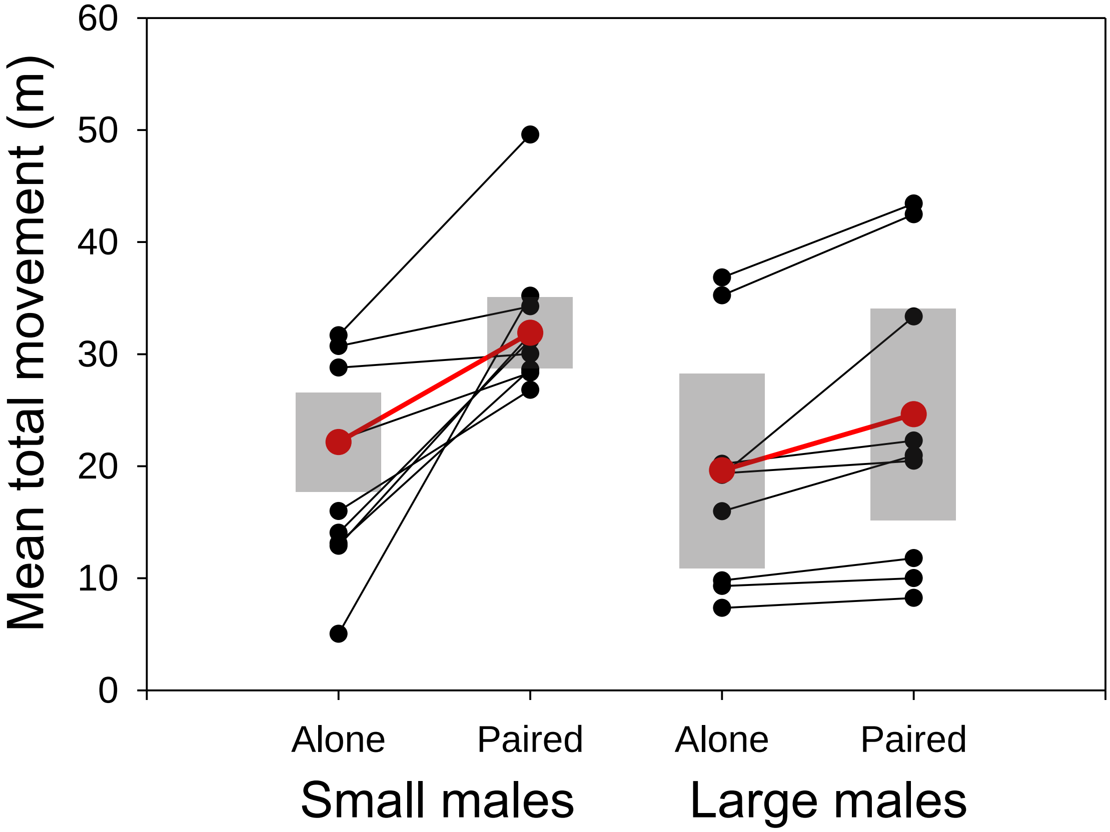


Fig 2.4. When paired, both large and small males circulated higher concentrations of corticosterone than when alone. This effect was noticeably greater on small males. Black symbols and connecting lines represent the concentrations of corticosterone in lizards following each treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

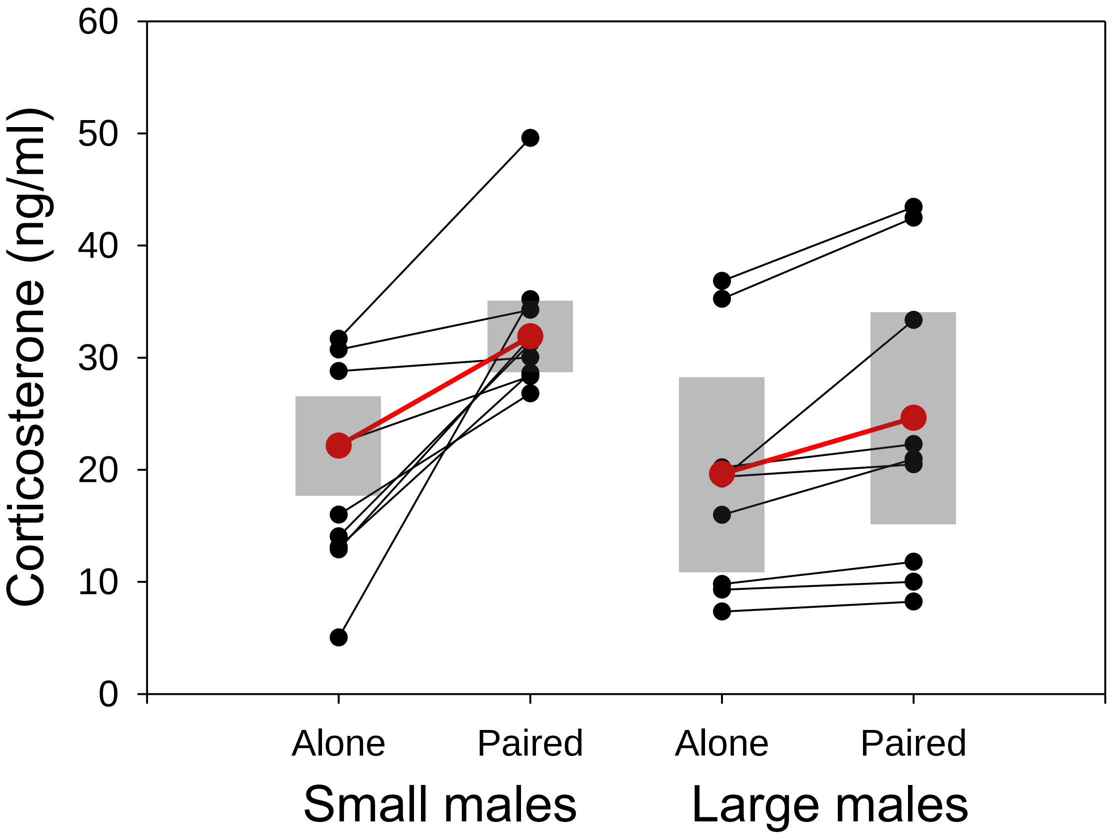
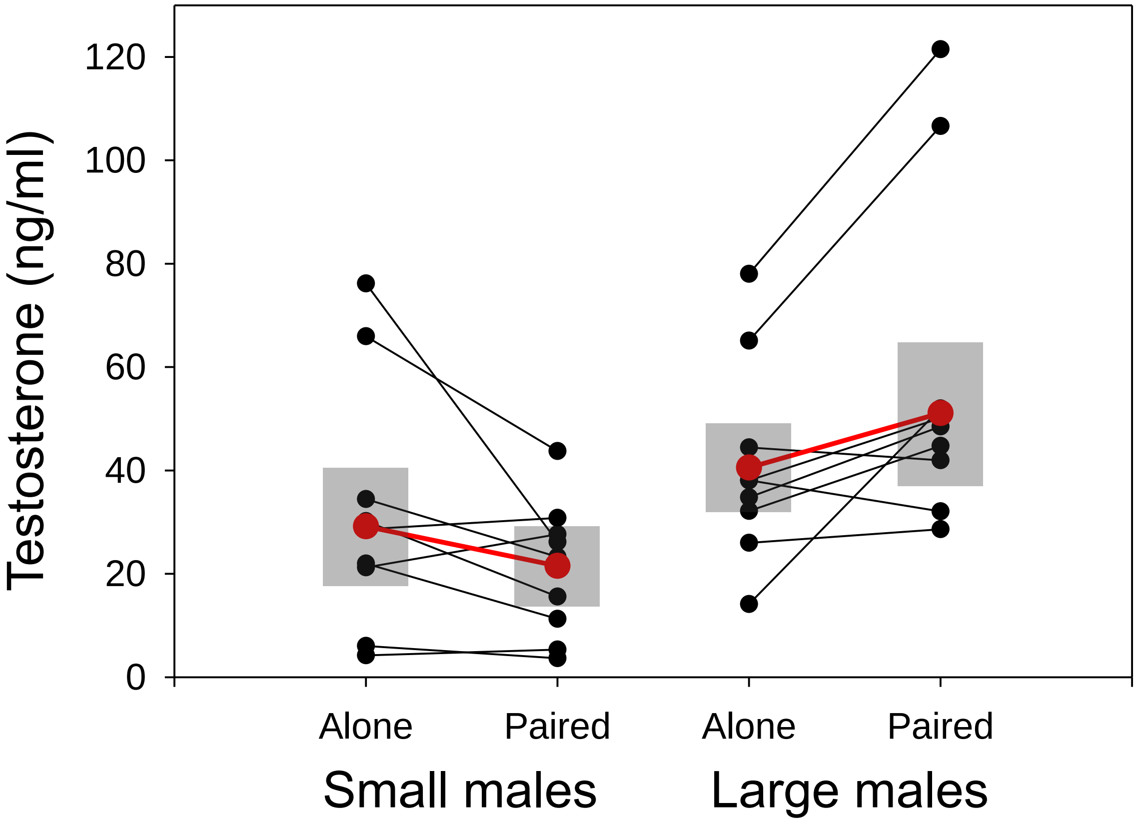


Fig 2.5. When paired, large males and small males circulated higher and lower concentrations of testosterone, respectively, than when alone. Black symbols and connecting lines represent concentrations of testosterone in lizards following each treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.



CHAPTER THREE:

Lizards Perceived Abiotic and Biotic Stresses Independently when Competing for Shade in Terrestrial Mesocosms

Abstract

Hormones such as glucocorticoids enable animals to respond adaptively to stresses in their environment. For this reason, circulating glucocorticoids became a popular biomarker for estimating the quality of an environment. Here, I show that access to thermal resources in an environment influence the hormones and behavior of male lizards (*Sceloporus jarrovi*). I exposed isolated and paired males to different thermal landscapes, ranging from one large patch of shade to sixteen smaller patches. Both the presence of a competitor and the patchiness of the thermal environment influenced hormone concentrations and movement patterns. When shade patches were rare, paired lizards competed more aggressively and circulated more corticosterone. Even without competitors, lizards circulated more corticosterone in landscapes with fewer patches of shade. Isolated males moved the farthest and covered the most area when shade was concentrated in a single patch, but paired males did the opposite. Because the total area of shade in each landscape was the same, these hormonal and behavioral responses of lizards were influenced by the ability to access shade in the landscape. Thus, circulating glucocorticoids should reflect the thermal quality of an environment when researchers can control for other factors. Moreover, a theory of stress during thermoregulation should help ecologists anticipate physiological and behavioral responses to changing climates.

Introduction

The spatial distributions of resources such as food, mates, shelter and even microclimates (Robinson and Holmes 1982, Duvall and Schuett 1997, Fisher 2000, Sears and Angilletta 2015, Sears et al. 2016) determine how animals locate and use these resources (Kronfeld-Schor and Dayan 2003). When multiple resources are concentrated in the same location, an animal can satisfy its needs while moving very little (Dunning et al. 1992, Taylor et al. 1993). However, disparate resources often occur in different locations, forcing animals to spend more time and energy to satisfy their needs (Schoener 1971, Possingham 1989, Houston and McNamara 2014). Furthermore, the extent to which disparate resources are close together or far apart depends on the time of day or year. For instance, preferred microclimates shift predictably as the sun moves across the sky, whereas food and mates shift in more complicated ways (Pyke et al. 1977, Ims 1995, Lima and Bednekoff 1999). Other resources, such as a burrow or nest, remain fixed in space. Thus, behaviors and the hormones that drive them will likely depend on the spatial distributions of resources.

To further complicate matters, members of a species often compete for the same resources. In territorial species, larger, faster, or more aggressive individuals exclude others from places where limiting resources occur (Connell 1961, Pianka 1981, Žagar et al. 2015). This phenomenon has been studied intensely from the perspective of competition for food, mates, and shelter (Ellis 1995, Giraldeau and Caraco 2000, Holbrook and Schmitt 2002), but less is known about competition for microclimates that enhance thermoregulation (Downes and Shine 1998, Angilletta 2009, Rusch and Angilletta In Press). Interactions between competitors impose a potent stress, often resulting in both physiological and behavioral changes for the loser and the winner (Gladue et al. 1989, Creel 2001, Summers 2002). Typically, both individuals experience elevated concentrations of glucocorticoids (e.g., corticosterone) following aggression, although losers often experience a greater increase than winners (Øverli et al. 1999, 2000, Summers 2002). Glucocorticoids mobilize energy needed to fight or flee (Wingfield et al. 1997, Sapolsky 2002, Dallman et al. 2004) and can increase food and heat seeking behaviors (Lohmus et al. 2006, Preest and Cree 2008). However, elevated glucocorticoids will deplete energy over time (Marra and Holberton 1998, Sapolsky 2002) and discourage aggression and courtship (Moore and Miller 1984, Denardo and Licht 1993, Morgan et al. 1999), potentially reducing an animal's home range (DeNardo and Sinervo 1994) and thus access to resources.

Although any competition can impose stress, the intensity of competition and thus the magnitude of stress, should depend on the quality of the environment. When resources are rare or aggregated, competition should be intense (Emlen and Oring 1977, Schoener 1983b, Dubois and Giraldeau 2005), presumably increasing both an animal's need to move and its circulating glucocorticoids (Ancona et al. 2010, Rusch and Angilletta In Press). Based on this reasoning, animals would compete more intensely when preferred microclimates are concentrated in space. And if competition impedes thermoregulation, animals will experience temperatures that fall outside their preferred range (Regal 1971, Downes and Shine 1998, Rusch and Angilletta In Press). By contrast, when preferred microclimates are dispersed in space, multiple animals can access these resources without occupying the same area and thus should thermoregulate equally well. In general, a patchy distribution of thermal resources enables individuals to thermoregulate effectively with relatively little movement (Sears and Angilletta 2015, Sears et al. 2016, Basson et al. 2017). Therefore, we expect the intensity of competition to decline as the thermal landscape becomes patchier. I tested this hypothesis by measuring the hormones and behaviors of male spiny lizards (*Sceloporus jarrovi*) in controlled thermal landscapes. I expected lizards to move greater distances and circulate more corticosterone when thermoregulating in a landscape with fewer patches of shade. Additionally, I expected subordinate males to circulate more corticosterone during competition than would dominant males. I also measured testosterone and aggression to infer how dominant and subordinate males compete for space in different thermal landscapes.

Methods

Collection and husbandry of animals

In August of 2012, I collected 24 adult males of *Sceloporus jarrovi* in the Chiricahua Mountains of Arizona (1500-2500 m). After capture, lizards were transported to the Sevilleta Field Station in New Mexico. Upon arrival, lizards were weighed (mean ± SD = 26.8 ± 5.1 g) and toe-clipped for identification (Perry et al. 2011).

Lizards were housed individually in plastic terraria (30 x 26 x 13 cm) lined with paper towels. Terraria were heated from below at one end to create a thermal gradient, thus allowing lizards to freely thermoregulate. The operative environmental temperatures along this gradient ranged from 23° to 42°C, as determined by hollow copper models of a lizard (Bakken and Gates 1975). Cardboard was placed between each terrarium to prevent lizards from viewing each other. Every other day, lizards were provided water and fed adult crickets (*Acheta domestica*) and larval beetles (*Tenebrio morio*) coated with a powder of vitamins and calcium (Rep-Cal, Los Gatos, CA, USA). Animals were maintained this way for two weeks before our experiment to ensure. All lizards ate regularly and were thus included in the study.

Experimental design and treatments

I recorded spatial positions and hormone levels of male lizards when alone and when paired in varying thermal environments. To manipulate the thermal environment, I followed methods of Sears et al. (2016). I used nine outdoor thermal arenas (20 x 20 m), consisting of sheet metal walls and a canopy of shade cloth (Greenhouse Megastore, Georgetown, IL) that blocked approximately 80% of solar radiation. Shade cloth was suspended 1.2 m above each arena on steel cables, which were fastened to iron posts outside the arena. I kept the total area shaded (36%) consistent for all arenas, but altered the distribution of shade using three distinct designs; 1 large patch (12 x 12 m), 4 medium patches (6 x 6 m), and 16 small patches (3 x 3 m). Because I had nine arenas, each of these spatial arrangements was replicated three times (Fig 3.1).

I paired lizards according to mass, predicting that a larger lizard would dominate thermal resources (i.e., shade patches) when paired with a smaller conspecific (Regal 1971, Ruby 1978, Downes and Shine 1998, Rusch and Angilletta In Press). Mean masses of large and small lizards were 30.3 ± 4.5 g and 23.3 ± 3.2 g, respectively. Lizards were divided into two groups, the 12 heaviest lizards (i.e., large) and 12 lightest lizards (i.e., small), and paired according to their relative mass in each group; the heaviest “large” lizard was paired with the heaviest “small” lizard, and so on. The average difference in mass between lizards in a pair was 6.9 ± 2.9 g. Each pair was then randomly assigned to one of two treatment orders: 1) isolation followed by competition, or 2) competition followed by isolation, and to one of three thermal environments 1) 1 patch, 2) 4 patches, or 3) 16 patches (Fig 3.1).

Prior to experiments, lizards underwent a 10 day habituation period to become familiar with the structure of his thermal arena without experiencing a competing male. Specifically, males were given five 24 h periods to explore their arenas; each day of exploration was separated by a day of rest, during which males were returned to the lab and offered food and water *ad libitum*. By separating the periods of habituation, we exposed both lizards in each pair to their thermal arena without interaction prior to the experiment. This repeated exposure to the arena was designed to facilitate social behaviors, such as territoriality, during the experimental period.

Following the habituation period, lizards were placed in their assigned thermal arenas (1 patch, 4 patches, or 16 patches) and under their assigned treatments (half in isolation and half paired) at ~1800 h the evening before experiments began. Then, during experiments, spatial positions (described below) and exposure behaviors (i.e., whether lizards were out in the open or under the shade cloth) were recorded at 20 min intervals from 0820-1240 h for a 2 day experimental period. From 0820-1240 h are the times when all shade from the shade patches were within the arenas due to the orientation of the sun; during this period, the total area of shade was equal among arenas.

The morning after the 2 day experimental period (0900-0930 h) I sampled blood from each lizard to measure total circulating levels of plasma corticosterone and testosterone (both free and bound). Each lizard was captured in the arena by hand and ~50 µL of blood was collected in a glass capillary tube by rupturing the orbital sinus. Once filled, each tube was sealed with Critoseal (Fisher Scientific, Pittsburgh, Pennsylvania, USA) and stored on ice. Blood samples were centrifuged within 1 h to separate red blood cells from plasma. Once separated, plasma was stored at -80 °C until assayed (see below). Blood samples were collected within 2 min of capture to minimize effects of handling stress on circulating corticosterone (Langkilde and Shine 2006). After bleeding, lizards were returned to terraria with food and water for 2 days. Following this period, the entire procedure was repeated, except that lizards in the competition treatment were switched to the isolation treatment, and vice versa (see Appendix; Table S3.1 for a description of events). At the end of the experiment, I had spatial positions, exposure behaviors, and blood samples for each lizard in isolation and in competition across three distinct thermal environments.

Movement analyses

I analyzed spatial positions of lizards to estimate the minimum total movement, the minimum area covered, and the probability of exposure in each treatment. A Cartesian coordinate system was painted on the walls of each arena, at 1 m intervals ranging from

0-20 m. During the experiment, I recorded an X-Y spatial position and noted whether each lizard was in shade or exposed to solar radiation, at 20 min intervals between 0820 and 1240 h. Following the experiment, I used triangulation to calculate the distance between successive positions and summed these distances to find the minimum total distance moved by each lizard.

I estimated the minimum area covered by creating a digital Cartesian coordinate system (Microsoft Excel, 2013) simulating the 20 x 20 m outdoor arenas. I plotted the spatial positions of each lizard on the digital Cartesian coordinate system. Once these data were plotted, I counted the number of blocks (i.e., 1 x 1 m) that each lizard traveled through to estimate the minimal area used within the arena. Lastly, I calculated the percentage of observations for which lizards were exposed to solar radiation, or the probability of exposure.

Aggression analysis

Interactions were observed every 20 minutes for 1 minute from 0820-1240 h for a 2-day experimental period. A scoring system was incorporated to capture the level of aggressive interactions; 1 point was given to the pair if one or both lizards were displaying (e.g., head bobs, pushups), 2 points was given to the pair if a chase ensued, and 3 points was given to the pair that engaged in fighting (e.g., biting, mounting). Scores were tallied at the end of each experimental day and summed for the two day treatment period.

Hormone assays

For each blood sample, I quantified total plasma concentrations (both free and bound fractions) of corticosterone and testosterone. Hormones were measured using commercial enzyme-linked immunoassay kits (Enzo Life Sciences, Farmingdale, NY). Samples were analyzed in duplicate on the same day, following instructions supplied with the kit. The assays were validated with standard curves, constructed from separate serial dilutions for corticosterone and testosterone (Fokidis et al. 2009). There were no differences between the slopes of a curve produced by serial plasma dilution for corticosterone (4- to 64-fold) or testosterone (8- to 200-fold) and a standard curve for each hormone. This approach enabled us to determine the appropriate dilutions for testing our samples, which was 32-fold for corticosterone and 128-fold for testosterone. Diluted samples were distributed randomly within a 96-well plate for each hormone. The sensitivities of these assays were 32.02 pg ml^{-1} for corticosterone and 7.81 pg ml^{-1} for testosterone. Mean coefficients of variation within assays were 3.32% and 3.89% for corticosterone (n = 2 plates) and 6.89% and 2.76% for testosterone (n = 2 plates). Mean coefficients of variation between assays were 3.60% for corticosterone and 4.82% for testosterone. A total of 48 samples (2 per lizard) were run in duplicate (n = 96 wells) for both corticosterone and testosterone (n = 2 plates for each hormone assay).

Statistical analyses

I modeled the effects of social context (alone vs paired) and thermal patchiness (1, 4 or 16 patches of shade) on multiple variables: minimum total movement, probability of exposure, minimum area covered, aggression score, and hormone concentrations. Each analysis included a mixture of fixed, continuous, and random factors. In addition to the fixed factors of social context (alone or paired) and thermal patchiness (1, 4, or 16), I included body size (large or small) and treatment order (paired then alone vs. alone then paired). Temporal block (1 or 2) and body mass (g) were covariates. The identity of the lizard was included as a random intercept when modeling all traits except aggression score, for which the pair of lizards was a random intercept.

Because operative temperatures likely influence exposure to solar radiation, I also included this information when modeling the probability of exposure. To obtain a single variable that characterized each thermal environment at each time, we used a principal component analysis to generate a linear combination of two highly correlated variables: the maximum operative temperature and the range of operative temperatures. The first principle component (PC1) captured 96% of the variation in these thermal variables (Table S3.14). Scores of this principle component were used as a covariate in my statistical model.

I used multimodel infer the most likely values of means and standard deviations. First, I used the procedure described by Zuur et al. (2009) to determine the most likely random component of the model. Then, I used the *nlme* library (Pinheiro et al. 2012) for analyses of corticosterone, testosterone, minimum total movement, minimum habitat use, and aggression score with the *MuMIn* library (Bartoń 2013) of the R Statistical Software (R-Core-Team 2015) to fit all possible models of fixed effects and to calculate the Akaike weight of each model. Similarly, I followed the same approach for the analysis of the probability of exposure, except we used and the *lme4* library (Bates et al. 2015) as this package enabled me to set the error structure to binomial so the models had a more appropriate fit to the data. The Akaike weight estimates the probability that a model describes the data better than other models. Finally, I used Akaike weights to calculate a weighted average of each parameter (see Appendix; Tables S3.2-S3.7). I practiced full model averaging, such that the weighted effect was considered zero for all factors excluded from a model (Burnham and Anderson 2002). The resulting values of parameters were used to calculate the most likely mean of a dependent variable for each treatment (see Appendix; Tables S3.8-S3.13). This approach eliminates the need to interpret *P* values, because all models (including the null model) contributed to the most likely value of each mean.

Results

Both social and thermal conditions determined the mean concentration of corticosterone, but only the social condition affected testosterone. In isolation, lizards circulated less corticosterone as the distribution of thermal resources became patchier (Fig 3.2). Compared to lizards in the patchiest arenas, isolated lizards in arenas with only 4 patches or 1 patch circulated 36% or 72% more corticosterone, respectively. Pairing a large and small lizard in a thermal arena caused both lizards to elevate corticosterone by a similar amount; lizards in 1- and 4-patch thermal arenas circulated 32.7 and 24.4% more corticosterone than paired lizards in 16-patch thermal arenas, respectively. The effects of thermal patchiness and social interactions on corticosterone were additive; therefore, pairing caused a greater relative increase in corticosterone in all environments, compared to lizards in isolation. Specifically, pairing raised corticosterone by 115% in arenas with 1 patch, by 155% in arenas with 4 patches, and by 179% in arenas with 16 patches (Fig 3.2). Pairing had opposing effects on testosterone. Large males circulated 50% more testosterone, while small males circulated 32% less. These opposite responses enhanced the difference in testosterone between large and small males that existed prior to pairing (Fig 3.3). Testosterone was unaffected by the thermal patchiness of the environment.

Both social and thermal conditions determined how lizards used the space. In isolation, lizards were more likely to occupy ground exposed to solar radiation as the patchiness of the arena increased; lizards were exposed 42%, 67%, and 72% of the time in arenas with 1-patch, arenas with 4-patches, and arenas with 16-patches. Pairing large and small lizards caused both lizards to increase their exposure to solar radiation to about 80% of the time, regardless of the thermal patchiness of their arena (Fig 3.4). Lizards in arenas with 1-patch moved greater distances and covered more area than lizards in either 4- or 16-patch environments, regardless of body size. However, paired lizards used more space or less space depending on the thermal patchiness (Figs 3.5 and 3.6). That is, lizards in arenas with 1-patch moved a shorter distance (47% decrease) and covered less area (39% decrease) when paired, whereas lizards in arenas with either 4- or 16-patches moved greater distances (41% or 19% increase, respectively) and covered more area (30% and 23% increases) when paired. And paired lizards had the greatest aggression scores in 1-patch thermal environments; lizards scored 4x and 2x higher in 1-patch thermal environments compared to lizards in either 4- or 16-patch thermal environments, respectively (Fig 3.7).

Discussion

Although a change in behavior often parallels a change in hormone levels, one still must establish cause and effect. In my study, for instance, both the distribution of microclimates and the presence of a competitor affected the hormones and behaviors of lizards. But did the hormonal response cause the behavioral response, or vice versa? Figure 3.8 summarizes the causal pathways that might be inferred from our data. Each pathway shows how the thermal landscape and social context can influence corticosterone and activity, but the pathways differ by whether the hormonal response stems from movement or from thermoregulation. For instance, increased patchiness increases thermoregulatory performance and reduces circulating corticosterone (Fig. 3.8A). Alternatively, an increase in thermal patchiness reduces the distance moved (i.e., energetic expenditure), which directly reduces circulating corticosterone (Fig. 3.8B). Another set of pathways focuses on the role of social interactions between lizards. An increase in thermal patchiness enables both males to thermoregulate effectively without moving long distances or occupying the same area, which would reduce aggressive interactions and thus result in lower circulating corticosterone (Fig. 3.8C, red arrows).

Furthermore, feedbacks between corticosterone and behavior can operate as well, such that the thermal landscape and the social context additively or synergistically alters corticosterone and behavior (Fig. 3.8C, green arrow).

A stress response in male lizards might have resulted from the effect of the thermal landscape on behavior. In my experiment, isolated lizards circulated more corticosterone when thermal resources were clumped into one large patch rather than dispersed into smaller patches (Fig 3.2). A previous study of the same species revealed that patchier landscapes enable better thermoregulation (Sears et al. 2016). This effect stems from the need to move greater distances when shuttling between sun and shade (Sears and Angilletta 2015), which directly affects thermoregulatory performance and energetic costs (Withers and Campbell 1985, Sears and Angilletta 2015, Basson et al. 2017). Because isolated lizards moved the farthest and covered the most area in arenas with only one patch (Figs 3.5 and 3.6), they likely expended more energy in this environment. The increase in circulating corticosterone should have helped lizards to meet the greater energetic demand, as corticosterone is well known for mobilizing energy stores (Rees et al. 1985, Gleeson et al. 1993, Girard and Garland 2001). This interpretation makes sense for lizards observed in isolation, which moved farther in landscapes with fewer patches. However, paired lizards moved the least when interacting in an environment with only one patch. Therefore, movement alone cannot account for the effect of the thermal landscape on corticosterone level.

Alternatively, lizards could have circulated more corticosterone as part of a response to thermal stress. In a previous experiment, males of *S. jarrovi* thermoregulated less precisely when moving in landscapes with fewer patches (Sears et al. 2016). Specifically, males in a landscape with only one patch of shade had at least a 10% greater variance of body temperatures compared to lizards in a landscape with more patches of shade. The greater variance of body temperature meant that lizards sometimes experienced a temperature that exceeded its preferred range. If the same phenomenon occurred during our experiment, lizards would have experienced the most thermal stress when moving in a landscape with only one patch of shade. To cope with such stress, animals often circulate more corticosterone, because these glucocorticoids encourage behaviors that restore homeostasis (Sapolsky et al. 2000, Landys et al. 2006, Dupoué et al. 2013). Thus, the pattern of circulating corticosterone that we observed among thermal environments could have resulted from the presumed thermal stress resulting from variation in thermoregulatory performance as well as the observed variation in movement.

The effect of social interactions on corticosterone reinforces the view that stress response was not entirely caused by the energetic cost of movement. Although lizards circulated the most corticosterone when forced to compete over a single patch of shade (Fig 3.2), they moved the least under this condition. Pairs of lizards in the 1-patch treatment concentrated their activity around the large patch of shade, moving shorter distances and using less space compared to pairs in either the 4-patch or 16-patch thermal environment (Figs 3.5 and 3.6). Therefore, the differences in corticosterone levels of paired males were not likely a response to the energetic demands of searching for thermal resources. Rather, the high levels of corticosterone in paired males likely reflects a greater frequency and intensity of aggression, such as chasing, fighting, or mounting. Indeed, aggression more than doubled as the number of shade patches decreased from sixteen to one (Fig 3.7). Moreover, the males shifted their levels of testosterone in opposite directions (Fig 3.3), as expected when a dominance hierarchy develops (Rose et al. 1975, Greenberg and Crews 1990, Rusch and Angilletta In Press). Aggression costs energy but also generates physiological stress because of increased activity and the risk of injury (Schuett and Grober 2000, Summers 2002). Some studies revealed that the sheer sight or scent of a conspecific caused an animal to circulate more corticosterone (Cockrem and Silverin 2002, Thaker et al. 2009b, Narayan et al. 2013). This response could prepare an animal for the physical exertion of displaying and or fighting, as well as aid in the recovery. Thus, the large increases in circulating corticosterone levels of paired males was likely a response to the frequency and intensity of social interactions, which depended on the movement patterns and habitat use of lizards, and ultimately the patchiness of the thermal environment (Fig 3.8).

Lizards were more likely to occupy an unshaded microhabitat when paired with a conspecific than when alone (Fig 3.4). Whether or not lizards were basking for thermoregulation, more frequent exposure to solar radiation likely led to higher body temperatures. In a previous study of *S. jarrovi*, large males basked more frequently in the presence of smaller males, which caused the larger males to exceed their preferred temperature range (Rusch and Angilletta In Press). Based on this observation, I hypothesize that exposure (i.e., basking intensity) in our experiment led to stressful temperatures, which in turn contributed to the elevation of corticosterone (Greenberg and Wingfield 1987, Girling and Cree 1995, Jessop et al. 2000). Alternatively, the elevated corticosterone levels triggered by aggression might have caused the greater frequency of basking. In another species of lizards (*Hoplodactylus maculatus*), artificial elevation of corticosterone caused individuals to seek heat more often and maintain higher body temperatures (Preest and Cree 2008). However, this result does not necessarily mean that the correlation between basking frequency (and presumably higher body temperatures) and corticosterone concentration in our experiment reflects cause and effect. I need to investigate the relationship between corticosterone and thermoregulation further, because hormones and temperature can each have a pervasive effect on organismal performance.

Because circulating concentrations of glucocorticoids indicate the health of an animal (Sapolsky et al. 2000, Romero and Wikelski 2001, Romero 2004), these hormones have been increasingly used by ecologists to infer the quality of environments (Marra and Holberton 1998, Newcomb Homan et al. 2003, Homyack 2010). In general, a population of animals with high concentrations of glucocorticoids suggest that this population experiences a more stressful (and hence lower quality) environment than do populations (of the same species) with low concentrations (Wingfield and Romero 2001, Homyack 2010). Our experiment provides the first evidence that the structure of a thermal landscape elicits a change in a circulating glucocorticoid, corticosterone.   Therefore, ecologists might be able to infer the thermal quality of an environment, something that has never been considered before. Traditionally, researchers defined the thermal quality of a habitat in terms of the mean and variance of operative temperatures relative to the preferred temperatures of a species (Christian et al. 1985, Hertz et al. 1993, Blouin-Demers and Nadeau 2005). Specifically, a greater difference between the mean of operative environmental temperatures and the mean (or central 50%) of preferred body temperatures would indicate a lower thermal quality of the environment. In our experiment, the mean and variance of operative temperature was roughly equal among the different thermal landscapes. Yet, lizards circulated more corticosterone as the patchiness of the thermal landscape decreased, independently of the social context (Fig 2). This result aligns with those of previous studies in which patchier thermal landscapes enhanced the thermoregulatory performance of lizards (Sears and Angilletta 2015, Sears et al. 2016). Thus, differences in circulating corticosterone between populations might tell us something about the quality of a thermal landscape that cannot be inferred from the mean and variance of operative environmental temperatures alone. Obviously, the quality of a habitat depends on many factors, but uncovering the mechanisms by which these factors mediate stress responses is vital for predicting how species will respond to anthropogenic changes (Kearney 2006, Gilman et al. 2010). Knowing how hormone profiles depend on the thermal landscape would help ecologists to identify vulnerable populations before they begin to decline.

Fig 3.1. Large, outdoor arenas (400 m^2) were used to manipulate the thermal landscape. Each arena contained one of three levels of patchiness; **(a)** 1 patch, **(b)** 4 patches, or **(c)** 16 patches.

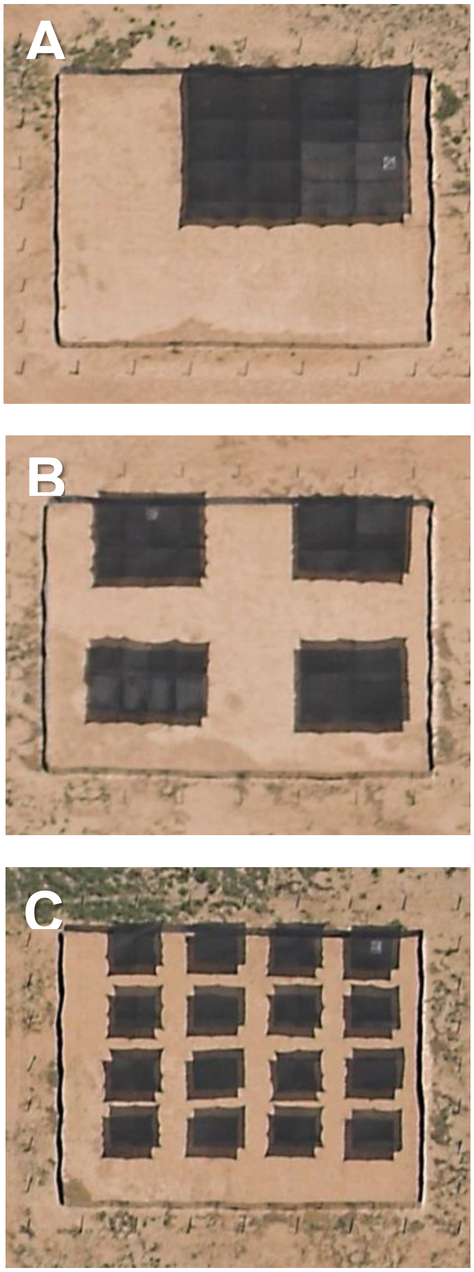


Fig 3.2. All lizards circulated more corticosterone as the patchiness of the thermal environment decreased, regardless of social context. This effect of additively amplified when lizards were paired. Diamond symbols and grey bars denote means and standard deviations computed by multimodel averaging. Open symbols denote corticosterone concentrations of lizards following a given treatment.

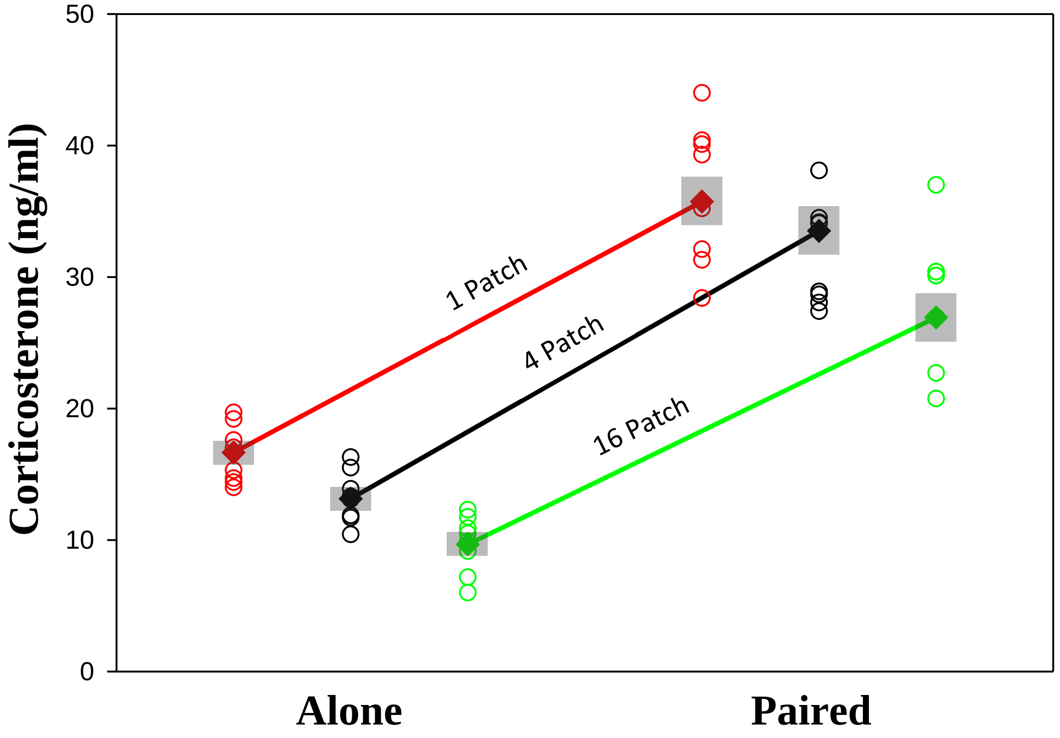


Fig 3.3. When paired, large lizards and small lizards circulated higher and lower concentrations of testosterone, respectively, than when alone. Diamond symbols and grey bars denote means and standard deviations computed by multimodel averaging. Open symbols denote testosterone concentrations of lizards following a given treatment.

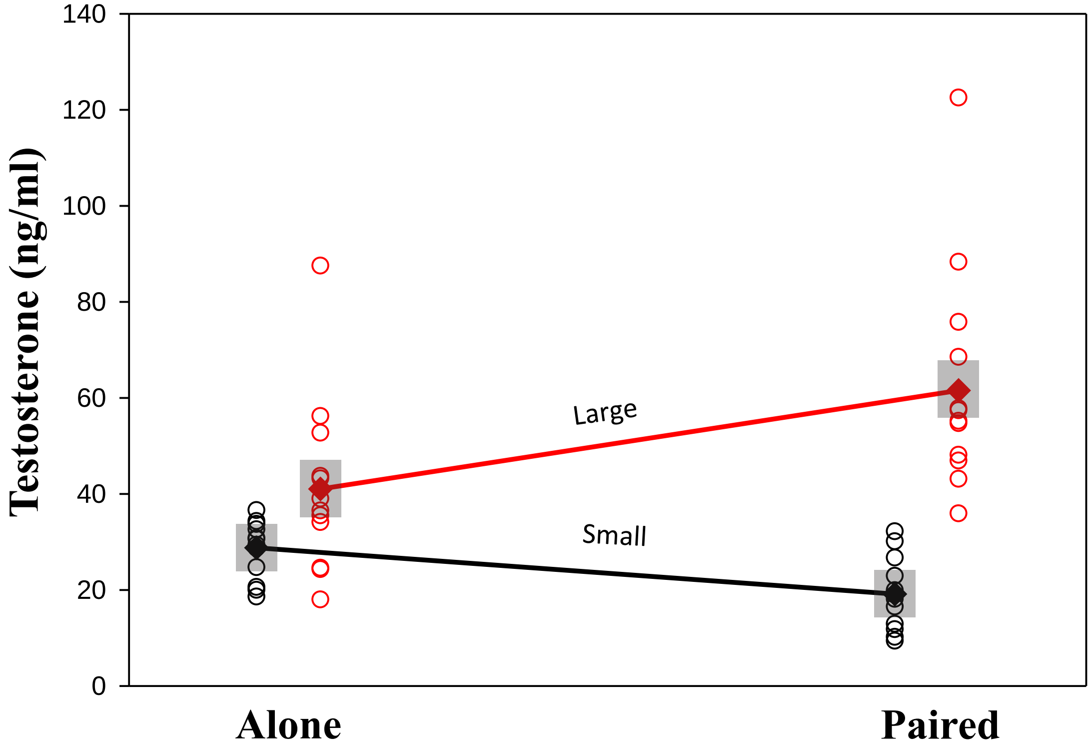


Fig 3.4. When alone, lizards had a greater probability of exposure as patchiness increased. When paired, all lizards had a higher probability of exposure compared to when alone, regardless of thermal patchiness. Black and grey bars denote mean probabilities of exposure when alone or paired with a conspecific under a given treatment.

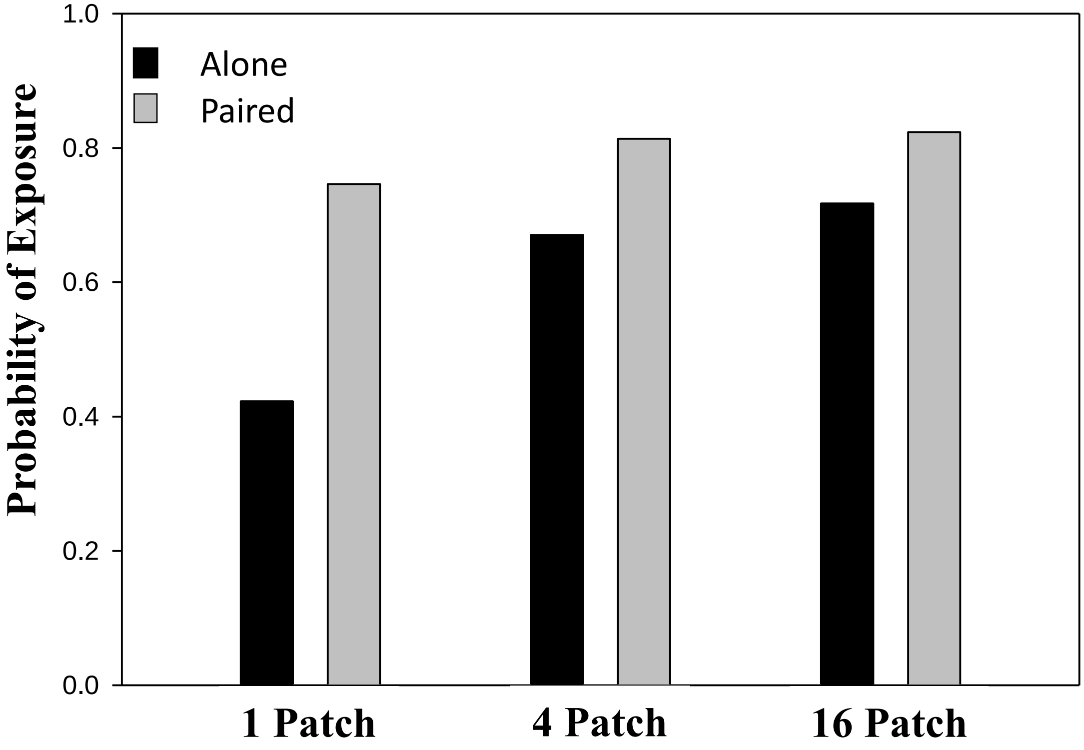


Fig 3.5. When alone, lizards move the greater distances in 1 patch thermal environments compared to lizards in either 4 or 16 patch thermal environments. When paired, this behavior was reversed; lizards moved greater distances in 4 and 16 patch thermal environments compared to lizards in 1 patch thermal environments. Diamond symbols and grey bars denote means and standard deviations computed by multimodel averaging. Open symbols denote minimum total movements under a given treatment.

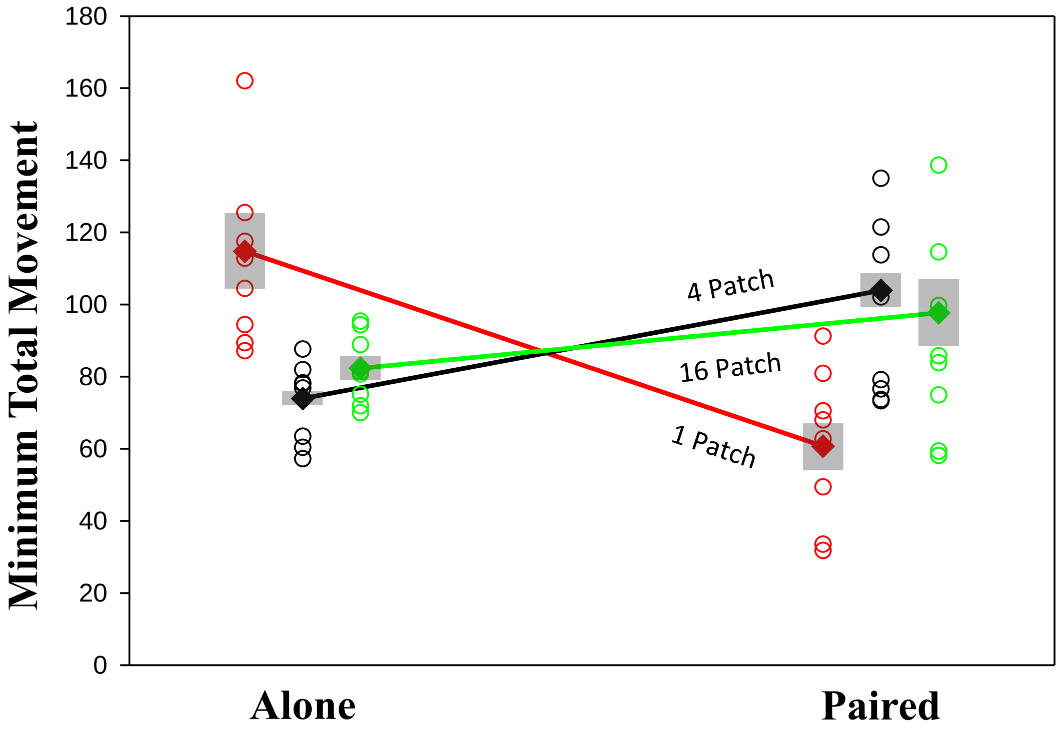


Fig 3.6. When alone, lizards used more habitat in 1 patch thermal environments compared to lizards in either 4 or 16 patch thermal environments. When paired, this behavior was reversed; lizards used more habitat in 4 and 16 patch thermal environments compared to lizards in 1 patch thermal environments. Diamond symbols and grey bars denote means and standard deviations computed by multimodel averaging. Open symbols denote minimum habitat use under a given treatment.

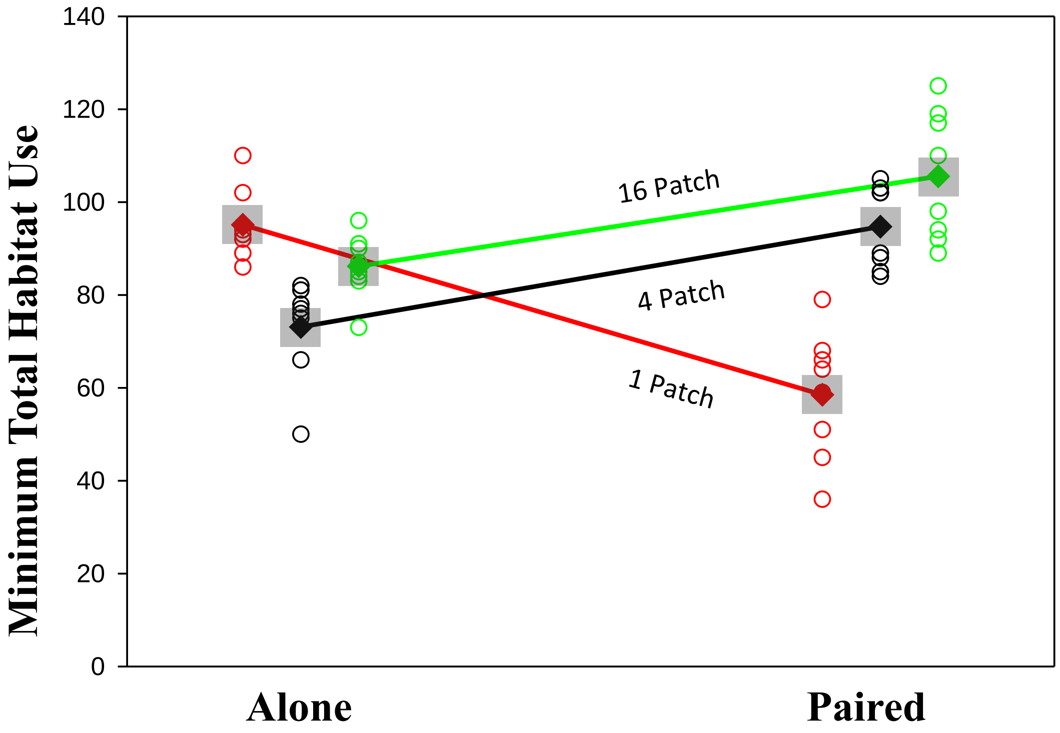


Fig 3.7. Paired lizards interacted more frequently and more aggressively in 1 patch thermal environments compared to either 4 or 16 patch thermal environments. Diamond symbols and grey bars denote means and standard deviations computed by multimodel averaging. Open symbols denote mean aggression score under a given treatment.

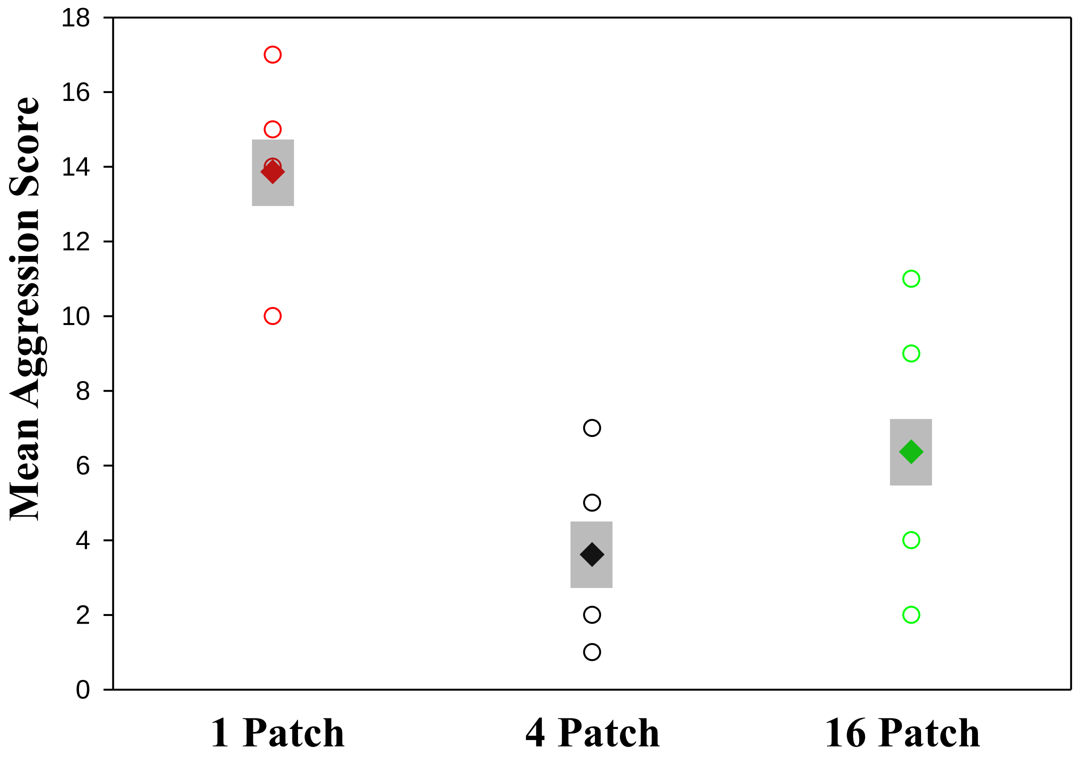
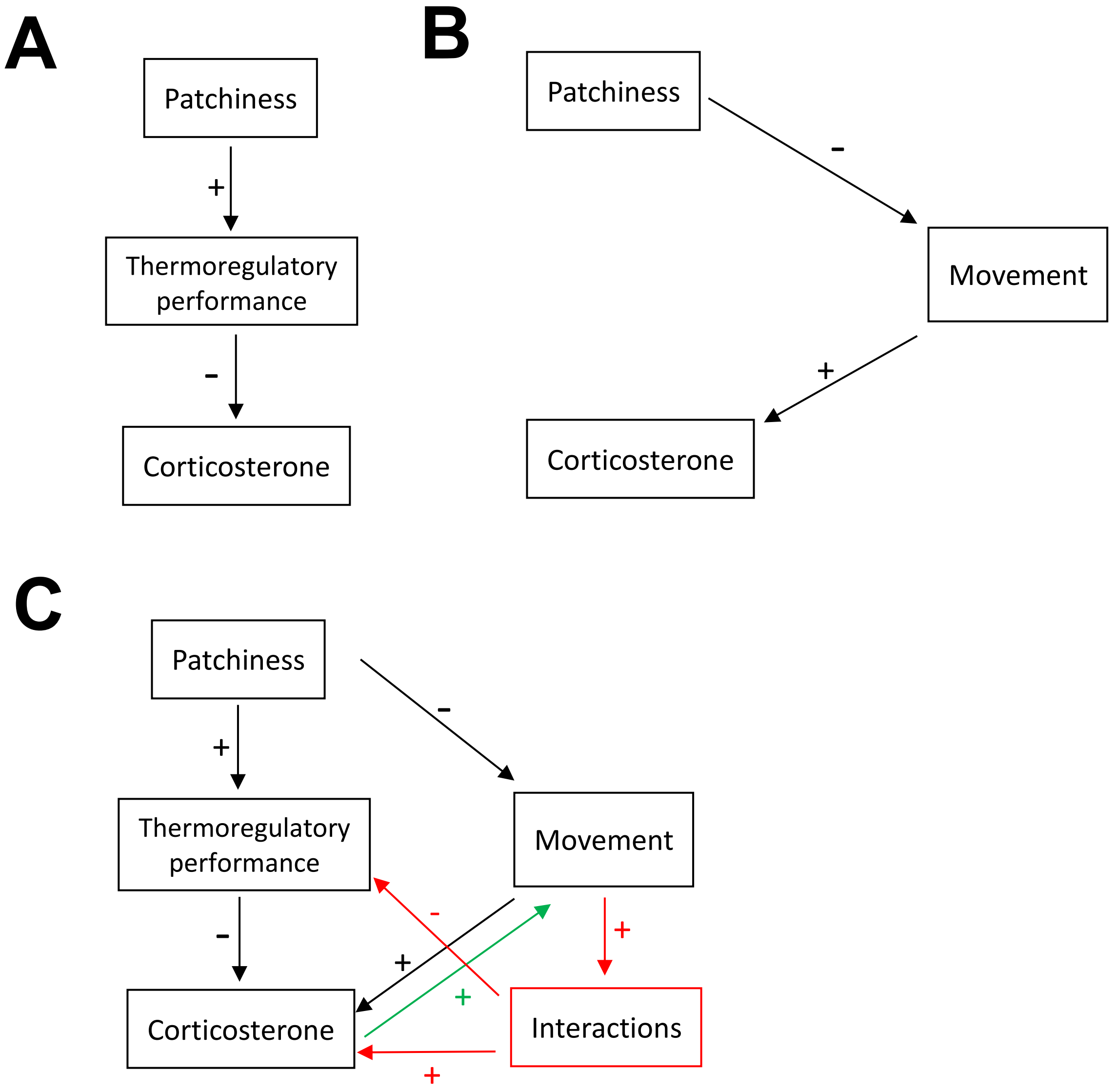


Fig 3.8. Causal pathways used to infer how the thermal landscape (patchiness) and social context (interactions) can influence corticosterone and activity of male lizards. **(a)** increased patchiness increases thermoregulatory performance, which decreases circulating corticosterone. **(b)** increased patchiness decreases movement, which decreases circulating corticosterone. **(c)** increased thermal patchiness enables both lizards to thermoregulate effectively without moving long distances or occupying the same area, which would reduce aggressive interactions and thus result in lower circulating corticosterone (red arrows). Furthermore, feedbacks between corticosterone and behavior can operate as well, such that the thermal landscape and the social context additively or synergistically alters corticosterone and behavior (green arrow).



CHAPTER FOUR:

The Structure of the Thermal Landscape Determined Movement, Thermoregulation, and Hormones under Simulated Predation

Abstract

Predation risk prevents animals from accessing microclimates needed to thermoregulate. However, the distribution of thermal resources should influence how animals perceive and respond to risk. By simulating predation, we showed that constrained movements and thermoregulation of male lizards (*Sceloporus jarrovi*) under risk depended on the distribution of shade. Under simulated risk, lizards moved less and thermoregulated worse than lizards in a control treatment. However, a patchy distribution of shade ameliorated predation risk because lizards in patchy arenas moved farther and thermoregulated better than lizards in clumped arenas. Furthermore, the patchiness of the landscape influenced physiological stress during simulated risk; lizards in clumped arenas circulated more corticosterone than lizards in patchy arenas. Even without simulated risk, lizards in clumped arenas circulated more corticosterone compared to lizards in patchy arenas, indicating the thermal quality of the landscape affected the energetic demands on lizards. Thus, models should incorporate species interactions and spatial structure when forecasting impacts of climate change on thermoregulation.

Introduction

As the planet continues to warm (IPCC 2014), predicting the response of organisms is of growing importance (Thomas et al. 2004, Sunday et al. 2011, Pacifici et al. 2015, Urban

2015, Bowler et al. 2017). Many species have already altered activity times and shifted geographic ranges to track preferred conditions (Parmesan et al. 1999, Walther et al. 2002, Root et al. 2003, Kerr et al. 2015), but genetic adaptations to climate change have been rare (Balanyá et al. 2006, Lavergne et al. 2010, Hoffmann and Sgrò 2011). Some warming could reduce thermoregulatory costs by enabling temperate ectotherms to maintain higher body temperatures with less effort (Deutsch et al. 2008, Sears and Angilletta 2015, Buckley and Huey 2016). However, excessive warming will constrain thermoregulation and likely lead to extinction events if species cannot disperse or adapt (Huey et al. 2009, Sinervo et al. 2010b, Buckley et al. 2015b). Mechanistic models, which link environmental conditions such as temperature to biological processes, have become a popular tool for assessing the impacts of climate change (Kearney and Porter 2004, Buckley 2008, Kearney and Porter 2009, Maino et al. 2016). These models define thermal constraints on activity, survivorship, and fecundity (Buckley et al. 2010, Bowler et al. 2017, Levy et al. 2017). Under projected climate change scenarios, many mechanistic models predict local or global extinctions (Carpenter et al. 2008, Sinervo et al. 2010b, Maclean and Wilson 2011). Although these models have greatly helped in our understanding of species limitations, they likely underestimate the impacts of climate change as they ignore the costs of biotic interactions, such as those between predators and prey.

A general assumption of existing mechanistic models is that if favorable microclimates exist, animals will access them at no cost (Buckley 2008, Kearney and Porter 2009, Buckley 2010, Elith et al. 2010, Leroux et al. 2013). In reality, however, many factors impose a cost of thermoregulation (Huey and Slatkin 1976b, Angilletta 2009, Sears and Angilletta 2015). In fact, perfect thermoregulation may be maladaptive in the presence of predators. Ecologists who study other behaviors, such foraging and mating, have long recognized the nonlethal costs imposed by risk of predation (Lima and Dill 1990, Brown 1992, Lima 1998a, b, Brown 1999, Brown and Kotler 2004, Jones and Dornhaus 2011). This perspective can be extended to thermoregulation (Downes and Shine 1998, Martín and López 2000, Polo et al. 2005), because temperature simply represents another ecological resource (Magnuson et al. 1979). To effectively thermoregulate, terrestrial ectotherms must seek sun and shade just as they seek food and mates (Cowles and Bogert 1944, Angilletta 2009). However, an animal that behaviorally thermoregulates by shuttling between sun and shade is more visible, and presumably more vulnerable to predators (Lima and Dill 1990, Smith 1992, Skelly 1994, Webb and Whiting 2005). Thus, in risky environments an animal might trade off thermoregulation with safety (Treves 2000, Ito and Mori 2010, Beauchamp 2015). For instance, prey typically respond to a predator by either fleeing to a shelter or freezing in place (Sih 1987, Lima and Dill 1990, Cooper 2008). Either behavior would hinder thermoregulatory performance, because an ectotherm will cool down when hiding in a refuge or heat up when stationary in the sun (Martín and López 1999, Polo et al. 2005, Angilletta 2009).

To further complicate matters, the tradeoff between regulating temperature and avoiding predators should depend on the spatial distribution of thermal resources. When resources occur throughout space, prey can play a “shell game” to reduce their risk of predation (Mitchell and Lima 2002, Laundré 2010). By moving among patches, the location of prey becomes less predictable to a searching predator. Moreover, a patchy thermal environment enables animals to thermoregulate effectively over a large area (Sears and Angilletta 2015, Sears et al. 2016). By contrast, animals cannot play this shell game and thermoregulate effectively when thermal resources are concentrated in space. Biologists have started to study how predation risk affects the way that organisms thermoregulate. For instance, Mitchell and Angilletta (2009) modeled the evolutionarily stable strategy for ectothermic prey thermoregulating in an environment with endothermic predators. According to their model, prey should occupy a wider range of microclimates in the presence of predators, consequently reducing their thermoregulatory performance. This model was partially supported by a study of larval newts (prey) and dragonfly nymphs (predators); newts spent less time in a warm patch in a treatment with dragonflies than in a control treatment (Gvoždík et al. 2013). However, a shell game between predators and prey can only emerge when preferred microclimates occur in several places at once. Biologists have yet to develop a theory or test hypotheses about this interaction between the thermal landscape and predation risk.

To see whether patchier environments reduce the perceived risk of predation, I measured the movement patterns and body temperatures of male spiny lizards (*Sceloporus jarrovi*) in controlled thermal landscapes with and without predation risk. When preferred microclimates are dispersed in space, prey can engage in an antipredator shell game by moving more throughout the environment to remain elusive to the predator, while still being able to thermoregulate carefully. By contrast, when thermal resources are aggregated in space prey cannot simultaneously move throughout the environment and carefully thermoregulate. Therefore, I predicted lizards would perceive less risk of predation when thermal resources are dispersed throughout space and would cover more ground, thermoregulate more efficiently, and to consequently experience less stress.

Methods

Collection and husbandry of animals

In April of 2013, I collected 80 adult males of *Sceloporus jarrovi* in the Chiricahua Mountains of Arizona (1500-2500 m). After capture, lizards were transported to the University of New Mexico's Sevilleta Field Station laboratory. Upon arrival to the laboratory, lizards were massed (mean mass = 17.2 g, SD = 3.8 g), measured (mean snout vent length = 85.3 mm, SD = 5.09 mm), and toe-clipped for identification (Perry et al. 2011).

Lizards were housed individually in plastic terraria (30 x 26 x 13 cm) lined with paper towels. Terraria were heated from below at one end to create a thermal gradient, thus allowing lizards to freely thermoregulate. The operative environmental temperatures along this gradient ranged from 23° to 42°C, as determined by hollow, copper models of a lizard (Bakken and Gates 1975). Cardboard was placed between each terrarium to prevent lizards from viewing each other. Every other day, lizards were provided water fed adult crickets (*Acheta domestica*) and larval beetles (*Tenebrio morio*) coated with a powder of vitamins and calcium (Rep-Cal, Los Gatos, CA, USA). Animals were maintained this way for two weeks before being used in our experiment. Only lizards that ate regularly were included in the study.

Preferred body temperatures

I measured the preferred body temperatures of lizards in artificial thermal gradients following the methods of Schuler and colleagues (2011). These measurements enabled me to establish that lizards would thermoregulate in our arenas and determine the temperatures that they prefer. Thermal gradients were created in plastic containers (112 x 35 x 30 cm) with a substrate of sand (~1 cm deep). These containers were kept in a room at 20 °C and uniformly illuminated from above by fluorescent lights. A 150-W infrared lamp (Exo-Terra, Mansfield, MA, USA), suspended above one end of each container, created a range of operative temperatures from 22° to 44°C. This type of gradient works well for lizards that thermoregulate by basking under natural conditions and forces the lizard to periodically retreat from the infrared lamp to avoid overheating (Angilletta 2009, Schuler et al. 2011).

Each lizard was placed in a thermal gradient at 2000 h, when infrared and fluorescent lights were off. The following morning, fluorescent and the infrared lights were turned on at 0600 and 0700 h, respectively, and were turned off at 2000 and 1700 h, respectively. On this day, lizards explored the thermal gradient undisturbed. On the next day, the bulbs were activated for the same periods, and body temperatures were recorded every 2 h between 0800 and 1600 h. To measure body temperature, each lizard was captured by hand and a quick-reading thermometer (T-4000, Miller & Weber, Inc., Queens, NY) was inserted in its cloaca. During the 44 h that each lizard spent in a thermal gradient (36 h of habituation and 8 h of measurements) no food or water was provided. Based on a previous study, I do not expect that preferred body temperatures of *S. jarrovi* would have differed if food and water were provided (Schuler et al. 2011). After these measurements, each lizard was returned to its terrarium, during which food and water were offered every other day.

Implantation of temperature loggers

Five days after we measured preferred body temperatures, I surgically implanted a miniature temperature logger (1.45 ± 0.05 g; Weedot, Alpha Mach, Inc., Qc, Canada) into the abdominal cavity of each lizard. Each logger was programmed to record temperature at a 10 min interval for the duration of the experiment. To exclude fluids, loggers were coated first with a plastic sealant (Plasti Dip, Plasti Dip International, Blaine, Minnesota, USA) and then with paraffin wax (Gulf Wax, Kalton, Ohio, USA). Surgical procedures followed those of Sears and colleagues (2016). Two weeks after surgery, I re-measured preferred body temperatures, as described above, to see whether the surgery affected thermoregulation. The mean and standard deviations of preferred body temperature estimated from statistical modeling (see *Statistical analyses*) were virtually identical: 34.8 ± 2.1 °C before surgery and 34.3 ± 2.1 °C after surgery. Furthermore, no individual showed a large change in preferred temperature (see Appendix; Fig. S4.1).

Experimental design and treatments

I recorded spatial positions and body temperatures of male lizards in controlled thermal environments with distinct levels of predation risk. To manipulate the thermal environment, I followed methods of Sears et al. (2016). Briefly, I used nine outdoor thermal arenas (20 x 20 m), consisting of sheet metal walls and a canopy of shade cloth (Greenhouse Megastore, Georgetown, IL) that blocked approximately 80% of solar radiation. Shade cloth was suspended 1.2 m above each arena on steel cables, which were fastened to iron posts outside the arena. I kept the total area shaded (36%) consistent for all arenas, but altered the distribution of shade using two distinct designs; 1 large patch (12 x 12 m) or 4 medium patches (6 x 6 m). Because I had nine arenas, each of these spatial arrangements was replicated four (1-patch) and five (4-patch) times (see Fig. 4.1). To simulate predation risk, I flew artificial red-tailed hawks (*Buteo jamaicensis*) along cable flyways above designated arenas 2 m above the ground (see Appendix; Fig S4.2) using fishing line (Shimano, Irvine, CA) and electric motors (Grainger, Lake Forest, IL). To reduce habituation, three flyways were constructed over each arena which allowed flights to occur at random times and trajectories twice an hour during data collection (0720-1220 h).

Each lizard was randomly assigned to one of six treatments: 1) clumped arena with no simulated risk for 2 days (Control), 2) patchy arena with no simulated risk for 2-days (Control), 3) simulated risk on day 1 in a clumped arena, followed by no simulated risk on day 2 (Predation D1), 4) simulated risk on day 1 in a patchy arena, followed by no simulate risk on day 2 (Predation D1), 5) no simulated risk on day 1, followed by simulated risk on day 2 in a clumped arena (Predation D2), or 6) no simulated risk on day 1, followed by simulated risk on day 2 in a patchy arena (Predation D2).

Prior to experiments, lizards underwent a 2 day habituation period to become familiar with the structure of their thermal arena without experiencing predation risk. Following the habituation period (~1230-1300 h), I sampled blood from each lizard to measure total (free plus bound) plasma corticosterone, a common proxy for assessing stress (Munck et al. 1984, Sapolsky et al. 2000, Angelier and Wingfield 2013). Each lizard was captured by hand while in its assigned thermal arean and ~50 µL of blood was collected in a capillary tube by rupturing the orbital sinus. Once filled, each tube was sealed with Critoseal (Fisher Scientific, Pittsburgh, Pennsylvania, USA) and stored on ice. Blood samples were centrifuged within 1 h to separate red blood cells from plasma. Once separated, plasma was stored at -80 °C until assayed (see below). Blood samples were collected within 2 min of capture to minimize effects of handling stress on circulating corticosterone (Langkilde and Shine 2006). After bleeding, lizards were given 1 day of rest where they were offered two crickets and one larval beetles coated in vitamin and calcium powder to supplement water and nutrient loss from blood collection. All lizards were observed consuming 1-3 food items. Following the rest period, each lizard was exposed to 2 days of treatment and data was collected from 0720-1220 h. Following data collection on the second treatment day (~1230-1300), I collected a second blood sample (~50 µL) from each lizard to measure changes in circulating levels of corticosterone following treatments. At the end of the experiment, I had spatial positions, body temperatures, exposure behaviors, and blood samples for each lizard under different predation risk in two distinct thermal environments (see Appendix; Table S4.1 for a description of events).

Movement analysis

I analyzed spatial positions of lizards to estimate the minimum total movement, the minimum area covered, and the probability of exposure in each treatment. A Cartesian coordinate system was painted on the walls of each arena, at 1 m intervals ranging from 0-20 m. During the experiment, I recorded an X-Y spatial position and noted whether each lizard was in shade or exposed to solar radiation, at 20 min intervals between 0820 and 1240 h. Following the experiment, I used triangulation to calculate the distance between successive positions and summed these distances to find the minimum total distance moved by each lizard.

I estimated the minimum area covered by creating a digital Cartesian coordinate system (Microsoft Excel, 2013) simulating the 20 x 20 m outdoor arenas. I plotted the spatial positions of each lizard on the digital Cartesian coordinate system. Once these data were plotted, I counted the number of blocks (i.e., 1 x 1 m) that each lizard traveled through to estimate the minimal area used within the arena. Lastly, I calculated the percentage of observations for which lizards were exposed to solar radiation, or the probability of exposure.

Hormone assays

For each blood sample, I quantified total plasma corticosterone. Hormones were measured using commercial enzyme-linked immunoassay kits (Enzo Life Sciences, Farmingdale, NY). Samples were analyzed in duplicate on the same day, following instructions supplied with the kit. The assay was validated with a standard curve, constructed from serial dilutions for corticosterone (Fokidis et al. 2009). There was no difference between the slopes of a curve produced by serial plasma dilution (4- to 64-fold) and a standard curve. This approach enabled me to determine the appropriate dilutions for testing our samples, which was 32-fold. Diluted samples were distributed randomly within a 96-well plate with a sensitivity of 32.02 pg ml^{-1}. Mean coefficients of variation within assays were 3.59%, 4.68%, 4.71%, and 3.31% while mean coefficient of variation between assays was 4.07%. A total of 144 samples (2 per lizard) were run in duplicate (n = 288 wells).

Statistical analyses

I modeled the effects of predation risk (none, day 1, or day 2) and thermal landscape (1 or 4 patches) on multiple variables: minimum total movement (m), minimum area covered (m^2), body temperature (°C), probability of exposure (0 or 1), and total circulating corticosterone (ng/ml). Each analysis included a mixture of fixed, continuous, and random factors. Temporal block (1-8), body mass (g), and snout vent length (mm) were covariates. The identity of the lizard was included as a random intercept in all models.

Because operative temperatures likely influence thermoregulatory behavior, such as basking, I also included this information when modeling the probability of exposure and body temperature. To obtain a single variable that characterized each thermal environment at each time, I used a principal component analysis to generate a linear combination of two highly correlated variables: the maximum operative temperature and the range of operative temperatures. The first principle component (PC1) captured 97% of the variation in these thermal variables (see Appendix; Table S4.12). Scores of this principle component were used as a covariate in our statistical model.

I used the R Statistical Software (R-Core-Team 2015) to infer the most likely values of means and standard deviations. First, I used the procedure described by Zuur et al. (2009) to determine the most likely random component of the model. Then, I used the *nlme* library (Pinheiro et al. 2012) for analyses of minimum total movement, minimum area covered, corticosterone, and preferred body temperature. To analyze the probability of exposure, I used the *lme4* library (Bates et al. 2015), which permits a binomial link function for discrete data. For body temperature, I used the *mgcv* library (Wood 2006), which enabled us to model the nonlinear relationship between operative temperature and body temperature. In each case, I used the *MuMIn* library (Bartoń 2013) to fit all possible models of fixed effects and interactions. For each model, this package computes the Akaike information criterion and the Akaike weight; the latter parameter estimates the probability that a model describes the data better than other models. Akaike weights were used to calculate a weighted average of each parameter (see Appendix; Tables S4.2-S4.6); we practiced full model averaging, such that the weighted effect was considered zero for all factors excluded from a model (Burnham and Anderson 2002). The resulting values of parameters were used to calculate the most likely mean of a dependent variable for each treatment (see Appendix;; Tables S7-S11). This approach eliminates the need to interpret *P* values, because all models (including the null model) contributed to the most likely value of each mean.

Results

When averaged across days, both simulated risk and thermal patchiness determined how lizards used space. Without a simulated risk of predation, lizards in clumped arenas moved 31% further and covered 15% more area than lizards in patchy arenas did (Figs 4.2 and 4.3, control boxes). However, this behavior reversed under a simulated risk of predation; lizards in patchy arenas moved 37% further and covered 41% more area than lizards in clumped arenas, (Figs 4.2 and 4.3, predation boxes), although both groups of lizards moved less and covered less area under simulated predation risk compared to lizards in control treatments. Furthermore, lizards that experienced simulated risk on day 1 still moved less and covered less area on day 2 than lizards in control treatments did (see Figs 4.2 and 4.3).

Similarly, simulated risk and thermal patchiness affected the probability that a lizard was exposed to solar radiation. Without simulated risk, lizards in patchy arenas were more likely to occupy positions exposed to solar radiation (68%) compared to lizards in clumped arenas (59%), though this trend was stronger on day 1 than on day 2 (Fig 4.4, control box). Under simulated risk, lizards reduced their exposure to solar radiation to 40% or 48% in clumped or patchy arenas, respectively (see Fig 4.4, Predation boxes); still, lizards in patchy arenas exposed themselves more compared to lizards in clumped arenas (Fig 4.4, predation boxes). When risk was removed on day 2, lizards returned to the baseline probability of basking in solar radiation (Fig 4.4 Predation D1 box).

Although most lizards thermoregulated accurately when possible (see Table 4.1 and Fig 4.5), predation risk and thermal patchiness interacted to influence the strategy of thermoregulation. Lizards in a clumped arena responded to simulated risk by shifting from a strategy of thermoregulation toward a strategy of thermoconforming, as evidenced by the linear relationship between operative environmental temperatures and body temperatures (Fig 4.5b). On days without simulated risk, lizards in the risky treatment maintained body temperatures comparable to those of lizards in the control treatment (see Table 4.1, Fig. 4.5c). The precision of body temperatures also depended on predation risk and thermal patchiness. On days without simulated risk, lizards in clumped arenas thermoregulated less precisely than lizards in patchy arenas, as evidenced by a greater standard deviation of body temperature (3.3 vs. 3.0°C; see Fig 4.6, control bars). With simulated risk, lizards maintained their preferred body temperature less precisely; the standard deviation of body temperature was 4.5 and 3.9 °C in the clumped arenas and patchy arenas, respectively (Fig 4.6, predation bars). On the day after simulated risk, lizards still thermoregulated with less precision than lizards in control treatments; this lag effect of predation risk occurred in clumped arenas and patchy arenas, as evidenced by slightly elevated standard deviations of body temperature (3.7 and 3.5°C; see Fig 4.6, bars for Predation D1).

Lizards likely perceived a risk of predation and a constraint on thermoregulation in our experimental arenas. By the end of the experiment, lizards exposed to simulated predation risk or clumped thermal resources circulated more corticosterone than did lizards under other conditions. Without simulated risk, lizards in clumped arenas circulated 74% more corticosterone than lizards in patchy arenas (see Fig 4.7, Control box). With simulated risk, lizards circulated several-fold greater levels of corticosterone; this effect of predation risk was amplified by thermal constraints, such that lizards in clumped arenas circulated 3.5-fold more corticosterone while lizards in patchy arenas circulated only 2.8-fold more corticosterone. Even with these large effects of predation risk, lizards in clumped arenas still circulated 47% more corticosterone than lizards in patchy arenas (see Fig 4.7 Predation boxes). On the day after simulated risk, lizards must have experienced a lag effect on the hypothalamic-pituitary-adrenal axis. One can infer this effect from the greater circulating corticosterone in lizards that experienced simulated risk on the first day of the experiment, relative to lizards that never experienced simulated risk (an increase of 256% or 343% in patchy or clumped arenas, respectively; see Fig 4.7, Predation D1 box). Thus, the effects of predation on movement and thermoregulation were tied to a hormonal response that would likely mobilize energy needed to overcome an environmental stress.

Discussion

Animals move according to several important but often conflicting demands. For instance, shuttling between sun and shade prevents overheating, but thermoregulating in the presence of a predator can lead to death (Huey 1974, Pitt 1999). Consequently, animals face numerous tradeoffs when making decisions, often favoring behaviors that ensure immediate survival at the expense of growth or reproduction (Lima and Dill 1990, Brown 1999, Gallagher et al. 2017). Thus, an individual should use space in a way that balances its need to secure resources and avoid predators. However, the structure of the "resource landscape" should influence how an individual balances these conflicting demands (Mitchell and Lima 2002, Arthur et al. 2004, Whittingham and Evans 2004). When critical resources are dispersed, animals can access them while moving throughout a larger area. Such a landscape helps prey become less predictable to predators (Mitchell and Lima 2002, Laundré 2010). By contrast, animals must remain within a smaller area when critical resources are concentrated. My results support this hypothesis: male lizards under perceived risk used more habitat, thermoregulated more precisely, and circulated less corticosterone in a patchy landscape than they did in a clumped landscape.

In general, lizards used less space (Figs 4.2 and 4.3) and avoided open areas (Fig 4.4) when exposed to a simulated predator than when exposed to a control treatment. This result makes sense, given that animals commonly avoid predators by running into burrows or hiding under vegetation (Dickman 1992, Cooper and Avalos 2010). No shelters or vegetation were available in my experimental arenas, however, lizards frequently ran under the shade cloth in response to a simulated predator. Although these behaviors reduce predation risk, they prevent animals from accessing solar radiation needed to effectively thermoregulate. Consequently, an animal in a refuge must contend with a body temperature that drops below its optimal temperature for physiological functions (Martín and López 1999, Polo et al. 2005, Angilletta 2009). In reptiles, numerous functions become impaired when body temperature falls substantially (Huey 1982b, Stevenson et al. 1985, Angilletta et al. 2002). In fact, even an animal's ability to flee a predator depends on its body temperature (Cooper and Blumstein 2015); a colder animal, which cannot attain maximal speeds, is more likely to avoid predators by crypsis than by fleeing (Hertz et al. 1982, Irschick and Losos 1998, Cooper 2000). Thus, lizards exposed to simulated risk in our experiment likely moved less and sought cover to reduce predation risk, with a loss of physiological performance (see Table 4.1; Figs 4.5 and 4.6).

Missed opportunities to acquire resources have consequences for growth and reproduction later in life, especially if they occur during crucial periods of the life cycle or activity season (Scrimgeour and Culp 1994, Brown 1999, Lind and Cresswell 2005). For example, Downes (2001) quantified long-term consequences of predation risk for the growth of lizards. Garden skinks were raised to maturity in outdoor enclosures under differing levels of predation risk: a snake scent or a control scent. Lizard exposed to a snake scent became active later in the day, moved less throughout the environment, and selected "safer" microhabitats than did lizards exposed to a control scent. These behavioral responses reduced opportunities to bask and forage. Over the course of the study, lizards gradually became less responsive to the olfactory cues, until activity patterns and microhabitat use became indistinguishable between the treatment groups. However, lizards exposed to predation scent grew slower and attained smaller body sizes as adults, which led to females producing lighter eggs and offspring. Thus, antipredator behavior, especially early in development, imposes a long-term cost that likely reduces fitness below levels achieved in safe environments (Downes 2001). Similarly, male spiny lizards (*S. jarrovi*) must forage during spring and summer after burning through fat in winter, and then store sufficient fat to fuel territoriality and courtship in the fall (Goldberg 1972, Ruby 1978). Males that grow less would suffer a disadvantage, because larger males secure more resources, attract more mates, and survive longer (Simon 1975, Ruby 1981, Rusch and Angilletta 2017). Additionally, males of *S. jarrovi* forage much less during the breeding season, spending most of their time on reproductive activities such as patrolling, displaying, and fighting (Ruby 1978, Marler and Moore 1988). Even when abundant food exists, predation risk can hinder a lizard’s ability to thermoregulate and forage, reducing muscle mass and thus competitive ability (Martín et al. 2003, Amo et al. 2007). Thus, landscapes that afford opportunities to thermoregulate and forage, while avoiding predators, would enhance the fitness of an animal.

Although perceived predation risk influenced the behavioral decisions of all lizards, the magnitude of the responses depended on the spatial distribution of thermal resources. Possibly, lizards perceived predation risk differently in patchy and clumped thermal landscapes and responded accordingly (Brown 1999, Arthur et al. 2004). For instance, if a habitat only has one or a few refuges, an animal will be more exposed when moving through the environment, making them more vulnerable to predators. On the other hand, habitats with many refuges enable an animal to hide throughout the environment, making active prey less vulnerable to predators. In fact, movement may even benefit prey in complex environments, as in a shell game in which an individual moves randomly to make its position less predictable to predators (Mitchell and Lima 2002, Laundré 2010). Because the distribution of thermal resources determines how effectively an individual can elude its predators, the patterns of movement in our experiment could have resulted from antipredator strategies tailored to the thermal landscape: low activity in a clumped landscape and high activity in a patchy landscape. Given this interaction between resource distribution and predation risk, the optimal behavior likely differs between patchy and clumped thermal landscapes (Mitchell and Angilletta 2009). Moving throughout the landscape in a shell game would simultaneously improve predator avoidance and thermoregulatory performance if preferred microclimates can be accessed in many places. Consistent with this idea, a simulated risk of predation caused lizards in patchy arenas to thermoregulate more accurately and more precisely than lizards in clumped arenas (see Table 4.1; Fig 4.5b and 4.6 Predation box). Thus, increased thermal patchiness likely buffers the effects of predation risk without impairing (and potentially improving) thermoregulation.

In addition to behavioral responses, perceived risk also increased circulating glucocorticoids. This result supports the idea that animals recognize potential predators and respond with a short-term increase in corticosterone, which then mediates antipredator behaviors to promote survival (Thaker et al. 2009a, Trompeter and Langkilde 2011, Barreto et al. 2014). For example, when Fijian ground frogs viewed a predatory cane toad, they increased circulating corticosterone and moved less frequently, compared to frogs exposed to conspecifics or a control object (Narayan et al. 2013). Consistent with these findings, lizards exposed to simulated predation risk increased their plasma corticosterone and reduced their movement during our experiment. However, an animal's perception of risk likely depends on its ability to escape. For instance, Cockrem and Silverin (2002) exposed both caged and free-ranging birds to a predator. Caged birds greatly increased their plasma corticosterone while free-ranging birds only moderately increased plasma corticosterone. The authors argued that birds perceived predation risk differently in each context because caged birds were unable to escape while free-ranging birds could escape (Cockrem and Silverin 2002). Therefore, lizards in patchy arenas might have circulated less corticosterone than lizards in clumped arenas because they had more sources of cover, which would ameliorate risk.

In the absence of simulated risk, plasma corticosterone was likely linked to energetic demands given the movement patterns and thermoregulatory performance of lizards in our thermal arenas. Because lizards moved more and thermoregulated worse in clumped arenas (see Fig 4.7 Control box), they likely spent more energy than lizards in patchy arenas did (Sears and Angilletta 2015, Basson et al. 2017). Thus, corticosterone might have increased to mobilize the energy needed to cover more ground for thermoregulation in a poorer quality thermal environment (Rees et al. 1985, Gleeson et al. 1993, Girard and Garland 2001). Alternatively, corticosterone might have been the cause of activity rather than a response to activity. If so, the effect of corticosterone must depend on a threshold. Without simulated risk, greater movement accompanied more corticosterone (see Figs 4.2 and 4.7 Control boxes); however, with simulated risk, less movement accompanied more corticosterone (see Figs 4.2 and 4.7 Predation boxes). Therefore, low and high levels of corticosterone must have opposing effects on activity if variation in corticosterone drove variation in movement. A previous study of birds revealed evidence for a threshold shift in the effect of corticosterone, where a slight artificial elevation of corticosterone increased activity but larger elevation decreased activity (Breuner and Wingfield 2000). Further investigation is needed to determine whether corticosterone was the cause or effect of thermoregulatory behavior.

I have shown that behavioral and physiological responses of lizards depended on the interaction between predation risk and the thermal landscape. These results underscore the need to consider abiotic and biotic factors simultaneously when predicting how species will respond to climate change (Angilletta 2009, Zarnetske et al. 2012, Post 2013). If predation risk limits access to thermal resources, the performance, dispersal, and ultimately survival of an animal will depend on the distribution of these resources. Thus far, studies investigating the effects of climate change have mainly focused on measuring changes in the mean or variance of temperature rather than the spatial distribution of temperatures (Kearney and Porter 2009, Buckley et al. 2010, Sinervo et al. 2010b). These models reveal costs of and constraints on activity but ignore factors that might influence these costs and constraints, such as the covariaton between thermal resources and predation risk (Lima 1998a, Sears and Angilletta 2015, Sears et al. 2016). Thus, great potential exists to extend current approaches, or develop new ones, that incorporate species interactions and spatial structure when forecasting impacts of climate change (Araújo et al. 2011, Kissling et al. 2012, Sears and Angilletta 2015, Levy et al. 2016, Sears et al. 2016). Biologists will ultimately need to embrace spatially-explicit models of thermoregulation to understand the behaviors of animals in warming landscapes (Angilletta 2009, Sears and Angilletta 2015, Basson et al. 2017).

Table 4.1. Mean body temperatures and % of observed temperatures within one standard deviation of the preferred temperature (32.5 – 36.7 °C). Means were estimated with a statistical model derived from multimodel averaging.

Treatment	*Patches*	*Mean T_B (°C)*	*T_B within PT*
Control	1	29.6	43%
Control	4	30.8	52%
Predation	1	28.6	35%
Predation	4	30.0	46%
Post Predation	1	29.3	40%
Post Predation	4	30.5	49%

Fig 4.1. Large, outdoor arenas (400 m^2) were used to manipulate the thermal landscape. Each arena contained one of two levels of patchiness: 1 patch **(A)** or 4 patches **(B)**.

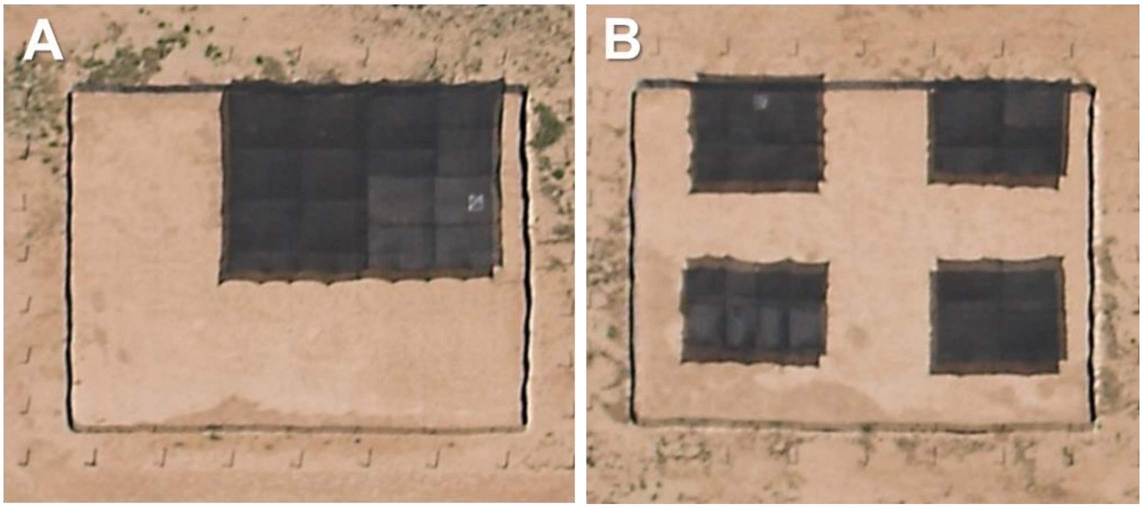


Fig 4.2. Without simulated risk, lizards in clumped arenas moved farther than lizards in patchy arenas (Control box). With simulated risk, this pattern was reversed (Predation D1 and D2 boxes). Furthermore, lizards that experienced simulated risk on day 1 still moved less on day 2 than lizards in control treatments did (Day 2 of Predation D1 box). Diamonds and grey bars denote means and standard deviations, respectively, computed by multimodel averaging. Each circle denotes the minimum total movement of a lizard. Black or red colors denote data for lizards in clumped or patchy arena, respectively.

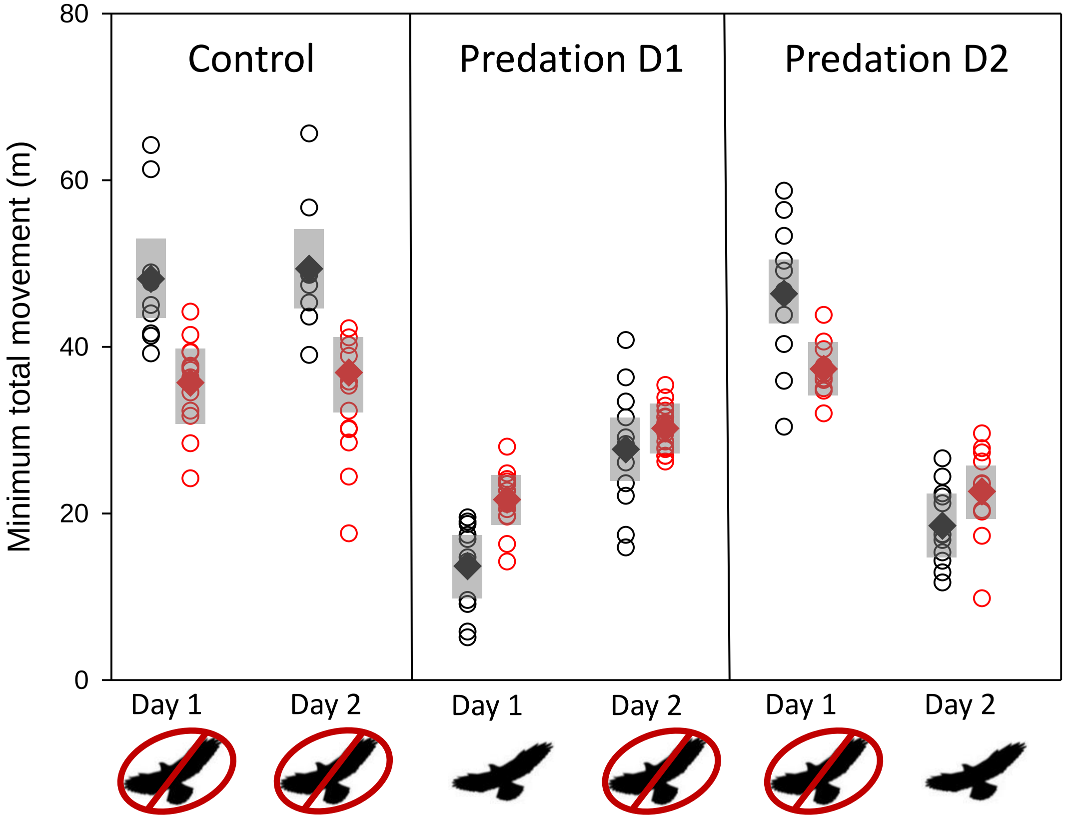


Fig 4.3. Without simulated risk, lizards in clumped arenas covered more area than lizards in patchy arenas (Control box). With simulated risk, this pattern was reversed (Predation D1 and D2 boxes). Furthermore, lizards that experienced simulated risk on day 1 still covered less area on day 2 than lizards in control treatments did (Day 2 of Predation D1 box). Diamonds and grey bars denote means and standard deviations, espectively, computed by multimodel averaging. Each circle denotes the area covered of a lizard. Black or red colors denote data for lizards in clumped or patchy arena, respectively.

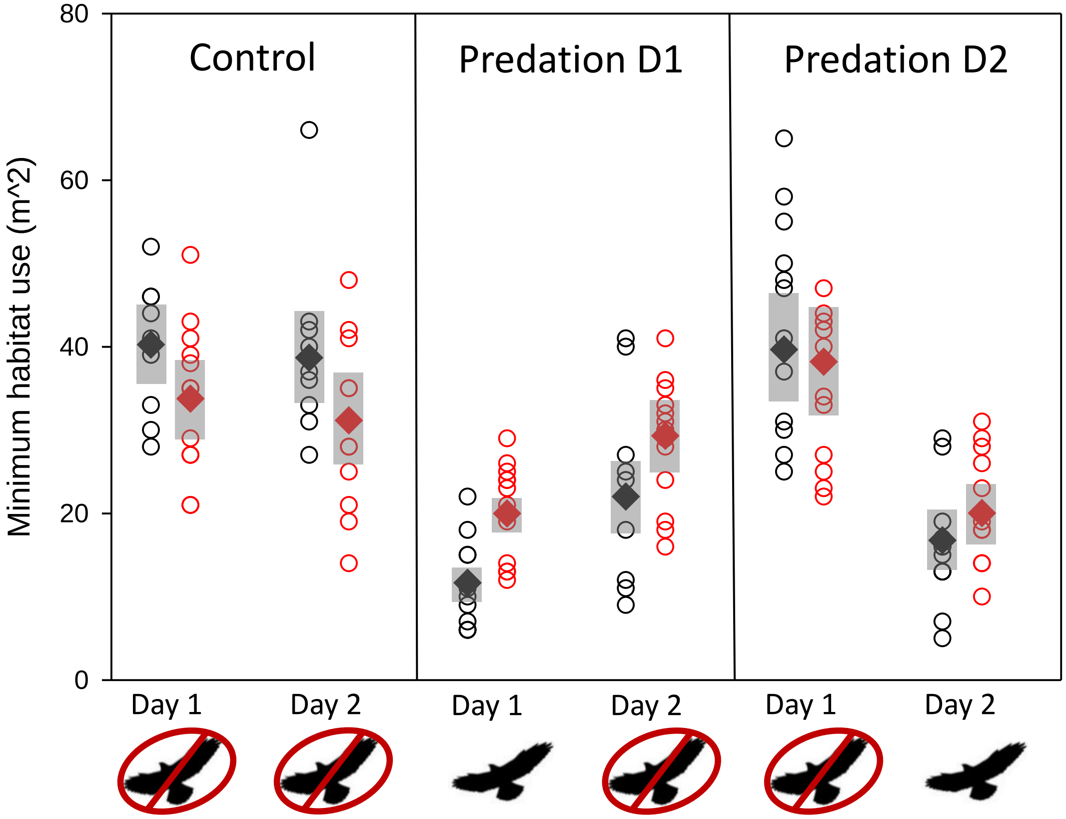


Fig 4.4. Without simulated risk, lizards in patchy arenas were more likely to expose themselves to open areas within the arena than were lizards in in clumped arenas (Control box). With simulated predation risk, all lizards were less likely to expose themselves to open areas, regardless of thermal patchiness (Predation D1 and D2 boxes). Lizards that experienced simulated risk on day 1 returned to control levels of exposure on day 2 in both clumped and patchy arenas (Day 2 of Predation D1 box). Black and red bars denote mean probabilities of exposure with and without simulated risk, respectively, computed by multimodel averaging.

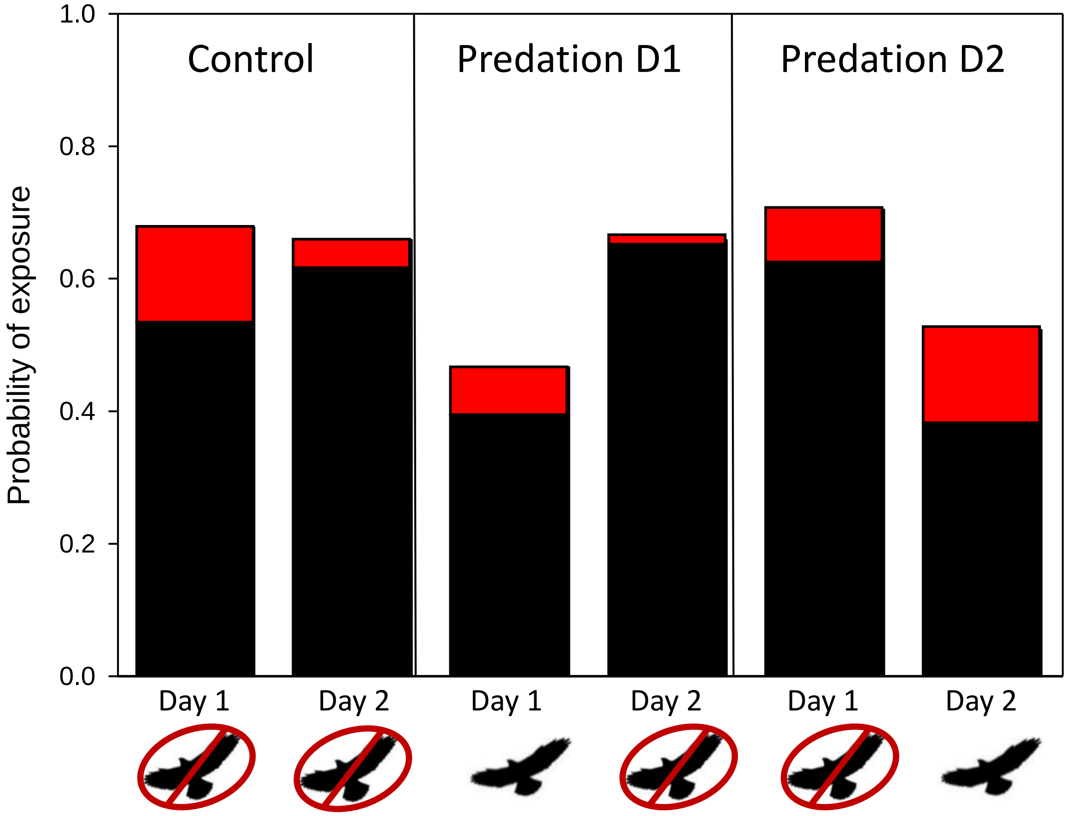
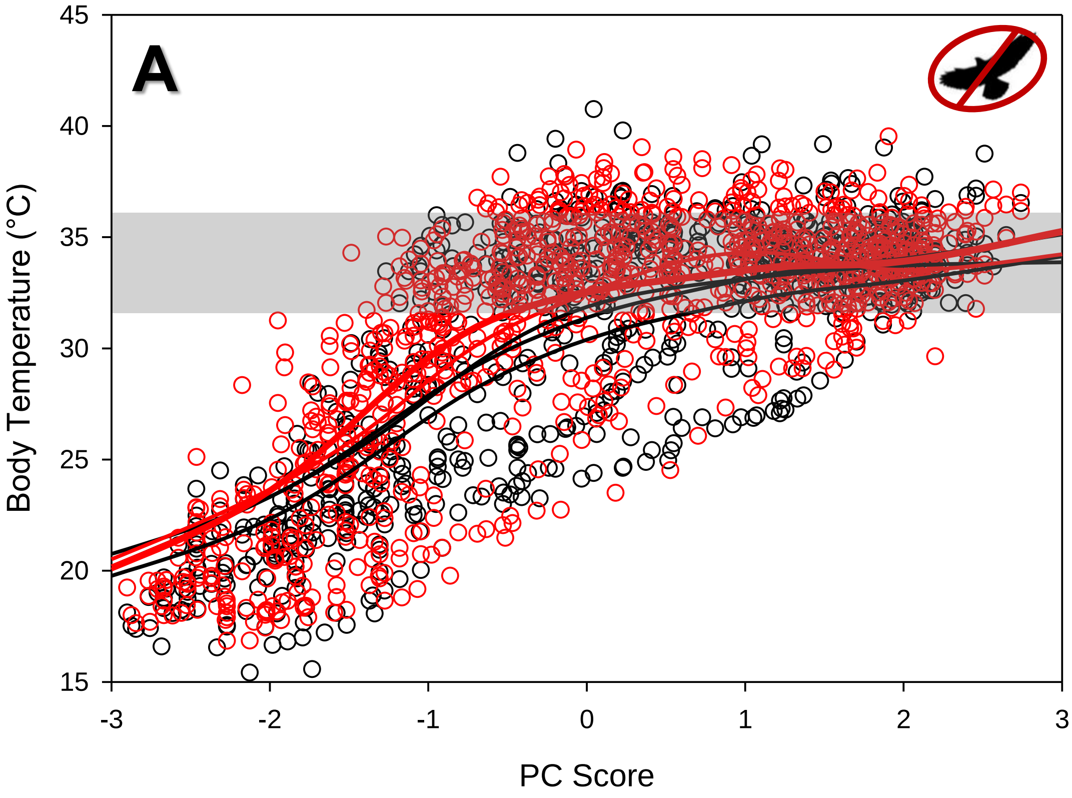
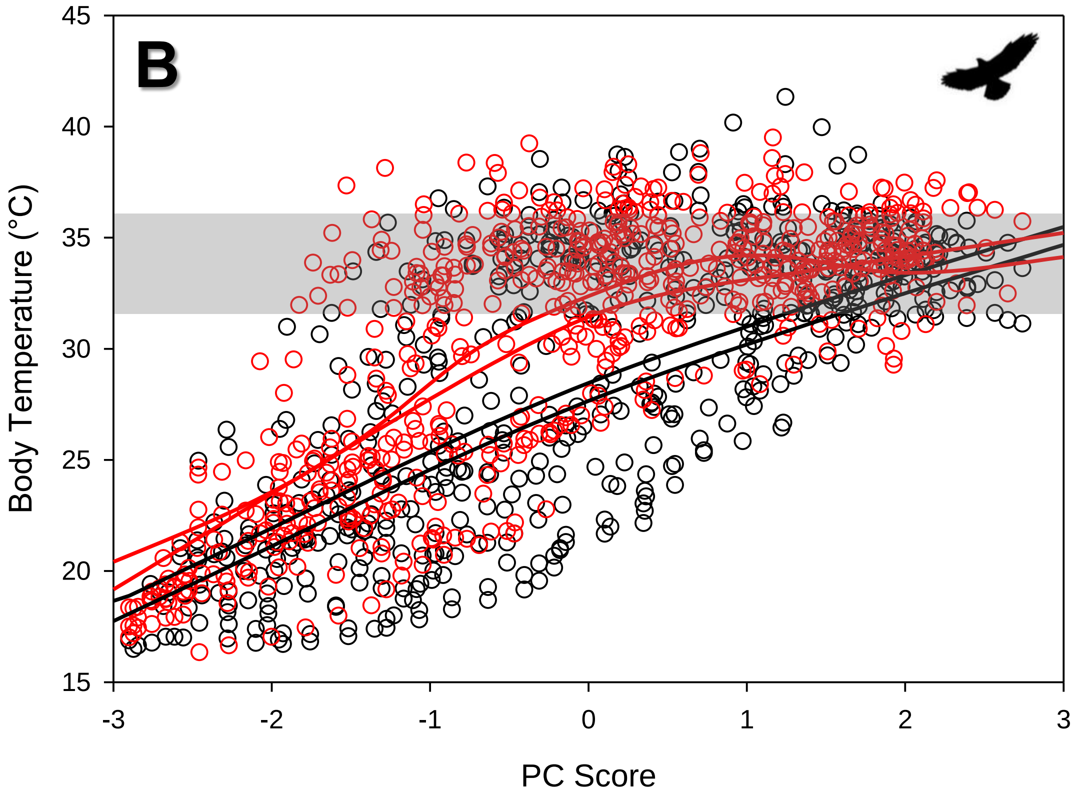


Fig 4.5. Body temperatures of lizards plotted against a principal component of environmental temperatures (Table S12). As PC1 increases, so does the maximum operative temperature and the range of temperatures (between sun and shade). Regardless of whether lizards experienced no simulated risk (A) or some simulated risk (B), lizards in patchier arenas thermoregulated more accurately. However, lizards in clumped arenas responded to simulated risk by shifting from a strategy of thermoregulation toward a strategy of thermoconforming, as evidenced by the linear relationship between operative environmental temperatures and body temperatures (B). Lizards that experienced simulated risk on day 1 thermoregulated nearly as accurate as lizards in control treatments (C). Black and red lines denote mean body temperatures of clumped and patchy arenas computed by multimodel averaging. Each circle denotes a body temperature of a lizard in a clumped arena (black) or patchy arena (red). The gray bar depicts the central 68% of preferred temperatures (32.5 – 36.7 °C), respectively.




B
Body Temperature (°C)
45
40
35
30
25
20
15
-3
-2
-1
0
1
2
3
PC Score

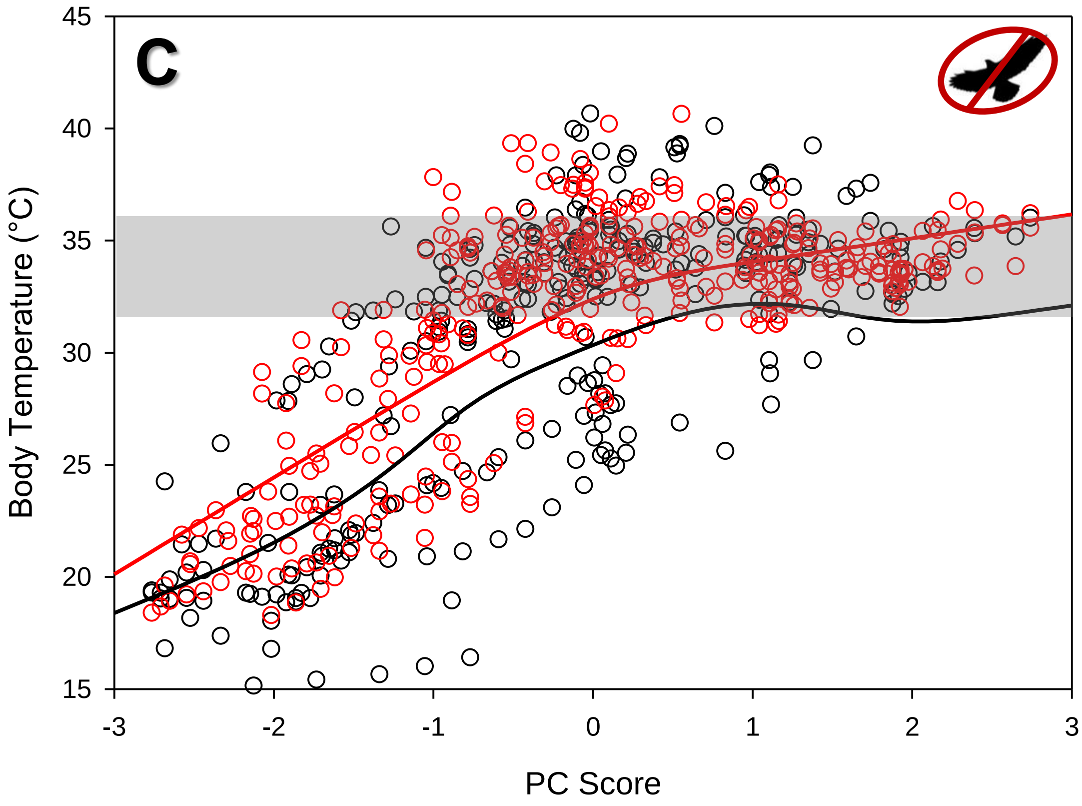

C
Body Temperature (°C)
45
40
35
30
25
20
15
-3
-2
-1
0
1
2
3
PC Score

Fig 4.6. Without simulated risk, lizards in patchy arenas thermoregulated more precisely than lizards in clumped arenas (Control box). With simulated risk, all lizards thermoregulated less precisely, regardless of thermal patchiness (Predation box). Lizards that experienced simulated risk on day 1 did not thermoregulate as precisely as lizards in control treatments, but thermoregulated more precisely than when exposed to simulated risk (Post Predation box). Black and red bars denote standard deviations computed by multimodel averaging.

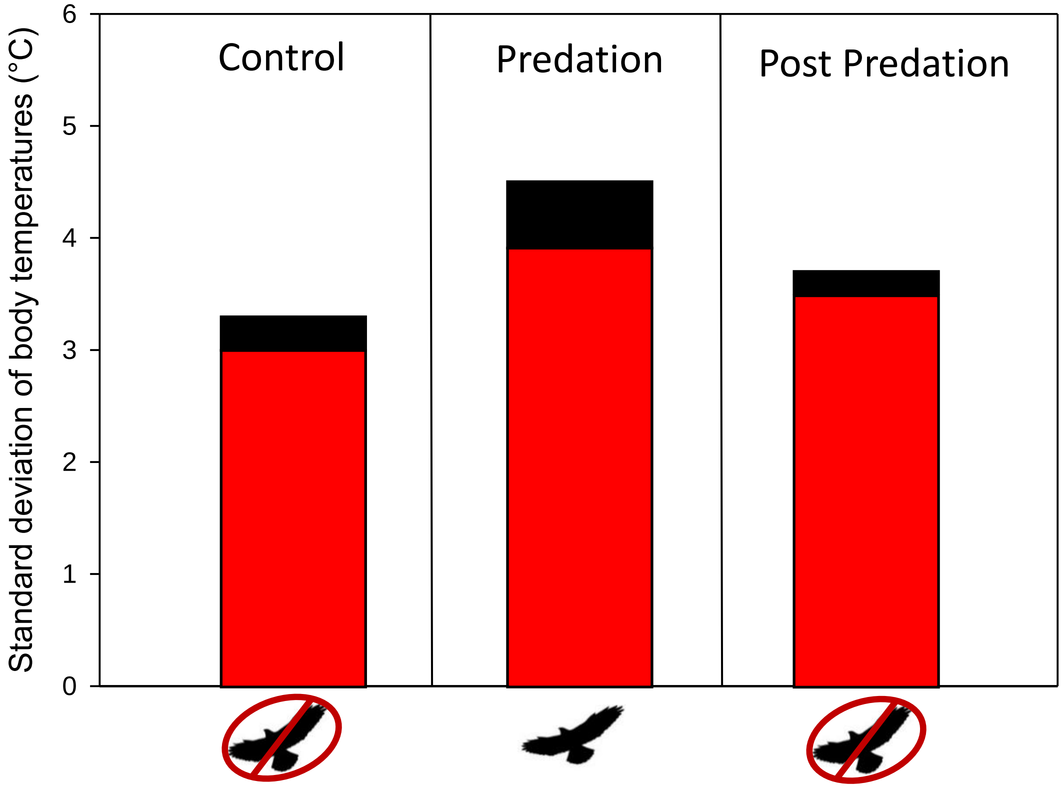
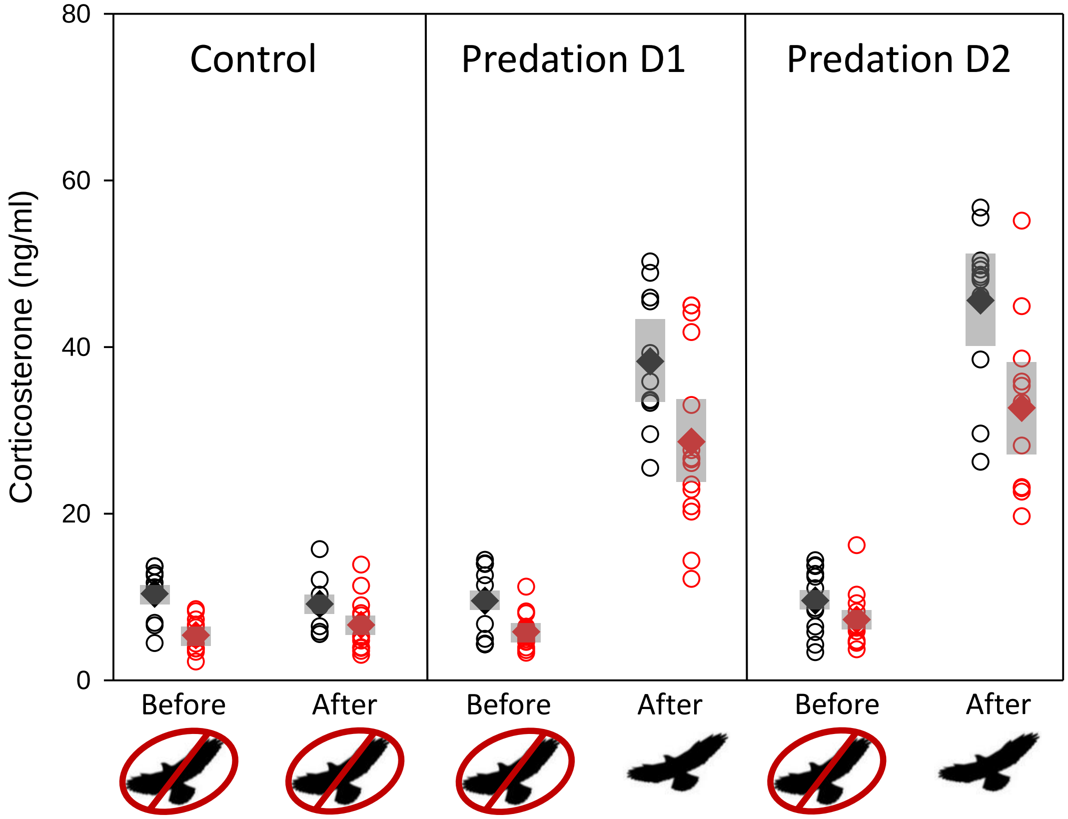


Fig 4.7. All lizards circulated more corticosterone in clumped arenas compared to patchy arenas, regardless of risk. However, this effect was amplified when lizards were exposed to simulated predation risk (Predation D1 and Predation D2 boxes). Diamonds and grey bars denote means and standard deviations, respectively, computed by multimodel averaging. Each circle denotes the circulating plasma corticosterone of a lizard. Black or red colors denote data for lizards in clumped or patchy arena, respectively.



CHAPTER FIVE:

Conclusions and Future Directions

My dissertation revealed the importance of considering abiotic and biotic factors of the environment when quantifying costs of thermoregulation. Both the presence of competitors and predators altered thermoregulation, movements, and hormones of lizards, but the magnitude depended on the spatial distribution of thermal resources. As thermal resources became patchier, lizards thermoregulated better and perceived less stress, as evidenced by lower plasma corticosterone.

Chapter two revealed male *S. jarrovi* will compete for limited thermal resources, with larger males outcompeting smaller males for access. Surprisingly, however, large males thermoregulated less accurately and less precisely than did small males during competition, presumably by overexploiting limited thermal resources. In fact, large males often warmed well beyond their preferred range of temperatures (34.0 ± 1.4 °C) while defending a heat source, sometimes approaching the mean critical thermal maximum for the species (41.0 ± 1.3 ºC; T. W. Rusch, unpublished). Therefore, large males incurred the risk of overheating to maintain priority access to the heat source in the presence of a conspecific. During the breeding season reproductive behaviors such as courtship and fighting take priority over other activities, such as foraging (Goldberg 1972, Ruby 1978, Marler and Moore 1989). Although such evidence for thermoregulation is scarce, Shillington (2002) found free-ranging male tarantulas regularly experience body temperatures above (24.7 – 35.1 °C) their preferred range (22.1 – 31.3 °C) when searching for females during the breeding season . And Regal (1971) observed that a captive male lizard fixated on a heat source in the presence of another male, and then basked less after the intruder was removed. Thus, male *S. jarrovi* may also sacrifice effective thermoregulation for mating opportunities, especially in the presence of rival males.

All data chapters revealed that both intraspecific competition and simulated predation caused an increase in plasma corticosterone. This result makes sense, because interactions with competitors or predators, such as chasing or fighting, induces a stress response and is energetically expensive (Hack 1997, Summers 2002, Ancona et al. 2010). In fact, even just the sight of a competitor or predator stimulates a corticosterone response in some species (Cockrem and Silverin 2002, Morgan and Tromborg 2007, Narayan et al. 2013). Elevated plasma corticosterone is an important adaptation to short-term changes in the environment, as it mobilizes energy and alters behaviors to aid immediate survival (Sapolsky et al. 2000, Summers 2002, Stephens et al. 2007). However, elevated corticosterone also imposes costs, such as reduced aggression, activity, and courtship (Schuett et al. 1996, Moore and Mason 2001, Cockrem and Silverin 2002), which can lead to missed opportunities and reduced fitness.

A major finding of my dissertation was that the costs of competition or predation were dependent on the distribution of thermal resources. As patchiness increased, thermoregulation improved (chapter four) and corticosterone decreased (chapters three and four). Possibly, lizards perceived risk differently in patchy and clumped thermal landscapes and responded accordingly (Brown 1999, Arthur et al. 2004). For instance, lizards in clumped arenas fought regularly for access to the single shade patch, which resulted in reduced thermoregulatory performance and highly elevated plasma corticosterone. Conversely, lizards in patchier arenas fought less as they were able to simultaneously occupy different thermal resources. This resulted in improved thermoregulation and lower plasma corticosterone, compared to lizards in clumped arenas. Similarly, lizards exposed to simulated predation in clumped arenas decreased their movements and increased use of cover, presumably in fear of predation. This resulted in decreased thermoregulatory performance and highly elevated plasma corticosterone. However, when lizards were exposed to simulated predation in patchy arenas, they moved greater distances and exposed themselves more. This resulted in improved thermoregulation and lower plasma corticosterone, compared to lizards in clumped arenas. In fact, movement may even benefit prey in complex environments, as in a shell game in which an individual moves randomly to make its position less predictable to predators (Mitchell and Lima 2002, Laundré 2010). Thus, increased thermal patchiness buffered the effects of competition and predation on thermoregulatory performance and stress levels.

Even without competitors or predators, lizards showed differences in plasma corticosterone in the different thermal arenas (chapters three and four). However, these corticosterone levels likely reflected the energetic demands of the observed movements and thermoregulation of lizards in the thermal arenas. Because lizards moved more and thermoregulated worse in clumped arenas, they likely spent more energy than lizards in patchy arenas did (Sears and Angilletta 2015, Basson et al. 2017). Thus, lizards may have circulated more corticosterone to mobilize the energy needed to cover more ground for thermoregulation in a poorer quality thermal environment (Rees et al. 1985, Gleeson et al. 1993, Girard and Garland 2001). Because plasma glucocorticoids are commonly used to indicate the health of an animal (Sapolsky et al. 2000, Romero and Wikelski 2001, Romero 2004), the results of my experiments provide the first evidence that the structure of the thermal landscape affects circulating glucocorticoid levels. Therefore, ecologists might be able to infer the thermal quality of an environment by measuring plasma glucocorticoids, something that has never been done before.

My dissertation has demonstrated that behavioral and physiological responses of lizards depends on both the thermal landscape and intraspecific competitors or predation risk. The results of control lizards underscore the need to move beyond the indice of d_e when quantifying the thermal quality of an environment (Christian et al. 1985, Hertz et al. 1993, Blouin-Demers and Nadeau 2005). In my experiments, the mean and variance of operative temperatures was roughly equal among the different thermal landscapes. Yet, lizards thermoregulated less effectively, move greater distances, and circulated more corticosterone as the patchiness of the thermal landscape decreased. Thus, my results underscore the need to better understand how abiotic and biotic factors interact to determine an organism’s thermoregulatory performance. Furthermore, my results are important when assessing current and future threats of climate change. If the predicted warming (Walther et al. 2002, Edenhofer et al. 2014) limits the abundance of preferred microclimates (Sinervo et al. 2010a, Sears et al. 2016), animals will likely increase competition for space, making animals more predictable, and presumably vulnerable, to predators (Mitchell and Lima 2002, Laundré 2010). Therefore, studies investigating the effects of climate change need to focus on more than just changes in the mean or variance of temperature by also considering the spatial distribution of temperatures (Sears and Angilletta 2015, Sears et al. 2016, Basson et al. 2017) and the covariaton between thermal resources and biotic factors, such as competitors and predators (Lima 1998a, Sears and Angilletta 2015, Sears et al. 2016). Luckily though, mechanistic models are flexible, thus providing opportunities to incorporate further biological detail, such as biotic interactions. Ultimately, biologists will need to embrace spatially-explicit models of thermoregulation to understand the behaviors of animals in warming landscapes (Angilletta 2009, Sears and Angilletta 2015, Basson et al. 2017).

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APPENDIX A

SUPPLEMENTAL MATERIAL

Fig S2.1. On average, lizards preferred the same body temperatures before and after surgical implantation of temperature loggers. Black symbols represent the mean temperature of each lizard in a thermal gradient. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

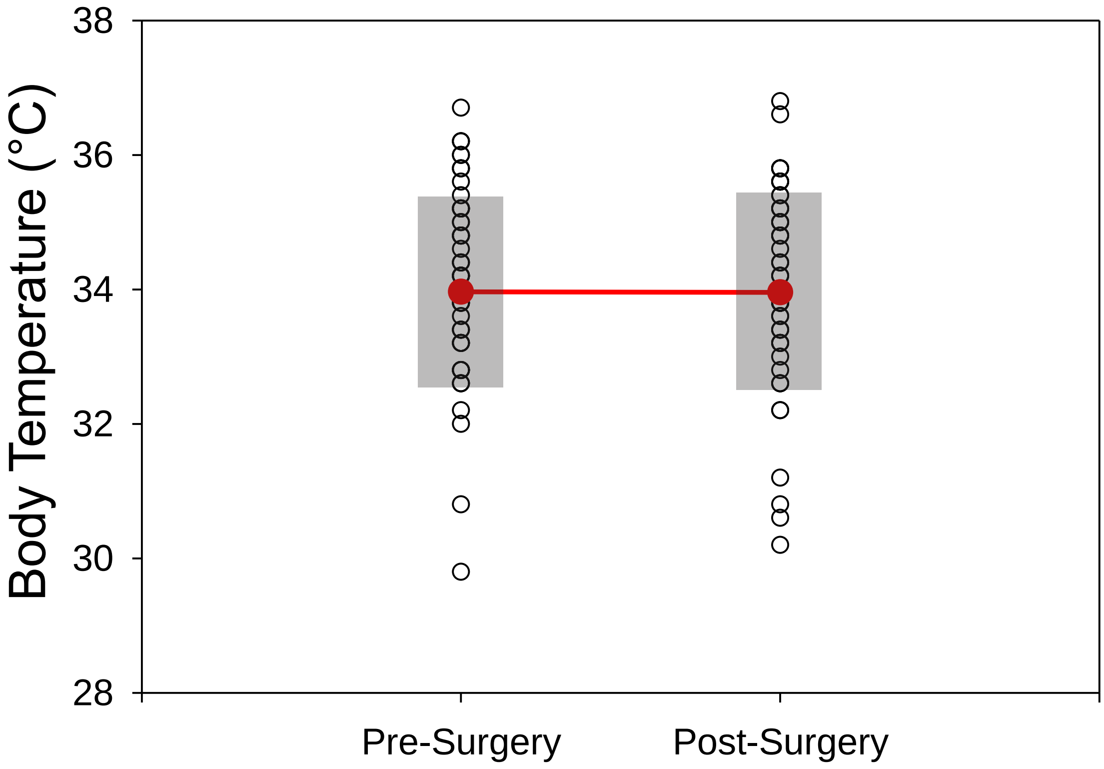

Table S2.1. Outline of experimental design indicating when specific events occurred.

Day	*Event*
1-2	Habituation in isolation
3-4	Treatment #1
5	Blood draw #1
6-12	Rest (provided food and water daily)
13-14	Habituation in isolation
15-16	Treatment #2
17	Blood draw #2

Table S2.2. A ranking of mean distance from heat lamp models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of rank and treatment, as well as the interaction among these variables. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
Models with likelihood > 0.01					
1. block + mass + rank + treatment + (treatment · rank)	8	-105.5	232.3	0	0.36
2. block + rank + treatment + (treatment · rank)	7	-107.3	232.5	0.15	0.33
3. mass + rank + treatment + (treatment · rank)	7	-108.8	235.6	3.30	0.07
4. block + order + rank + treatment + (treatment · rank)	8	-107.2	235.7	3.36	0.07
5. block + mass + order + rank + treatment + (treatment · rank)	9	-105.4	235.8	3.42	0.06
6. rank + treatment + (treatment · rank)	6	-111.2	237.3	4.98	0.03
7. block + order + rank + treatment + (order · treatment) +	9	-106.9	238.8	6.46	0.01

(treatment · rank)					
8. mass + order + rank + treatment + (treatment · rank)	8	-108.8	238.9	6.55	0.01
9. block + mass + order + rank + treatment + (order ·treatment) + (treatment · rank)	10	-105.1	239.0	6.67	0.01
Full model (ranked 22nd). block + mass + treatment + rank + order + (treatment · rank) + (treatment · order) + (rank · order) + (treatment · rank · order)	12	-104.4	246.3	13.93	0.00
Null model (ranked 48th). intercept only	4	-121.9	253.2	20.85	0.00

Table S2.3. A ranking of body temperature models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of rank, treatment, and order, as well as the interaction among these variables. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
Models with likelihood > 0.01					
1. day of trial + block + order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	17	-9695.7	19425.6	0	0.28
2. block + order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	16	-9696.8	19425.6	0.12	0.27
Full Model. day of trial + block + mass + order + rank + time of day + treatment + (order · rank) + (order · treatment) +	18	-9695.8	19425.7	1.96	0.11

(rank · treatment) + (order · rank · treatment)					
4. block + mass + order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	17	-9696.7	19427.5	2.08	0.10
5. day of trial + order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	16	-9698.4	19427.6	3.39	0.05
6. order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	15	-9699.5	19429.1	3.53	0.05
7. day of trial + block + order + rank + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	16	-9699.3	19429.1	4.91	0.02
8. block + order + rank +	15	-9700.2	19430.5	5.04	0.02

treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)					
9. day of trial + mass + order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	17	-9698.4	19430.6	5.33	0.02
10. order + rank + time of day + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	16	-9699.5	19430.9	5.46	0.02
11. day of trial + block + mass + order + rank + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	17	-9699.2	19431.0	6.86	0.01
Null model (ranked 297th). intercept only	7	-9739.9	19493.9	68.28	0.00

Table S2.4. A ranking of total movement models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. mass + treatment	5	-301.5	615.0	0	0.19
2. treatment	4	-302.9	615.2	0.25	0.17
3. rank + treatment	5	-302.1	616.2	1.21	0.10
4. mass + order + treatment	6	-301.1	617.1	2.17	0.06
5. order + treatment	5	-302.9	617.8	2.84	0.05
6. block + treatment	5	-302.9	617.8	2.87	0.05
7. mass + rank + treatment	6	-301.5	617.8	2.89	0.04
8. block + mass + treatment	6	-301.5	617.9	2.89	0.04
9. rank + treatment + (rank · treatment)	6	-301.5	617.9	2.93	0.04
10. order + rank + treatment	6	-302.0	618.9	3.98	0.03
11. block + rank + treatment	6	-302.1	619.0	4.01	0.03
12. mass + order + treatment + (order · treatment)	7	-300.6	619.1	4.15	0.02
13. order + treatment + (order · treatment)	6	-302.4	619.6	4.62	0.02

14. mass + rank + treatment + (rank · treatment)	7	-300.9	619.8	4.81	0.02
15. mass + order + rank+ treatment	7	-301.0	620.1	5.10	0.02
16. block + mass + order + treatment	7	-301.1	620.2	5.25	0.01
17. block + order + treatment	6	-302.8	620.6	5.61	0.01
18. order + rank + treatment + (rank · treatment)	7	-301.4	620.9	5.90	0.01
19. block + rank + treatment + (rank · treatment)	7	-301.4	620.9	5.93	0.01
20. order + rank + treatment + (order · treatment)	7	-301.46	620.9	5.96	0.01
Null model (ranked 43rd). **i**ntercept only	3	-309.8	626.3	11.33	0.00
Full model (ranked 74th). block + mass + order + rank + treatment + (order · rank) +(order · treatment) + (rank · treatment) + (order · rank · treatment)	12	-299.4	636.3	21.33	0.00

Table S2.5. A ranking of corticosterone models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC*$_c$	Δ*AIC*$_c$	*Weight*
1. rank + treatment + (rank · treatment)	9	-121.6	268.2	0	0.26
2. treatment	7	-126.0	270.0	1.81	0.11
3. treatment + mass	8	-124.6	270.5	2.38	0.08
4. order + rank + treatment + (rank · treatment)	10	-120.9	270.7	2.50	0.08
5. mass + order + treatment	9	-122.9	270.8	2.65	0.07
6. rank + treatment	8	-124.7	270.8	2.65	0.07
7. rank + treatment + mass + (rank · treatment)	10	-121.3	271.4	3.29	0.05
8. block + rank + treatment + (rank · treatment)	10	-121.5	271.8	3.66	0.04
9. block + mass + order + rank + treatment + (rank · treatment)	11	-119.8	272.6	4.50	0.03
10. order + treatment	8	-125.7	272.8	4.68	0.03
11. order + rank + treatment	9	-124.0	273.0	4.85	0.02

12. block + treatment	8	-126.0	273.3	5.11	0.02
13. block + mass + treatment	9	-124.3	273.5	5.34	0.02
14. order + rank + treatment + (order · rank) + (rank · treatment)	11	-120.4	273.8	5.68	0.02
15. block + rank + treatment	9	-124.6	274.2	6.01	0.01
16. mass + order + treatment + (order · treatment)	10	-122.9	274.5	6.39	0.01
17. order + rank + treatment + (order · treatment) + (rank · treatment)	11	-120.8	274.6	6.47	0.01
18. block + order + rank + treatment + (rank · treatment)	11	-120.9	274.8	6.60	0.01
19. block + mass + rank + treatment + (rank · treatment)	11	-121.1	275.2	7.01	0.01
20. mass + order + rank + treatment + (order · rank) + (rank · treatment)	12	-119.1	275.7	7.52	0.01
21. order + rank + treatment + (order · rank)	10	-123.5	275.9	7.71	0.01
Null model (ranked 36th). **i**ntercept only	6	-132.49	280.0	11.74	0.00
Full model (ranked 67th). block + mass + order + rank + treatment + (order · rank) +(order · treatment) +	15	-118.0	289.9	21.75	0.00

(rank · treatment) +

(order · rank · treatment)

Table S2.6. A ranking of testosterone models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. rank + treatment + (rank · treatment)	9	-151.6	328.2	0	0.40
2. rank	7	-156.4	330.7	2.52	0.11
3. rank + treatment + order + (rank · treatment)	10	-151.4	331.6	3.45	0.07
4. rank + treatment + block + (rank · treatment)	10	-151.6	332.0	3.78	0.06
5. rank + treatment + mass + (rank · treatment)	10	-151.6	332.1	3.88	0.06
6. mass	7	-157.6	333.2	4.97	0.03
7. rank + order	8	-156.1	333.6	5.42	0.03
8. treatment	7	-158.0	334.0	5.75	0.02
9. rank + block	8	-156.3	334.0	5.75	0.02
10 Null model. intercept only	6	-159.5	334.0	5.77	0.02
11. rank + treatment	8	-156.4	334.0	5.84	0.02
12. rank + mass	8	-156.4	334.1	5.85	0.02

13. rank + treatment + order + (rank · treatment) + (order · treatment)	11	-151.1	335.3	7.07	0.01
14. treatment + mass	8	-157.2	335.6	7.44	0.01
15. rank + treatment + order + (rank · treatment) + (order · rank)	11	-151.4	335.8	7.58	0.01
16. rank + treatment + order + block + (rank · treatment)	11	-151.4	335.8	7.63	0.01
17. rank + treatment + order + mass + (rank · treatment)	11	-151.4	335.8	7.64	0.01
18. order + mass	8	-157.4	336.2	7.95	0.01
19. rank + treatment + block + mass + (rank · treatment)	11	-151.6	336.2	7.97	0.01
20. block + mass	8	-157.6	336.5	8.30	0.01
21. order	7	-159.4	336.8	8.57	0.01
22. treatment + order	8	-157.8	336.9	8.70	0.01
Full model (ranked 72nd). block + mass + order + rank + treatment + (order · rank) + (order · treatment) + (rank · treatment) + (order · rank · treatment)	15	-151.0	355.9	27.73	0.00

Table S2.7**.** Coefficients and standard errors for the model of distance from heat lamp, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	24.92	13.18
block	4.48	2.31
mass	-0.36	0.44
rank	11.96	3.87
treatment	8.97	1.85
order	0.04	0.92
rank · treatment	-18.06	3.83
order · treatment	-0.07	0.72
order · rank	-0.05	0.76
order · rank · treatment	0.01	0.34

Table S2.8**.** Coefficients and standard errors for the model of body temperatures, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	38.75	1.88
day of trial	-0.06	0.09
block	-0.73	0.45
order	-2.23	0.68
rank	-5.46	1.34
time of day	-0.04	0.02
treatment	-2.59	0.56
mass	-0.00	0.04
order · rank	2.45	0.81
order · treatment	1.22	0.35
rank · treatment	4.15	0.68
order · rank · treatment	-1.20	0.04

Table S2.9**.** Coefficients and standard errors for the model of total movement, based on full model averaging.

Independent variable	*Coefficient*	*SE*
Intercept	5323.03	2324.24
mass	-49.72	75.00
treatment	-1268.91	474.62
rank	152.04	560.10
order	-115.07	358.51
block	20.68	235.05
rank · treatment	-59.37	254.56
order · treatment	45.46	224.06
order · rank	13.62	172.23
order · rank · treatment	-0.16	19.80

Table S2.10**.** Coefficients and standard errors for the model of corticosterone, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	35.01	9.79
rank	5.36	6.08
treatment	-5.04	1.67
mass	-0.32	0.64
order	-1.66	3.65
block	-0.28	1.84
rank · treatment	-4.74	5.15
order · rank	-0.29	2.16
order · treatment	0.04	0.60
order · rank · treatment	0.00	0.11

Table S2.11. Coefficients and standard errors for the model of testosterone, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	48.24	28.36
rank	-28.78	16.32
treatment	-10.59	10.57
order	-0.956	4.32
mass	0.12	0.80
block	-0.22	3.35
rank · treatment	18.17	15.34
order · treatment	0.096	1.29
order · rank	-0.06	2.25
order · rank · treatment	-0.00	0.23

Table S3.1. Outline of experimental design indicating when specific events occurred.

Day	*Event*	*Time*
1	Placed in arenas	1800
2-3	Treatment #1	0820-1240
4	Blood draw #1 Returned to laboratory	0900-930
5-6	Rest (provided food and water)	Whole day
7	Placed in arenas	1800
8-9	Treatment #2	0820-1240
10	Blood draw #2	0900-930

Table S3.2. A ranking of mean circulating corticosterone models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of patches and treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. group + patches + rank + treatment + (rank · treatment)	10	-115.2	256.4	0.00	0.27
2. patches + rank + treatment + (rank · treatment)	9	-117.4	257.6	1.16	0.15
3. group + patches + treatment	8	-119.5	258.8	2.36	0.08
4. patches + treatment	7	-121.1	259.0	2.62	0.07

5. group + order + patches + rank + treatment + (rank · treatment)	11	-115.2	259.8	3.38	0.05
6. group + mass + patches + rank + treatment + (rank · treatment)	11	-115.2	259.8	3.39	0.05
7. group + patches + rank + treatment	9	-118.8	260.4	3.93	0.04
8. mass + patches + rank + treatment + (rank · treatment)	10	-117.4	260.8	4.34	0.03
9. patches + rank + treatment	8	-120.5	260.8	4.35	0.03
10. order + patches + rank + treatment + (rank · treatment)	10	-117.4	260.8	4.36	0.03
11. group + mass + patches + treatment	9	-119.1	260.9	4.48	0.03
12. mass + patches + treatment	8	-120.8	261.4	4.94	0.02
13. group + order + patches + treatment	9	-119.5	261.8	5.39	0.02
14. order + patches + treatment	8	-121.1	261.9	5.50	0.02
15. group + patches + rank + treatment + (patches · treatment) + (rank · treatment)	12	-115.0	262.9	6.47	0.01
16. group + patches + rank + treatment + (patches · rank) + (rank · treatment)	12	-115.1	263.1	6.64	0.01
17. group + mass + order + patches +	12	-115.2	263.4	6.96	0.01

rank + treatment + (rank · treatment)					
18. group + mass + patches + rank + treatment	10	-118.8	263.6	7.13	0.01
19. group + order + patches + rank + treatment	10	-118.8	263.6	7.13	0.01
20. patches + rank + treatment + (patches · treatment) + (rank · treatment)	11	-117.2	263.8	7.33	0.01
21. order + patches + rank + treatment	9	-120.5	263.8	7.39	0.01
22. mass + patches + rank + treatment	9	-120.5	263.8	7.40	0.01
23. patches + rank + treatment + (patches · rank) + (rank · treatment)	11	-117.3	263.9	7.47	0.01
24. group + mass + order + patches + treatment + (rank · treatment)	10	-119.1	264.1	7.66	0.01
25. mass + order + patches + rank + treatment + (rank · treatment)	11	-117.4	264.2	7.72	0.01
26. mass + order + patches + treatment	9	-120.8	264.4	7.96	0.01
Full model (raked 97th). group + mass + order + patches + rank + treatment + (patches · rank) +	18	-114.7	289.0	32.57	0.00

(patches · treatment) + (rank · treatment) + (patches · rank · treatment)					
Null model (ranked 137th). intercept only	4	-168.9	346.8	90.37	0.00

Table S3.3. A ranking of mean circulating testosterone models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of rank and treatment, as well as their interaction. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. group + rank + treatment + (rank · treatment)	8	-178.9	377.5	0.00	0.39
2. group + order + rank + treatment + (rank · treatment)	9	-177.6	377.9	0.39	0.32
3. group + mass + rank + treatment + (rank · treatment)	9	-178.9	380.6	3.03	0.09
4. group + mass + order + rank + treatment + (rank · treatment)	10	-177.6	381.1	3.60	0.06
5. rank + treatment + (rank · treatment)	7	-182.6	382.1	4.56	0.04
6. group + patches + rank + treatment + (rank · treatment)	10	-178.5	382.9	5.40	0.03
7. order + rank + treatment + (rank · treatment)	8	-181.7	383.1	5.54	0.02
8. group + order + patches + rank + treatment + (rank · treatment)	11	-177.1	383.6	6.04	0.02

9. mass + rank + treatment + (rank · treatment)	8	-182.6	384.8	7.28	0.01
Full model (raked 50th). group + mass + order + patches + rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment) + (patches · rank · treatment)	18	-174.9	409.3	31.79	0.00
Null model (ranked 78th). intercept only	1	-203.0	414.9	37.4	0.00

Table S3.4. A ranking of mean probability of exposure models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of patches, treatment, and the first principle component analysis (PC1). Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. group + patches + PC1 + treatment + (patches · treatment)	8	-770.2	1556.5	0.00	0.19
2. group + mass + patches + PC1 + treatment + (patches · treatment)	9	-769.6	1557.3	0.83	0.13
3. group + order + patches + PC1 + treatment + (patches · treatment)	9	-769.6	1557.4	0.92	0.12
4. group + mass + order + patches + PC1 + treatment + (patches · treatment)	10	-768.9	1558.0	1.53	0.09
5. group + patches + PC1 + rank + treatment + (patches · treatment)	9	-770.0	1558.0	1.56	0.09
6. group + order + patches + PC1 + rank + treatment + (patches · treatment)	10	-769.4	1559.0	2.49	0.06
7. group + mass + patches + PC1 +	10	-769.6	1559.3	2.84	0.05

rank + treatment + (patches · treatment)					
8. group + mass + order + patches + PC1 + rank + treatment + (patches · treatment)	11	-768.9	1560.0	3.52	0.03
9. group + patches + PC1 + rank + treatment + (patches · treatment) + (rank · treatment)	10	-770.0	1560.1	3.59	0.03
10. group + order + patches + PC1 + rank + treatment + (patches · treatment) + (rank · treatment)	11	-769.4	1561.0	4.52	0.02
11. group + patches + PC1 + rank + treatment + (patches · rank) + (patches · treatment)	11	-769.5	1561.1	4.62	0.02
12. group + mass + patches + PC1 + rank + treatment + (patches · treatment) + (rank · treatment)	11	-769.6	1561.4	4.88	0.02
13. group + patches + PC1 + treatment	6	-774.7	1561.5	4.97	0.02
14. group + order + patches + PC1 + rank + treatment + (patches · rank) +	12	-768.9	1562.0	5.55	0.01

(patches · treatment)					
15. group + mass + order + patches + PC1 + rank + treatment + (patches · treatment) + (rank · treatment)	12	-768.9	1562.0	5.55	0.01
16. group + mass + patches + PC1 + rank + treatment + (patches · treatment) + (patches · rank)	12	-769.0	1562.3	5.77	0.01
17. group + mass + patches + PC1 + treatment	7	-774.1	1562.3	5.81	0.01
18. group + order + patches + PC1 + treatment	7	-774.1	1562.4	5.90	0.01
19. group + mass + order + patches + PC1 + rank + treatment + (patches · rank) + (patches · treatment)	13	-768.3	1562.9	6.43	0.01
20. group + mass + order + patches + PC1 + treatment	8	-773.4	1563.0	6.50	0.01
21. group + patches + PC1 + rank + treatment	7	-774.5	1563.0	6.54	0.01
22. group + patches + PC1 + rank + treatment + (patches · rank) +	12	-769.5	1563.1	6.66	0.01

(patches · treatment) + (rank · treatment)					
Full model (raked 49th). group + mass + order + patches + PC1 + rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment) + (patches · rank · treatment)	16	-768.25	1568.9	12.43	0.00
Null model (ranked 289th). intercept only	1	-846.2	1694.4	137.90	0.00

Table S3.5. A ranking of mean minimum total movement models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of patches and treatment, as well as their interaction. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. group + mass + order + patches + treatment + (patches · treatment)	16	-173.0	395.6	0.00	0.36
2. group + order + patches + rank + treatment + (patches · treatment)	16	-173.3	396.1	0.51	0.28
3. group + order + patches + treatment + (patches · treatment)	15	-176.4	397.9	2.34	0.11
4. group + mass + order + patches + rank + treatment + (patches · treatment)	17	-172.0	398.4	2.85	0.09
5. group + order + patches + rank + treatment + (patches · treatment) + (rank · treatment)	17	-172.3	399.0	3.42	0.06
6. group + mass + patches + treatment + (patches · treatment)	15	-177.7	400.4	4.89	0.03
7. group + patches + treatment +	14	-180.0	400.7	5.18	0.03

(patches · treatment)					
8. group + mass + order + patches + rank + treatment + (patches · treatment) + (rank · treatment)	18	-170.9	401.3	5.78	0.02
9. group + order + patches + rank + treatment + (patches · rank) + (patches · treatment)	18	-171.5	402.6	7.10	0.01
10. group + patches + rank + treatment + (patches · treatment)	15	-179.3	403.6	8.08	0.01
Full model (raked 46th). group + mass + order + patches + rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment) + (patches · rank · treatment)	22	-169.4	423.2	27.65	0.00
Null model (ranked 106th). intercept only	8	-213.0	445.6	50.07	0.00

Table S3.6. A ranking of mean minimum habitat use models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of patches and treatment, as well as their interaction. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	Δ*AIC$_c$*	*Weight*
1. group + patches + rank + treatment + (patches · rank) + (patches · treatment)	12	-165.5	364.0	0.00	0.18
2. group + order + patches + rank + treatment + (patches · rank) + (patches · treatment)	13	-164.0	364.7	0.72	0.12
3. group + patches + rank + treatment + (patches · treatment)	10	-169.6	365.2	1.18	0.10
4. group + patches +rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment)	13	-164.5	365.7	1.73	0.08
5. group + mass + patches + treatment + (patches · treatment)	10	-169.9	365.8	1.80	0.07
6. group + order + patches + rank +	11	-168.3	366.0	1.98	0.07

treatment + (patches · treatment)					
7. group + patches + treatment + (patches · treatment)	9	-171.9	366.5	2.52	0.05
8. group + order + patches + rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment)	14	-162.9	366.5	2.53	0.05
9. group + patches + rank + treatment + (patches · treatment) + (rank · treatment)	11	-168.7	366.8	2.78	0.04
10. group + mass + order + patches + treatment + (patches · treatment)	11	-168.9	367.1	3.08	0.04
11. group + mass + patches + rank + treatment + (patches · rank) + (patches · treatment)	13	-165.2	367.1	3.13	0.04
12. group + order + patches + treatment + (patches · treatment)	10	-170.8	367.6	3.57	0.03
13. group + order + patches + rank + treatment + (patches · treatment) + (rank · treatment)	12	-167.4	367.7	3.73	0.03
14. group + mass + patches + rank + treatment + (patches · treatment)	11	-169.3	368.0	4.02	0.02
15. group + mass + order + patches +	14	-163.8	368.3	4.28	0.02

rank + treatment + (patches · rank) + (patches · treatment)					
16. group + mass + patches + rank + treatment + (patches · rank) + (patches · treatment)	14	-164.2	369.1	5.05	0.01
17. group + mass + order + patches + rank + treatment + (patches · treatment)	12	-168.1	369.2	5.20	0.01
18. group + mass + patches + rank + treatment + (patches · treatment) + (rank · treatment)	12	-168.5	369.8	5.82	0.01
19. group + mass + order + patches + rank + treatment + (patches · rank) + (patches · treatment) + (rank · treatment)	15	-162.7	370.3	6.33	0.01
20. group + mass + order + patches + rank + treatment + (patches · treatment) + (rank · treatment)	13	-167.2	371.1	7.14	0.01
Full model (raked 34th). group + mass + order +patches + rank + treatment + (patches · rank) + (patches · treatment) +	17	-161.7	377.8	13.81	0.00

(rank · treatment) +					
(patches · rank · treatment)					
Null model (ranked 72nd).					
intercept only	3	-208.2	423.0	58.97	0.00

Table S3.7. A ranking of mean minimum habitat use models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of patches and treatment, as well as their interaction. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. patches	5	-29.9	79.7	0.00	0.74
2. Null model. intercept only	3	-36.9	82.7	3.01	0.16
3. Full model. group + patches	6	-27.8	84.3	4.59	0.07
4. group	4	-36.3	86.3	6.56	0.03

Table S3.8. Coefficients and standard errors for the model of corticosterone, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	34.7	2.3
group	-0.9	1.0
4-patches	-3.6	1.1
16-patches	-7.0	1.1
rank	3.1	2.6
treatment	-17.6	1.7
rank · treatment	-3.0	2.7
order	0.0	0.3
mass	0.0	0.0
4-patches · treatment	0.1	0.6
16-patches · treatment	0.0	0.5
4-patches · rank	0.0	0.3
16-patches · rank	0.0	0.3
4-patches · rank · treatment	0.0	0.0
16-patches · rank · treatment	0.0	0.0

Table S3.9. Coefficients and standard errors for the model of testosterone, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	67.4	10.7
group	-12.4	5.9
rank	-43.7	6.6
treatment	-21.6	2.8
rank · treatment	30.8	3.9
order	3.2	4.8
mass	0.0	0.3
4-patches	-0.2	1.8
16-patches	-0.3	1.9
4-patches*treatment	0.0	0.2
16-patches · treatment	0.0	0.2
4-patches · rank	0.0	0.5
16-patches · rank	0.0	0.5
4-patches · rank · treatment	0.0	0.0
16-patches · rank · treatment	0.0	0.0

Table S3.10. Coefficients and standard errors for the model of probability of exposure, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	0.7	0.4
group	0.4	0.1
4-patches	0.4	0.2
16-patches	0.5	0.3
PC1	0.4	0.0
treatment	-1.4	0.2
4-patches · treatment	0.6	0.3
16-patches · treatment	0.8	0.4
mass	0.0	0.0
order	-0.1	0.1
rank	0.0	0.1
rank · treatment	0.0	0.1
4-patches · rank	0.0	0.1
16-patches · rank	0.0	0.1
4-patches · rank · treatment	0.0	0.0
16-patches · rank · treatment	0.0	0.0

Table S3.11. Coefficients and standard errors for the model of minimum total movement, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	62.8	7.0
group	-18.5	1.5
mass	0.2	0.2
order	5.1	2.1
4-patches	43.6	6.7
16-patches	36.9	5.1
treatment	50.9	8.3
4-patches · treatment	-81.5	11.2
16-patche · treatment	-66.5	9.9
rank	-1.9	2.3
rank · treatment	0.5	2.1
4-patches · rank	0.0	0.8
16-patches · rank	0.1	1.1
4-patches · rank · treatment	0.0	0.1
16-patches · rank · treatment	0.0	0.0

Table S3.12. Coefficients and standard errors for the model of minimum habitat use, based on full model averaging

Independent variable	*Coefficient*	*SE*
intercept	64.9	9.1
group	-9.6	2.7
4-patches	33.5	5.5
16-patches	43.0	6.3
rank	-9.4	7.2
treatment	35.9	4.7
4-patches · rank	5.4	6.8
16-patches · rank	8.1	9.0
4-patches · treatment	-58.3	6.2
16-patches · treatment	-56.0	6.2
order	1.4	2.4
rank· treatment	1.5	3.7
mass	0.1	0.2
4-patches · rank · treatment	0.0	0.9
16-patches · rank · treatment	-0.1	1.2

Table S3.13. Coefficients and standard errors for the model of aggression score, based on full model averaging

Independent variable	*Coefficient*	*SE*
intercept	13.0	2.9
4-patches	-10.3	2.4
16-patches	-7.5	2.4
group	-0.3	2.2

Table S3.14 Principal components describing the covariation between operative environmental temperatures.

Variable	*PC1*	*PC2*
Maximal operative temperature	0.71	-0.71
Range of operative temperature	0.71	0.71
Eigenvalue	1.91	0.09
% of variance	95.6	4.4
Cumulative	95.6	100

Fig S4.1. On average, lizards preferred the same body temperatures before and after surgical implantation of temperature loggers. Black symbols represent the mean temperature of each lizard in a thermal gradient. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

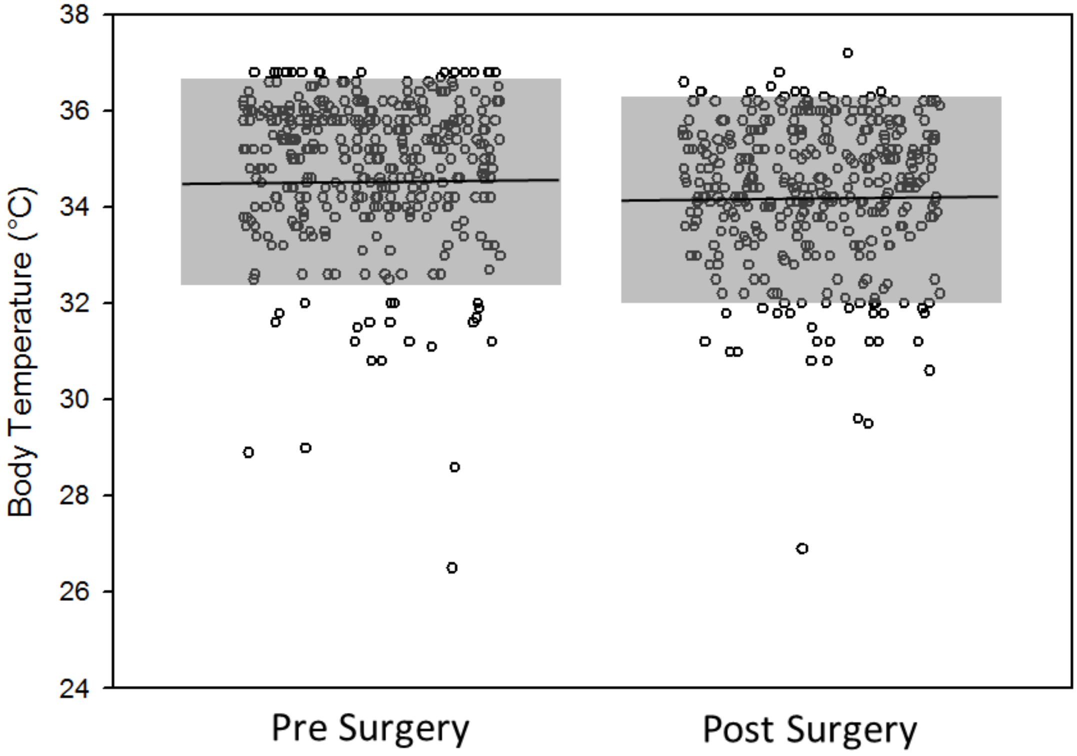

Fig S4.2. Schematic of aggregated (1-patch) thermal arena with cable flyways. Note, only one predator was flown at a time during experiments.

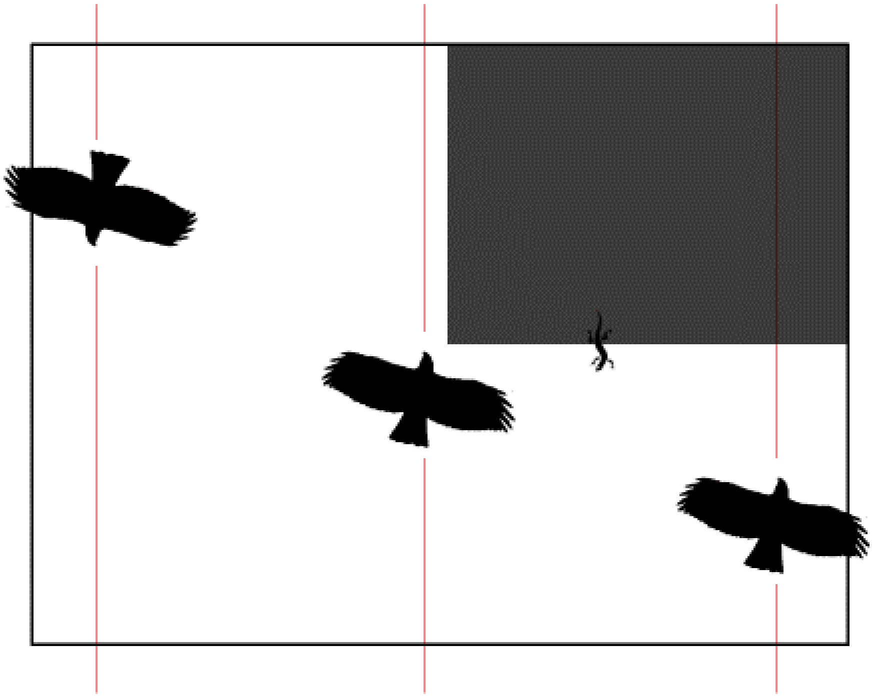

Table S4.1. Outline of experimental design indicating when specific events occurred.

Day	*Event*	*Time*
1	Placed in arenas	1800
2-3	Habituation	Whole day
3	Blood draw #1	1230-1300
4	Rest (provided food)	Whole day
5-6	Treatment	0720-1220
6	Blood draw #2	1230-1300

Table S4.2. A ranking of mean minimum total movement models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of day, patches, and treatment, as well as their interaction. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC_c*	*ΔAIC_c*	*Weight*
1. day + patches + treatment + (day · patches · treatment)	19	-436.0	916.2	0	0.72
2. day + mass + patches + treatment + (day · patches · treatment)	20	-435.7	918.4	2.23	0.24
3. day + group + patches + treatment + (day · patches · treatment)	26	-429.3	922.9	6.73	0.02
4. Full Model. day + group + mass + patches + treatment + (day · patches · treatment)	27	-428.7	924.6	8.42	0.01
Null model (ranked 65th). intercept only	8	-534.7	1086.4	170.22	0.00

Table S4.3. A ranking of mean minimum habitat use models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of day, patches, and treatment, as well as their interactions. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. day + patches + treatment + (day · treatment) + (patches · treatment)	16	-495.7	1027.7	0	0.33
2. day + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment) + (day · patches · treatment)	19	-492.0	1028.3	0.65	0.24
3. day + mass + patches + treatment + (day · treatment) + (patches · treatment)	17	-495.6	1030.1	2.39	0.1
4. day + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment)	17	-495.7	1030.2	2.58	0.09
5. day + mass + patches + treatment + (day · treatment) + (day · patches) +	20	-492.0	1030.9	3.19	0.07

(patches · treatment) + (day · patches · treatment)					
6. day + group + patches + treatment + (day · treatment) + (patches · treatment)	23	-487.8	1031.0	3.38	0.06
7. day + group + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment) + (day · patches · treatment)	26	-484.1	1032.4	4.75	0.03
8. day + mass + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment)	18	-495.6	1032.7	5.02	0.03
9. day + mass + patches + treatment + (day · treatment) + (patches · treatment)	24	-487.3	1032.9	5.22	0.02
10. day + group + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment)	24	-487.8	1033.9	6.28	0.01
11. Full Model. day + group + mass + patches + treatment + (day · treatment) + (day · patches) +	27	-483.6	1034.4	6.70	0.01

(patches · treatment) + (day · patches · treatment)					
12. day + group + mass + patches + treatment + (day · treatment) + (day · patches) + (patches · treatment)	25	-487.3	1035.8	8.17	0.01
Null model (ranked 66th).					
intercept only	8	-555.2	1127.5	99.85	0.00

Table S4.4. A ranking of mean body temperature models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of day, patches, PC1, and treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. day + patches + PC1 + treatment + (day · treatment)	38	-7156.4	14389.6	0	0.66
2. Full Model. day + patches + PC1 + treatment + (day · patches) + (day · treatment) + (patches · treatment) + (day · patches · treatment)	43	-7152.8	14392.7	3.13	0.14
3. day + patches + PC1 + treatment + (day · patches) + (day · treatment) + (patches · treatment)	41	-7155.1	14393.2	3.62	0.11
4. day + patches + PC1 + treatment + (patches · treatment)	34	-7162.8	14394.3	4.73	0.06
5. day + patches + PC1 + treatment	36	-7161.9	14396.6	7.05	0.02
Null Model (ranked 10th).					
intercept only	21	-7468.1	14978.5	588.94	0.00

Table S4.5. A ranking of mean probability of exposure models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of day, patches, and treatment, as well as the interaction of day and treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. day + patches + treatment + (day · treatment)	8	-1499.5	3015.1	0	0.22
2. day + patches + treatment + (day · patches) + (day · treatment)	9	-1499.0	3016.1	0.98	0.14
3. day + patches + treatment + (day · treatment) + (patches · treatment)	10	-1498.4	3016.9	1.79	0.09
4. day + mass + patches + treatment + (day · treatment)	9	-1499.5	3017.1	1.97	0.08
5. day + patches + PCA + treatment + (day · treatment)	9	-1499.5	3017.2	2.02	0.08
6. day + patches + treatment + (day · patches) + (day · treatment) + (patches · treatment)	11	-1497.8	3017.8	2.67	0.06
7. day + mass + patches + treatment +	10	-1499.0	3018.1	2.95	0.05

(day · patches) + (day · treatment)					
8. day + patches + PCA + treatment + (day · patches) + (day · treatment)	10	-1499.0	3018.1	3.00	0.05
9. day + mass + patches + treatment + (day · treatment) + (patches · treatment)	11	-1498.4	3018.9	3.81	0.03
10. day + patches + PCA + treatment + (day · treatment) + (patches · treatment)	11	-1498.4	3018.9	3.81	0.03
11. day + mass + patches + treatment + (day · treatment)	10	-1499.5	3019.1	3.99	0.03
12. day + patches + treatment + (day · patches) + (day · treatment) + (patches · treatment) + (day · patches · treatment)	13	-1496.6	3019.4	4.31	0.03
13. day + mass + patches + treatment + (day · patches) + (day · treatment) + (patches · treatment)	12	-1497.8	3019.8	4.69	0.02
14. day + patches + PCA + treatment + (day · patches) + (day · treatment) +	12	-1497.8	3019.8	4.69	0.02

(patches · treatment)					
15. day + mass + patches + treatment + (day · patches) + (day · treatment)	11	-1499.0	3020.1	4.97	0.02
16. day + mass + PCA + patches + treatment + (day · treatment) + (patches · treatment)	12	-1498.4	3021.0	5.83	0.01
17. day + mass + patches + treatment + (day · patches) + (day · treatment) + (patches · treatment) + (day · patches · treatment)	14	-1496.6	3021.5	6.33	0.01
18. day + PCA + patches + treatment + (day · patches) + (day · treatment) + (patches · treatment)	14	-1496.6	3021.5	6.34	0.01
19. day + mass + patches + PCA + treatment + (day · patches) + (day · treatment) + (patches · treatment)	13	-1497.8	3021.8	6.71	0.01
20. Full Model. day + mass + patches + PCA + treatment + (day · patches) + (day · treatment) +	15	-1496.6	3023.5	8.36	0.00

(patches · treatment) +					
(day · patches · treatment)					
Null model (ranked 69th).	2	-1549.6	3103.2	88.06	0.00
intercept only					

Table S4.6. A ranking of mean circulating corticosterone models based on the likelihood of being the best model. For each model, we provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed, in addition to the full model and the null model. All likely models included effects of measure, patches, and treatment, as well as the interaction of measure and treatment. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. measure + patches + treatment + (measure · patches) + (measure · treatment) + (measure · patches · treatment)	16	-440.6	917.5	0	0.25
2. measure + patches + treatment + (measure · treatment)	11	-447.3	918.6	1.08	0.15
3. measure + patches + SNL + treatment + (measure · patches) + (measure · treatment) + (measure · patches · treatment)	17	-440.2	919.4	1.90	0.10
4. mass + measure + patches + treatment + (measure · patches) + (measure · treatment) + (patches · treatment) + (measure · patches · treatment)	17	-440.4	919.8	2.24	0.08

5. measure + patches + treatment + (measure · treatment) + (patches · treatment)	13	-445.5	919.8	2.28	0.08
6. measure + patches + SVL + treatment + (measure · treatment)	12	-447.1	920.7	3.14	0.05
7. mass + measure + patches + treatment + (measure · treatment)	12	-447.2	920.8	3.32	0.05
8. measure + patches + treatment + (measure · patches) + (measure · treatment)	12	-447.3	921.0	3.46	0.04
9. measure + patches + SNL + treatment + (measure · treatment) + (patches · treatment)	14	-445.2	921.6	4.08	0.03
10. mass + measure + patches + treatment + (measure · treatment) + (patches · treatment)	14	-445.3	921.9	4.42	0.03
11. mass + measure + patches + SVL + treatment + (measure · patches) + (measure · treatment) + (patches · treatment) + (measure · patches · treatment)	18	-440.2	922.0	4.50	0.03
12. measure + patches + treatment +	14	-445.5	922.2	4.72	0.02

(measure · patches) + (measure · treatment) + (patches · treatment)					
13. mass + measure + patches + SVL + treatment + (measure · treatment)	13	-447.1	923.1	5.54	0.02
14 measure + patches + SVL + treatment + (measure · patches) + (measure · treatment)	13	-447.1	923.1	5.56	0.02
15. mass + measure + patches + treatment + (measure · patches) + (measure · treatment)	13	-447.2	923.3	5.73	0.01
16. mass + measure + patches + SVL + treatment + (measure · treatment) + (patches · treatment)	15	-445.1	924.1	6.55	0.01
17. measure + patches + SVL + treatment + (measure · patches) + (measure · treatment) + (patches · treatment)	15	-445.1	924.1	6.57	0.01
18. mass + measure + patches + treatment + (measure · patches) + (measure · treatment) +	15	-445.3	924.4	6.90	0.01

(patches · treatment)					
Full Model (ranked 32nd). group + mass + measure + patches + SVL + treatment + (measure · patches) + (measure · treatment) + (measure · patches · treatment)	25	-434.8	930.9	13.36	0.00
Null Model (ranked 145th). intercept only	5	-555.5	1121.4	203.86	0.00

Table S4.7. Coefficients and standard errors for the model of minimum total movement, based on full model averaging.

Independent variable	*Coefficient*	*SE*
(Intercept)	48.4	3.0
day	1.2	3.9
group 2	0.1	0.6
group 3	0.0	0.3
group 4	0.1	0.6
group 5	0.1	0.4
group 6	0.0	0.3
group 7	0.1	0.8
group 8	0.0	0.3
mass	0.0	0.1
patches	-12.4	3.3
P1-treatment	-34.5	3.4
P2-treatment	-1.8	3.4
day · patches	-3.6	4.6
day · P1-treatment	12.8	4.8
day · P2-treatment	-29.1	4.8
patches · P1-treatment	20.4	3.9
patches · P2-treatment	3.4	4.1
day · patches · P1-treatment	-1.8	5.5
day · patches · P2-treatment	16.8	5.8

Table S4.8. Coefficients and standard errors for the model of minimum habitat use, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	40.2	3.5
day	-1.6	3.5
group 2	0.7	1.9
group 3	0.3	1.2
group 4	0.7	1.9
group 5	1.0	2.6
group 6	0.3	1.3
group 7	1.1	2.8
group 8	-0.1	1.0
mass	0.0	0.1
patches	-6.5	3.5
P1-treatment	-28.6	3.2
P2-treatment	-0.7	5.0
day · patches	-1.0	3.7
day · P1-treatment	11.9	3.8
day · P2-treatment	-21.2	6.0
patches · P1-treatment	14.8	4.0
patches · P2-treatment	5.1	7.4
day · patches · P1-treatment	0.0	3.8
day · patches · P2-treatment	5.6	9.0

Table S4.9. Coefficients and standard errors for the model of probability of exposure, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	0.2	0.2
day	0.1	0.2
mass	0.0	0.0
patches	0.4	0.1
PC1	0.0	0.0
P1-treatment	-0.7	0.2
P2-treatment	0.2	0.2
day · patches	-0.1	0.2
day · P1-treatment	0.8	0.2
day · P2-treatment	-1.0	0.2
patches · P1-treatment	-0.1	0.2
patches · P2-treatment	0.0	0.2
day · patches · P1-treatment	0.0	0.1
day · patches · P2-treatment	0.0	0.2

Table S4.10. Coefficients and standard errors for the model of body temperature, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	29.2	0.5
day	0.6	0.6
patches	1.4	0.5
P1-treatment	-1.3	0.7
P2-treatment	0.5	0.6
day · patches	-0.2	0.6
day · P1-treatment	1.4	0.9
day · P2-treatment	-1.1	0.9
patches · P1-treatment	0.2	0.6
patches · P2-treatment	-0.2	0.6
day · patches · P1-treatment	-0.2	0.7
day · patches · P2-treatment	0.2	0.8

Table S4.11. Coefficients and standard errors for the model of corticosterone, based on full model averaging.

Independent variable	*Coefficient*	*SE*
intercept	8.6	4.7
group 2	3.2	1.3
group 3	0.6	1.5
group 4	1.6	1.3
group 5	0.0	1.5
group 6	3.3	1.3
group 7	0.2	1.5
group 8	1.6	1.4
mass	0.0	0.1
measure	-0.4	1.4
patches	-4.6	1.2
P1-treatment	-0.1	2.3
P2-treatment	0.3	2.5
SVL	0.1	0.1
measure · patches	1.9	2.1
measure · P1-treatment	27.3	3.8
measure · P2-treatment	33.7	4.4
patches · P1-treatment	0.0	3.5
patches · P2-treatment	0.6	4.4
measure · patches · P1-treatment	-8.4	4.5

measure · patches · P2-treatment	-13.1	4.9

Table S4.12. Principal components describing the covariation between operative environmental temperatures.

Variable	*PC1*	*PC2*
Maximal operative temperature	-0.71	0.71
Range of operative temperature	-0.71	0.71
Eigenvalue	1.39	0.23
% of variance	97.3	2.7
Cumulative	97.3	100

APPENDIX B

COAUTHOR APPROVAL

All coauthors of published chapters granted permission to use those chapters in this dissertation.