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## **Behavior Plasticity Mitigates the Effect of Climate Warming in White-Tailed Deer**

Carter L. Wolff

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Behavior plasticity mitigates the effect of climate warming in white-tailed deer

By

Carter L. Wolff

A Thesis  
Submitted to the Faculty of  
Mississippi State University  
in Partial Fulfillment of the Requirements  
for the Degree of Master of Science  
in Biological Sciences  
in the College of Arts and Sciences

Mississippi State, Mississippi

August 2018

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2018

Behavior plasticity mitigates the effect of climate warming in white-tailed deer

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Climate change can alter the ecology of natural systems through various mechanisms, such as direct thermal effects on a consumer. However, consumers may employ behavioral mechanisms in response to warming. Among these may be spatial or temporal shifts in activity, making use of thermal heterogeneity on the landscape. Despite this, few studies consider the role of behavioral plasticity and spatial or temporal heterogeneity in the context of climate change. I conducted experiments to evaluate the importance of behavior in mediating the net effects of warming at the population and the individual level using captive white-tailed deer (*Odocoileus virginianus*). I created thermal heterogeneity over feeding stations using opaque and translucent roofing material. Feeding activity and consumption were monitored at these feeders. Activity patterns revealed deer disproportionately used the shaded feeder during the daytime and the unshaded feeder during crepuscular periods. I found that deer consumed less feed in group and individual experiments when feeders were unshaded. My results suggest that deer can use heterogeneity in the environment that may mediate the net effects of climate change. Furthermore, maintaining thermal heterogeneity may mitigate the direct effects

of climate change on the consumer, but may lead to indirect effects at the community level.

## ACKNOWLEDGEMENTS

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CHAPTER I  
BEHAVIORAL PLASTICITY MITIGATES THE EFFECT OF  
CLIMATE WARMING IN WHITE TAILED DEER

**1.1 Introduction**

Anthropogenic greenhouse gases are leading to increases in mean global temperatures (Easterling et al., 2000; Harvell et al., 2002; IPCC 2014) that may alter communities through several mechanisms. Rising temperatures may impact organisms directly by altering a species' behavior or physiology (Tomanek and Zuzow, 2010; Kingsolver et al., 2013; Long et al., 2014). Alternatively, a species may be affected indirectly if changes in temperature affect other species that it interacts with (Olofsson et al., 2009; Li et al., 2011; Blois et al., 2013). As global climate continues to change, it is important to assess how environmental factors may affect species and their interactions with ecological communities.

Much effort has been put into understanding how climate change will affect a species' abundance, distribution, and function in a community. For example, climate envelope models are a common approach that use a species current distribution to estimate future distributions based on predictions of future climate conditions (Berry et al., 2002; Martínez-Meyer et al., 2004; Hijmans and Graham, 2006; Araújo and Peterson, 2012; Brooks et al., 2012). However, climate envelope modeling and similar approaches generally make simplistic assumptions about behavior and environmental heterogeneity

(Schmitz et al., 2003; Van Der Putten et al., 2010; Angert et al., 2013; Abram et al., 2017). Implicit within these approaches is the potentially faulty assumption that animals behave the same way in response to current and future environmental conditions (Harmon and Barton, 2013) and that climate conditions are uniform below the model resolution that these approaches use (Davis and Shaw, 2001; Pearson and Dawson, 2003).

Animal behavior is likely to influence the net effects of climate change in two ways. First, climate change may directly affect animal behavior, altering inter- and intra-specific interactions and generating indirect effects within a community (Lensing and Wise, 2006; Martin, 2007; Aublet et al., 2009; Barton and Schmitz, 2009; Blaustein et al., 2010; Cornelissen, 2011; Auer and Martin, 2013; Goyer et al., 2014; Carla et al., 2016). For example, studies across a broad range of taxa, including ectothermic and endothermic species, have shown some of the first responses to environmental change are behavioral shifts by consumers. These shifts can generate indirect effects on their resources at lower trophic levels (Post et al., 1999; Voigt et al., 2003; Urban et al., 2017; Barton and Schmitz, 2018). Second, behavioral plasticity may allow animals to mitigate the effects of climate change so that they maintain their abundance, distribution, and function in a community. For example, organisms in thermally stressful environments may behaviorally thermoregulate by making use of spatial (Block et al., 2001; Bacigalupe et al., 2003; van den Berg et al., 2015; Street et al., 2016) and temporal microclimates (Hutchison and Maness, 1979; Aublet et al., 2009; Carla et al., 2016; Levy et al., 2016). These microclimates may offer thermal refuge within a landscape, which animals can use to mitigate the effects of stressful abiotic conditions.

Unfortunately, the role of thermal heterogeneity and its implications for climate change effects are poorly understood (Dobrowski, 2011; Sears et al., 2011; Elmore et al., 2017). Spatial and temporal thermal heterogeneity may give animals the opportunity to alter their behaviors in ways that mitigate the effects of stressful environments. A large amount of research has focused on how animals move between microenvironments to thermoregulate (Huey and Slatkin, 1976; Bowyer and Kie, 2009; Kearney et al., 2009; Long et al., 2014; Carroll et al., 2015), and evidence suggests that ignoring thermal heterogeneity can result in over- or underestimation of the effects of warming (Huey et al., 2003; Sears et al., 2016). The importance of thermal heterogeneity for understanding the net effects of climate change has been demonstrated in some arthropod systems, where consumers use cooler thermal refuges during hot periods in order to remain within the broader landscape and continue their functional role in the ecosystem (Harley, 2011; Barton and Schmitz, 2018). However, it remains unclear if the importance of behavioral plasticity and use of temporal or spatial thermal-heterogeneity generalizes to other systems, such as endotherms.

To evaluate how animal behavior may mediate the effects of warming in a vertebrate herbivore, I studied temporal and spatial patterns of white-tailed deer (*Odocoileus virginianus*) using a controlled, replicated experiment. I created thermal heterogeneity within deer enclosures using shaded and unshaded feeding stations and monitored feeding activity 24-hours per day. My approach allowed us to evaluate how deer may alter their behavior to capitalize on spatial (shaded or unshaded feeders) and temporal (day and night) variation in temperature to meet their nutritional and

thermoregulatory demands and maintain their functional role as herbivores in the community.

## **1.2 Methods**

### **1.2.1 Study System**

Deer are a common herbivore in North America, and available thermal research has focused on deer response to cold, winter conditions at higher latitudes. However, deer at lower latitudes are exposed to high air temperatures in summer months, correlating with elevated internal temperature (Demarais et al., 1986). The summer is an important time for deer as adult females are lactating, which is energetically expensive and rising summer temperatures are likely to impact the energetic demand of reproduction (Rogowitz, 1996; Johnson et al., 2001).

I conducted my research at the Mississippi State University Rusty Dawkins Memorial Deer Unit (Starkville, MS, USA). The outdoor facility houses wild captured deer from Mississippi, as well as some captive born offspring. Each enclosure had naturally occurring vegetation and ambient shade produced by large hardwood trees and enclosure walls that were covered with 70% shade cloth. Transportation of deer during the experiment was facilitated using BAM™ (Zoo-Pharm, Laramie, WY, USA) delivered with a Pneu-Dart projection system (Pneu-Dart, Inc., Williamsport, PA, USA).

### **1.2.2 Comparison of temperature between shaded and unshaded feeders**

I created shaded treatments using opaque roofing material and unshaded treatments using translucent roofing material. Translucent roofing allowed us to create

warmer environments without removing the canopy roof. Removing the roof may have biased the effect of shade in my experiment.

I suspended temperature data loggers (Onset Hobo, Bourne, MA, USA) 1 m from the top of each feeder in the group experiment. I recorded temperature at each feeder at 30-minute intervals throughout the duration of the group experiment. I compared the mean ambient temperature between the shaded and unshaded feeders using a paired t-test. Presumably, the difference in ambient temperature between shaded and unshaded feeders is driven by solar radiation. Therefore, I also compared the mean ambient temperature between shaded and unshaded feeders during the daytime (6:00 hr – 18:00 hr) with a paired t-test. In addition, I calculated the difference in temperature at the unshaded feeder minus the shaded feeder and compared the difference across the 24-hour day.

### **1.2.3 Group Experiment**

I conducted a group experiment using four large enclosures (~ 0.75 ha each) from April to September 2017. Each enclosure contained two identical wooden feeders with six metal troughs (0.52 x 0.32 x 0.15 m) per feeder placed in areas lacking in natural shade (10 m away from the eastern edge of the enclosure, with feeders 5 m apart). I placed a canopy over each feeder, constructed from a PVC frame (3.7 m x 3.4 m x 2.2 m) and corrugated roofing material. Each enclosure had both a shaded and unshaded canopy. I monitored visitation to each feeder using infrared, motion-triggered camera traps (Bushnell Trophy HD Essential, Overland Park, KS, USA) placed 2.5 m away at a height of 1.5 m.

To initiate the experiment, I added known amounts of commercially-available, pelletized feed to the feeders (Cargill Sportsman's Choice Record Rack, Cargill, Inc.,

Minneapolis, MN, USA). Every 48-hours I quantified consumption by returning to the enclosure and weighing the remaining feed. I then refilled feeders and weighed them to determine initial feed available. If strong precipitation led to feed saturated with water, I discarded the feed from the feeder and excluded that data from the analysis. To reduce potential bias in treatment location, I rotated the opaque and translucent canopy covers every two weeks.

The total number of deer per enclosure in the group experiment ranged from 5-19 over the course of the experiment. However, I maintained similar deer densities ( $\pm$  1-2 deer between enclosures) within the four enclosures at any point in time. I averaged measurements of consumption across the two-day sampling period to estimate a daily rate of consumption. To account for differences in density, I adjusted consumption data to a per animal basis based on the number of deer in each enclosure.

I observed discrete camera photos for instances of feeding behavior at each feeder. I considered a feeding event as any picture that included a deer with its head and neck within the perimeter of the feeder canopy. However, if an individual was bedded down underneath the canopy, I did not consider that as a feeding event. I evaluated each photograph and recorded if a deer was feeding. Thus, my data reflected the frequency of feeder use throughout the day for both the unshaded and shaded feeder. Approximately 33% of the deer within one of the enclosures died during the experiment. Due to the higher mortality observed in this enclosure compared to the other three enclosures, I excluded all data from that enclosure in my analyses.

#### **1.2.4 Individual Experiment**

I conducted feeding trials on individual deer in four small enclosures (~0.05 – 0.07 ha each) from May 2017 to September 2017. In each enclosure, deer had access to water, a shaded refuge, and a feeder with either a shaded or unshaded roof. I constructed shaded refuges using a PVC frame (2.4 x 2.5 x 2.5 m) that supported an opaque roof. Feeders were constructed from a wooden frame (1.2 x 2.4 x 1.5 m), with two metal feeding troughs (0.52 x 0.32 x 0.15 m) per feeder and covered with corrugated roofing material. In each enclosure, deer were presented with either a shaded or unshaded feeder. Each feeder was monitored continuously using an infrared video camera positioned 10 m away from the feeder and a digital video recorder system (Lorex Technology Inc., Markham ON, CAN).

The experiment was separated into nine two-week blocks and each block consisted of four trials. One deer was randomly assigned to each of the four enclosures. To minimize the effects of the relocation process, deer were placed in the experimental enclosures for 36 hours to acclimate. After 36 hours, I rotated deer counterclockwise to the adjacent enclosure to begin the first trial. During this rotation, I added and recorded initial weight of feed in the feeder (Cargill Sportsman's Choice Record Rack, Cargill, Inc., Minneapolis, MN, USA). I repeated this process for each of the four enclosures. After each 72-hour interval, I rotated deer into adjacent enclosures and repeated the feed processing. At the end of the four-trial block, deer were removed from the small enclosures and returned to the large enclosures used for the Group experiment. Before initiating the next block, shaded and unshaded feeders were randomized among the four enclosures to minimize the potential for an enclosure effect on treatment. I averaged

measurements of consumption across the three-day sampling period to estimate a daily rate of consumption per deer.

I observed video data for instances of feeding at each feeder. I considered a feeding event as any video that captured a deer with its head and neck within the perimeter of the feeder canopy. However, if an individual was bedded down underneath the canopy, I did not score that as a feeding event. I recorded the time each feeding bout was initiated. Because deer may engage in other, non-feeding activities while at a feeder (e.g., vigilance, resting), I did not quantify total feeding activity based on duration at the feeder. Additionally, it was logistically infeasible to quantify deer behavior at a finer scale (e.g., minute by minute) using the video data. Thus, I used the video data to determine the initiation of feeding events and used the feed weight data to measure consumption.

### **1.2.5 Statistical Analysis**

Analyses were completed using the statistical computing language R (R Core Team, 2016). Temporal effects of shade treatments were analyzed using a temporal overlap analysis in the Overlap Package in R (Meredith and Ridout, 2017). I fitted camera and video data to a kernel density and estimated a coefficient of overlap,  $\Delta$ , between shaded and unshaded feeders during a 24-hour day (Ridout and Linkie, 2009; Biggerstaff et al., 2017). The coefficient of overlap is defined as the area under the curve formed from taking the minimum density of feeder use in the shaded and translucent feeder. This value ranges from zero and one, with one being identical activity patterns. In addition, I obtained 95% confidence intervals of the coefficient of overlap from bootstrap

estimates with 1000 samples. On its own, the coefficient of overlap does not indicate differences in activity patterns. Therefore, I used the Watson's U2 statistic in the CircStats package in R (Lund and Agostinelli, 2012) to compare activity patterns (*sensu* Lashley et al., 2018). The Watson's U2 statistic computes the probability that two sets of data (i.e., camera data from shaded and unshaded feeders) are from the same population.

I analyzed the effects of shade treatments on consumption using general linear mixed effects models in the LME4 package in R (Bates et al., 2015), assuming a Gamma distribution to account for non-normal data. In the individual experiment, I treated deer as a random effect to account for individual variation. Similarly, in the group experiment the enclosure was treated as a random effect. In addition to using shade treatment as a binary predictor, I also included three different models with minimum, maximum, and average temperature. Temperature data for Starkville, MS was accessed from the Soil Climate Analysis Network station (<https://www.wcc.nrcs.usda.gov/scan/>) and averaged across the two or three-day sampling period for the group and individual experiments respectively. I compared models from each experiment using AICc values, from the the MuMIn package in R (Bartoń, 2018).

## **1.3 Results**

### **1.3.1 Comparison of temperature between shaded and unshaded feeders**

The mean ambient temperature under the unshaded feeder was approximately 0.2 °C warmer than the shaded feeder (paired t-test,  $p < 0.001$ ; See Appendix 1). The greatest difference between shaded and unshaded feeders occurred from approximately 12:00 - 20:00 hr when the unshaded feeder was approximately 1 – 3 °C warmer than the shaded feeder (See Appendix 2). During this period, the mean ambient temperature at the

unshaded feeder was 1.4 °C warmer than the unshaded feeder (paired t-test,  $p < 0.001$ ; see appendix 3).

### **1.3.2 Temporal Analysis**

Activity patterns of the group experiment resulted in a coefficient of overlap of 0.826 (bootstrap 95% CI 0.818 – 0.836; Figure 1). Further analysis of these activity patterns indicated that shaded and unshaded feeders were used differently throughout the 24-hour day (Watson's U2 test,  $p < 0.001$ ). This was most evident during the mid-day where feeding activity at the shaded feeder was proportionally greater compared to the unshaded feeder and crepuscular periods where feeding activity at the unshaded feeder was proportionally greater compared to the shaded feeder.

The individual experiment also showed differences in activity patterns, with a coefficient of overlap of 0.855 (bootstrap 95% CI 0.838 – 0.861; Figure 2). As with the group experiment, deer used shaded and unshaded feeders differently across the 24-hour day (Watson's U2 test,  $p < 0.001$ ). Again, this was most evident during the mid-day where feeding activity at the shaded feeder was proportionally greater compared to the unshaded feeder and crepuscular periods where feeding activity at the unshaded feeder was proportionally greater compared to the shaded feeder.

### **1.3.3 Consumption Analysis**

In the group experiments, the model with average temperature reported a lower AICc value than either minimum or maximum temperature. However, AICc values did not differ compared to the model that only used shade treatment (Table 1). Consumption at shaded feeders was  $0.57 \pm 0.02$  (mean  $\pm$  1 SE) kg per deer per day while consumption

at unshaded feeders was  $0.50 \pm 0.02$  (mean  $\pm$  1 SE) kg per deer per day (Figure 3). Daily per deer consumption rate was 13% lower at unshaded feeders, which was significantly different in the model with shade treatment and average temperature (Wald test,  $p = 0.0494$ ). Neither average temperature or the interactive effect of shade treatment and temperature were significant.

In the individual experiment, models that included temperature had higher AICc values than the model with shade treatment only (Table 2). Deer consumed  $1.00 \pm 0.04$  (mean  $\pm$  1 SE) kg of feed per day at shaded feeders and  $0.85 \pm 0.05$  (mean  $\pm$  1 SE) kg of feed per day at unshaded feeders (Figure 4), suggesting that deer ate 17% less feed per day when feeders were unshaded (Wald test,  $p = 0.0169$ ).

#### **1.4 Discussion**

I show that deer altered their behavior to meet conflicting thermal and nutritional demands in ways that may allow them to maintain their functional role as herbivores as climate warms. Consistent with previous work (Carranza et al., 1991; Relyea and Demarais, 1994; Ager et al., 2003), the deer in my experiments were largely crepuscular. However, in the cooler shaded treatments, deer often fed more during mid-day when temperatures were hottest. This may be because deer were able to forage in a location in which solar energy did not influence their internal temperature, which may have led to responses such as changes in metabolic rate (Renecker and Hudson, 1986; Baumgard and Rhoads, 2012) and altered diet preference (Dearing et al., 2008). When feeders were unshaded, deer fed less during the daytime. However, deer compensated for this reduced daytime feeding by increasing feeding activity near sunrise and sunset (Figure 1 and 2), although the amount that deer ate was reduced.

In addition to deer using feeders differently throughout the 24-hour day, results from the group experiment in which deer had access to both types of feeder suggest that deer made use of spatial thermal heterogeneity to mitigate the effects of warming. Deer fed from shaded and unshaded feeders at similar levels during the night when the two shade treatments didn't differ in temperature. However, during the day deer showed a strong preference for the shaded feeder (Figure 1). The important message to learn from this is that deer did not continue with the status quo, behaving identically in the more stressful environment. Instead, deer exhibited behavioral plasticity, using their environment in a different way in response to the changed thermal landscape.

Although deer were able to alter their feeding behavior in ways that may mitigate the effects of warming, there may be consequences for energetic balances. In the group experiment, deer ate less when feeders were unshaded (Figure 3 and 4), suggesting that access to cooler microclimates may be important for vertebrate herbivores facing climate warming. My individual experiment corroborated this, showing a 17% reduction in feed consumption when restricted to unshaded feeders. While this may not be detrimental during short periods of time, chronic reduction of feeding could have consequences, such as reduction in body size and reduced fecundity, that may impact species at both the individual and population level (White, 1983; Milner et al., 2014). Although it is unclear how deer would respond at longer time periods, my results reinforce the importance of landscape thermal heterogeneity (Elmore et al., 2017) and its role in potential behavioral adjustments to climate warming.

It is also unclear how changing patterns of deer herbivory would affect lower trophic levels. While my results suggest that deer could capitalize on thermal

heterogeneity to maintain their role as an herbivore within a community, my results also suggest that indirect effects may arise due to changed spatial and temporal patterns of herbivory. Even if deer were able to consume the same amount of food (i.e., plants) in a future, warmed world, a behavioral shift in when and where they feed could have top-down effects on plant communities (Tylianakis et al., 2008; Cahoon et al., 2012). For example, increasing temperatures may concentrate deer activity into isolated, cooler microhabitats analogous to my shaded feeders, and thereby differentially affect plants in those areas by increasing herbivory. Similarly, by altering when and where deer feed, interactions with predators may also change. My study did not include predators, although it is possible that predation risk may mediate how deer and other herbivores balance nutritional and thermal demands (Geist, 1974; Monteith et al., 2014). Evaluating these potential top-down and bottom-up effects that arise from altered deer behavior is beyond the scope of this study, but a laudable next step in understanding the net effects of climate change on deer and their ecosystems.

As with any manipulative experiment, the price of control and replication is a reduction in realism. Confining deer to areas much smaller than their natural home ranges may introduce variation or experimental artifacts. Movement patterns in ungulates are commonly driven by forage availability and restricting this movement may lead to an under or overestimation the natural activity patterns of my deer (Frair et al., 2005; Tylianakis et al., 2008). Furthermore, my study used pelletized feed to allow systematic measurement of consumption rates. The feed is more nutritious than many plants available to wild deer, and it is unclear if the nutritional quality of food may alter the outcomes of consumption and time spent foraging (Wilmshurst et al., 2000; Parker et al.,

2009). In the group experiment, social behavior of a species such as deer, could influence the results of this experiment. Previous research has suggested that group size may increase the time spent feeding by deer (Lashley et al., 2014), meaning that altering group size throughout the experiment may bias my estimation of consumption. While, I reduced this bias by implementing a paired design within enclosures and by maintaining similar densities of deer in each enclosure, it is still important to consider. Furthermore, my feeders limited the number of deer that could feed simultaneously, which differs from natural foraging where animals would be spaced across a larger patch. Deer may have been discouraged from using an already crowded feeder, especially if individuals exhibited dominance behavior to other individuals within the group (Stone et al., 2017). Ultimately, this could bias my assessments of feeder use if individuals were using a suboptimal feeder due to lower social rank. However, this effect is weakened when food is abundant (Michel et al., 2016), as it was in my experiment.

## **1.5 Conclusion**

Deer do not passively respond to changing environmental conditions, behaving identically despite temperature and other conditions. Instead, I show that deer can alter their behavior to make use of spatial and temporal patterns of thermal heterogeneity on the landscape. This highlights the importance of incorporating behavior into future studies of species' responses to climate change, as well as the importance of thermal heterogeneity within an environment. At this point, my understanding of the relationship between vertebrate herbivores and climate change in southern environments is limited. I recommend that further studies explore this relationship, potentially using experimental manipulation.

1.3 Model selection for consumption analysis in the group experiment.

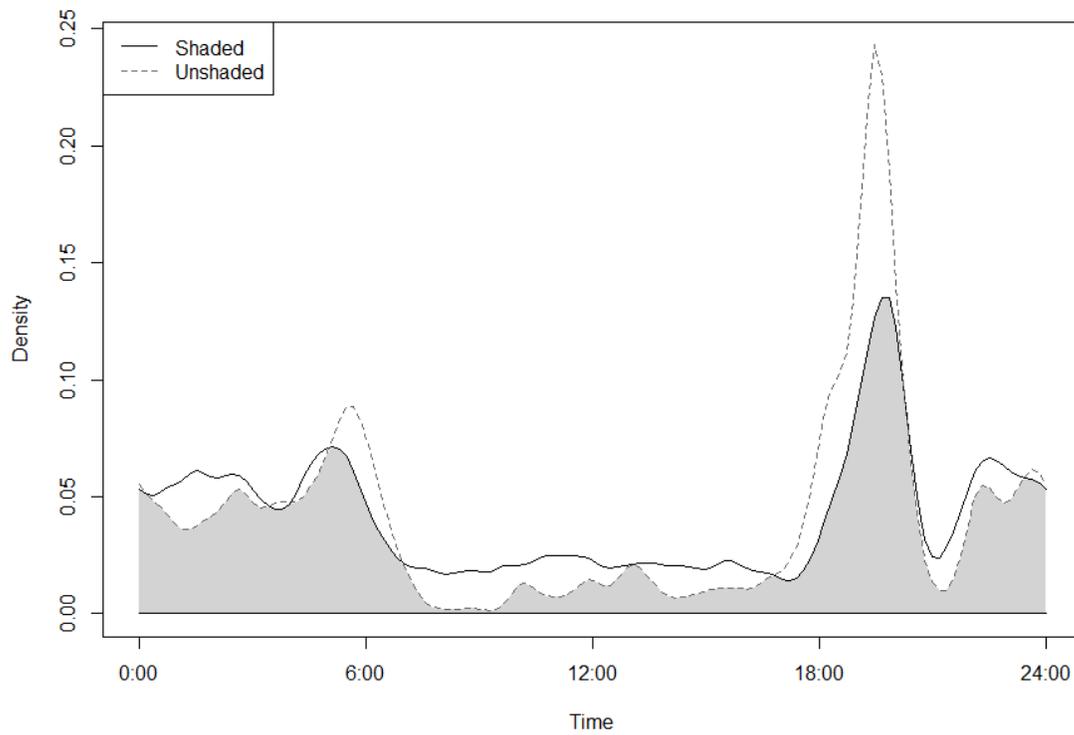
<b>Model</b>	<b>df</b>	<b>Negative Log Likelihood</b>	<b>AICc</b>	<b>ΔAIC</b>
Feeder	4	-122.225	252.5	0.00
Feeder * Average Temperature	6	-120.638	253.5	0.93
Feeder * Maximum Temperature	6	-120.800	253.60	1.26
Feeder * Minimum Temperature	6	-121.824	255.65	3.31

I used AICc values to compare models including the shade treatment at the feeder and different measurements of temperature as an assessment of thermal comfort.

1.4 Model selection for consumption analysis in the individual experiment.

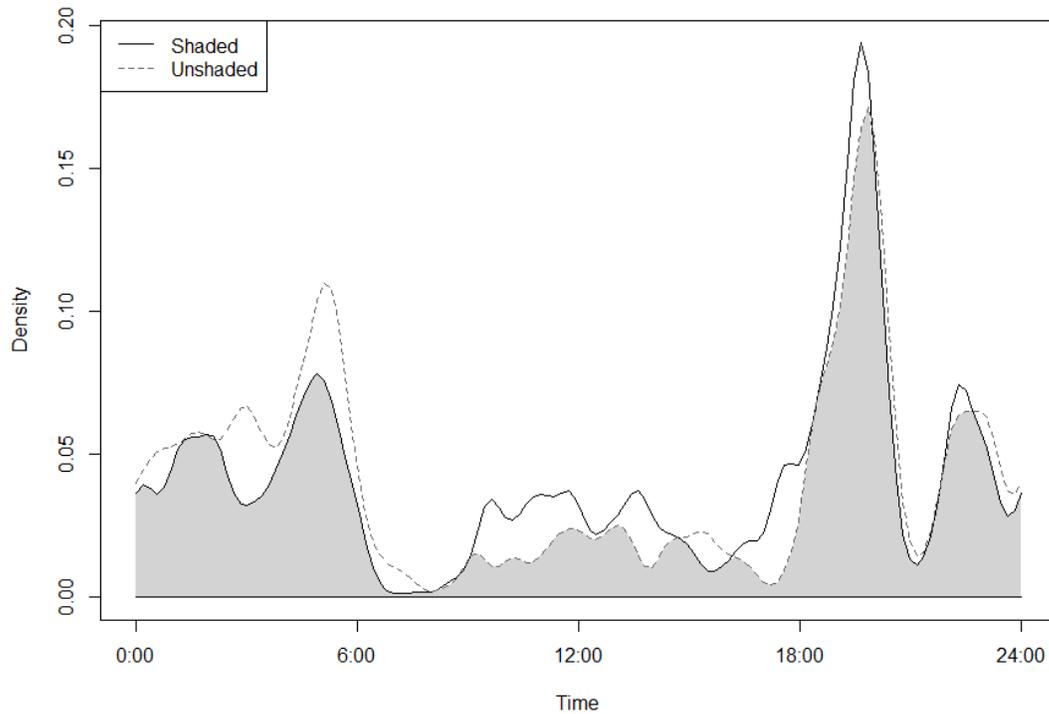
<b>Model</b>	<b>df</b>	<b>Negative Log Likelihood</b>	<b>AIC</b>	<b>ΔAIC</b>
Feeder	4	-42.453	92.91	0.00
Feeder * Minimum Temperature	6	-40.954	93.91	1.36
Feeder * Maximum Temperature	6	-42.262	96.83	3.98
Feeder * Average Temperature	6	-42.416	96.52	4.28

I used AICc values to compare models including the shade treatment at the feeder and different measurements of temperature as an assessment of thermal comfort.



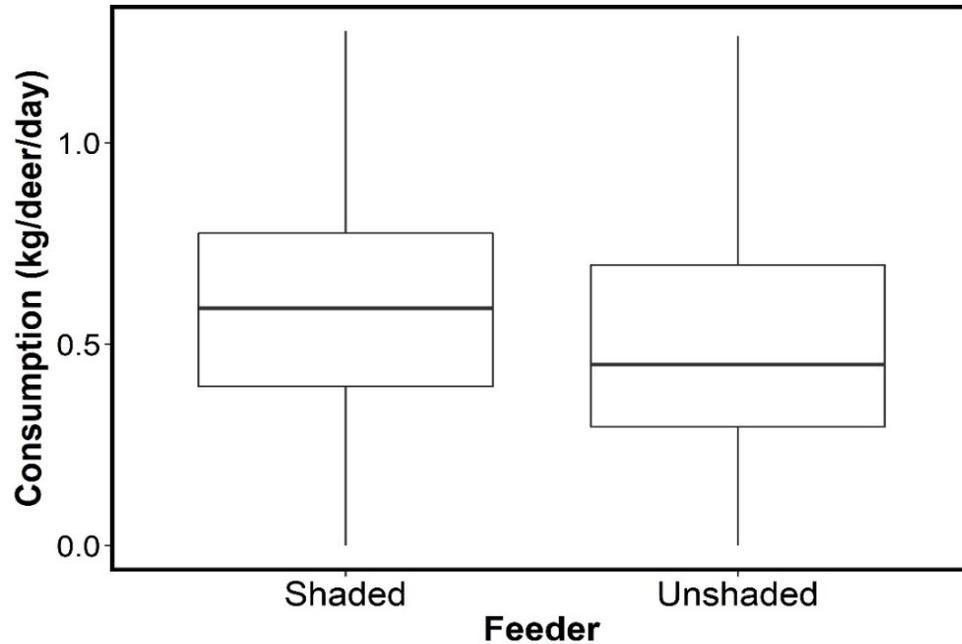
### 1.1 Overlap plot of feeding activity in the group experiment.

Feeding activity patterns of deer were different between shaded (solid black line) and unshaded (dashed grey line) feeders (coefficient of overlap = 0.826; Watson's U2 statistic,  $p < 0.001$ ). The grey area represents areas of overlap between the two activity patterns.



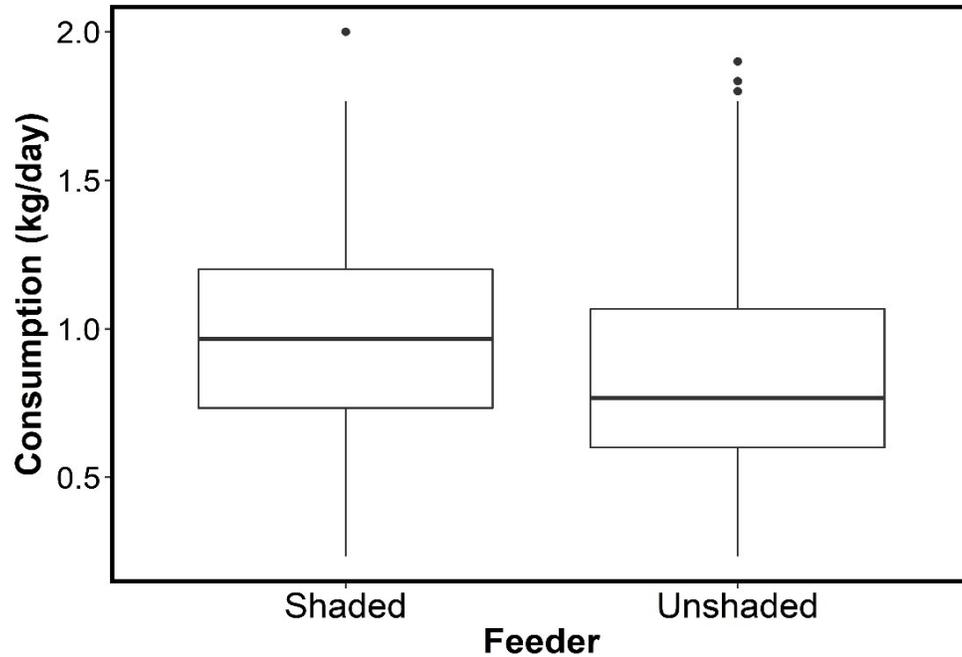
### 1.2 Overlap plot of feeding activity curves in the individual experiment.

Feeding activity patterns of individual deer were different between shaded (solid black line) and unshaded (dashed grey line) feeders (coefficient of overlap = 0.855; Watson's U2 statistic,  $p < 0.001$ ). The grey area represents areas of overlap between the two-activity pattern



### 1.3 Consumption in the group experiment.

Consumption differed among shaded and unshaded feeder treatments. Deer consumed 13% less in unshaded feeders (Wald test,  $p = 0.0494$ ). Shade treatment and average temperature across the two-day sampling period influenced daily consumption. Daily consumption rates were averaged across the sampling period and by the total number of deer per trial.



#### 1.4 Consumption in the individual experiment

Consumption differed among shaded and unshaded feeder treatments. Deer consumed 17% less food in unshaded feeders (Wald test,  $p = 0.0169$ ). Measurements were taken across a three-day sample period and averaged to estimate a daily rate of consumption. The dots beyond the boxplots are outlying points and are defined as samples beyond the  $1.5 * \text{IQR}$  (interquartile range).

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APPENDIX A

COMPARISON OF TEMPERATURE AT SHADED AND UNSHADED FEEDERS

### **A.1 Mean of temperature between shaded and unshaded feeders**

I suspended temperature data loggers (Onset Hobo, Bourne, MA, USA) 1 m from the top of each feeder in the group experiment. I recorded temperature at each feeder at 30-minute intervals throughout the duration of the group experiment. I compared the mean ambient temperature between shaded and unshaded feeders.

### **A.2 Difference in temperature between unshaded and shaded feeder during the 24-hour day**

I suspended temperature data loggers (Onset Hobo, Bourne, MA, USA) 1 m from the top of each feeder in the group experiment. I recorded temperature at each feeder at throughout the duration of the group experiment. I calculated the difference in temperature as the temperature at the unshaded feeder minus the temperature at the shaded feeder. The difference in these microclimates was most evident during the mid-day when opaque roofing material prevented solar radiation from warming the shaded feeder.

### **A.3 Mean ambient temperature during periods of high solar radiation**

The difference in ambient temperature between shaded and unshaded feeders is driven by solar radiation. Therefore, I also compared the mean ambient temperature between shaded and unshaded feeders during the period where solar radiation is likely to have the greatest effect between treatments (6:00 hr – 18:00 hr; see to Appendix 2) with a paired t-test. I used the same data loggers used to compare mean ambient temperature in Appendix 1.

#### **A.4 Ambient temperature in the large enclosures for the group experiment**

I placed temperature data loggers (Onset Hobo, Bourne, MA, USA) across the large enclosures at a height of 0.5 m. In each enclosure I placed three loggers in ambient shade areas and three loggers in sunny areas. I recorded temperature at 30 min intervals during my experiment. I calculated the difference in temperature from sunny and shaded areas and observed that over the course of the 24-hour day.

#### **A.5 Ambient temperature at feeders in the individual experiment**

I suspended temperature data loggers (Onset Hobo, Bourne, MA, USA) 1 m from the top of each feeder in the individual experiment. I recorded temperature at 30 min intervals at each feeder over the duration of the group experiment. I calculated the difference in temperature as the temperature at the unshaded feeder minus the temperature at the shaded feeder.

#### **A.6 Ambient temperature at the thermal refuge in the individual experiment**

I suspended temperature three data loggers (Onset Hobo, Bourne, MA, USA) at each thermal refuge in the individual experiment at a height of 0.3 m, 0.6m, and 2.5 m. I recorded temperature at 30 min intervals throughout the duration of the individual experiment. I average the temperature from the three loggers to estimate average ambient temperature at the refuge each hour of the 24-hour day.

#### **A.7 Thermal heat index**

I obtained weather information for Starkville, MS from the Soil Climate Analysis Network station (<https://www.wcc.nrcs.usda.gov/scan/>). I used hourly measurements of air temperature and relative humidity to calculate a temperature humidity index according

to (Dikmen and Hansen, 2009) and observed changes in temperature humidity index over the 24-hour day.

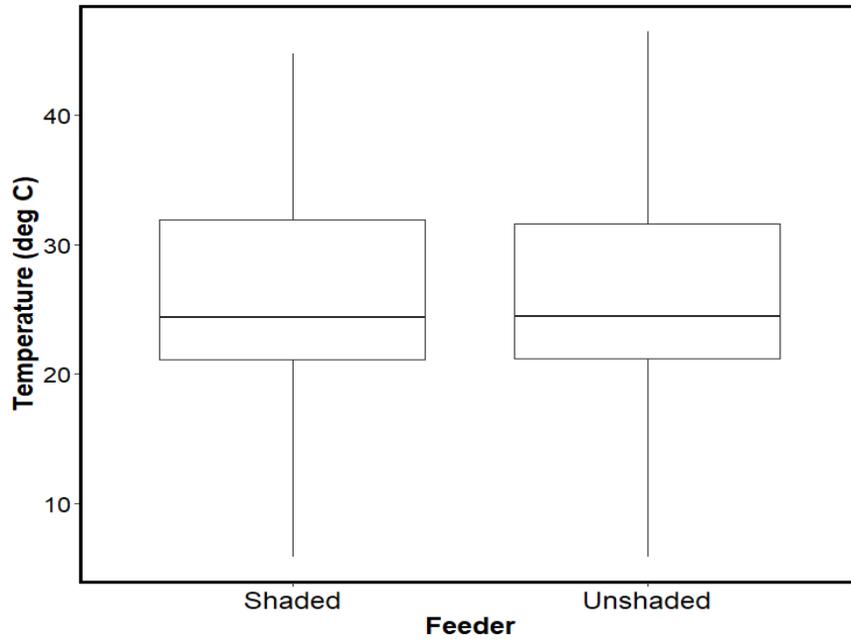


Figure A.1 Ambient temperature at shaded and unshaded feeders.

Mean ambient temperature between was 0.2 °C warmer at unshaded feeders (paired t-test,  $p < 0.001$ ).

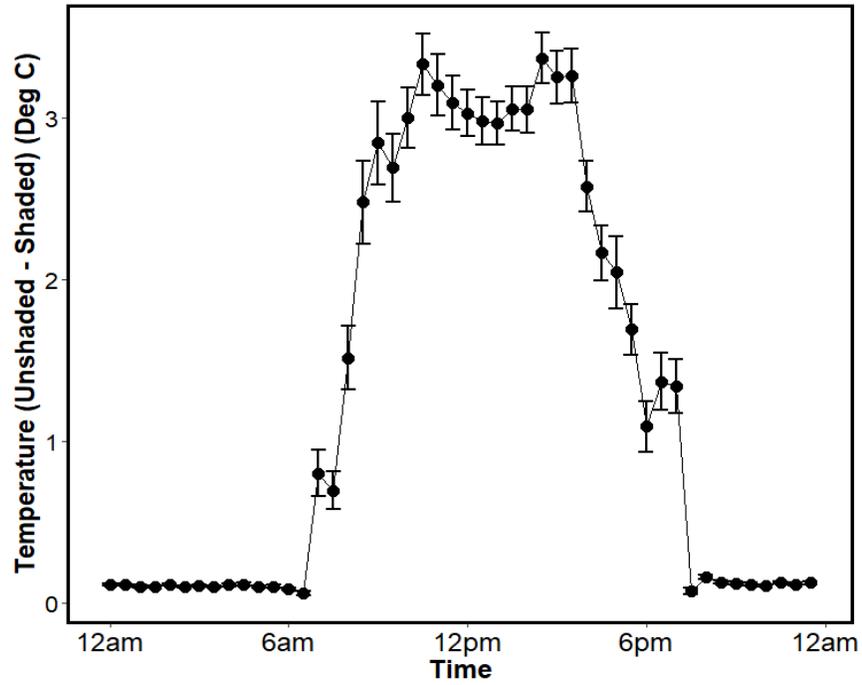


Figure A.2 Difference in temperature between unshaded and shaded feeder during the 24-hour day.

Difference in temperature as the temperature at the unshaded feeder minus the temperature at the shaded feeder. The difference in these microclimates was most evident during the mid-day when opaque roofing material prevented solar radiation from warming the shaded feeder. Error bars are  $\pm 1$  SE.

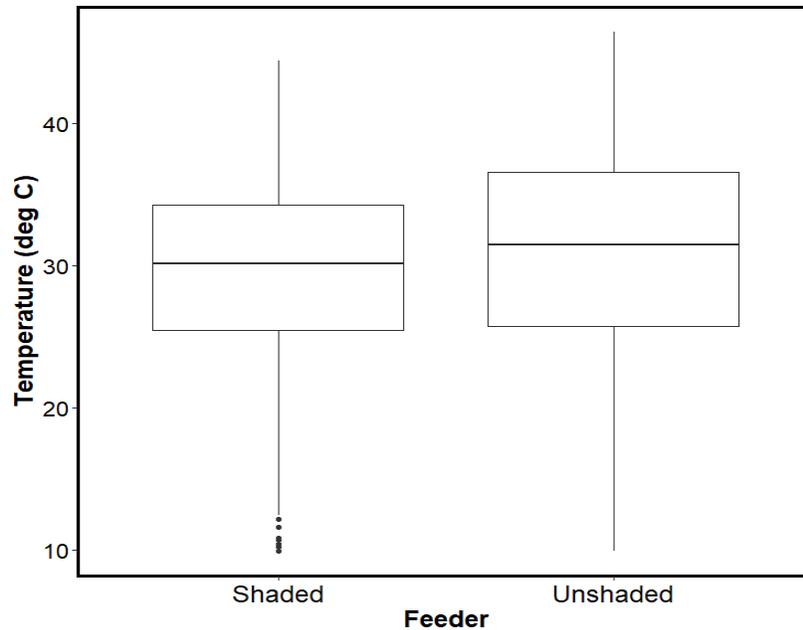


Figure A.3 Ambient temperature during high solar radiation

The difference in ambient temperature between shaded and unshaded feeders is driven by solar radiation. Therefore, I also compared the mean ambient temperature between shaded and unshaded feeders during the period where solar radiation is likely to have the greatest effect between treatments (6:00 hr – 18:00 hr). Mean ambient temperature at unshaded feeders was approximately 1.4 °C warmer than shaded feeders (paired t-test,  $p < 0.001$ ).

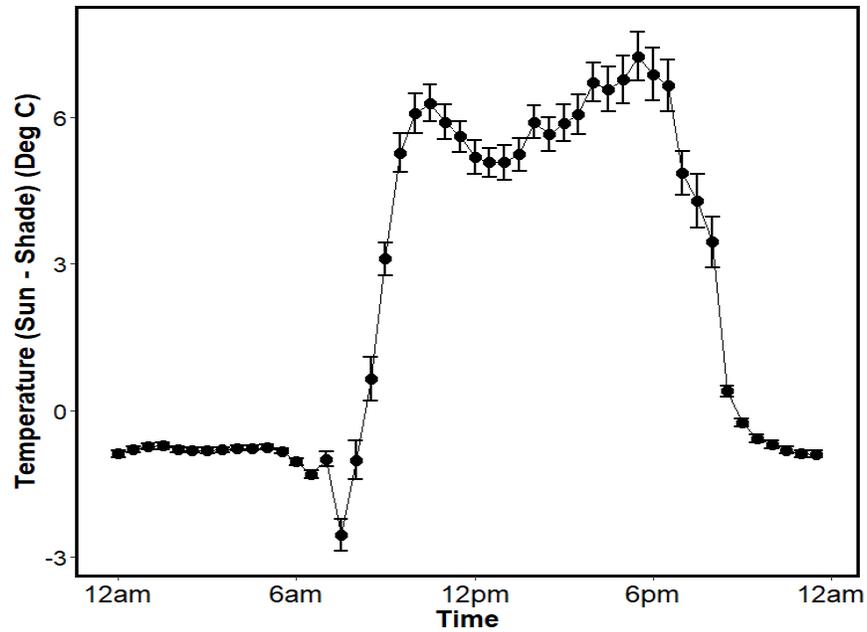


Figure A.4 Ambient temperature in the large enclosures for the group experiment.

In each enclosure I placed three loggers in ambient shade areas and three loggers in sunny areas. I recorded temperature at 30 min intervals during my experiment. The y axis is the difference in temperature from sunny and shaded areas each hour of the 24-hour day.

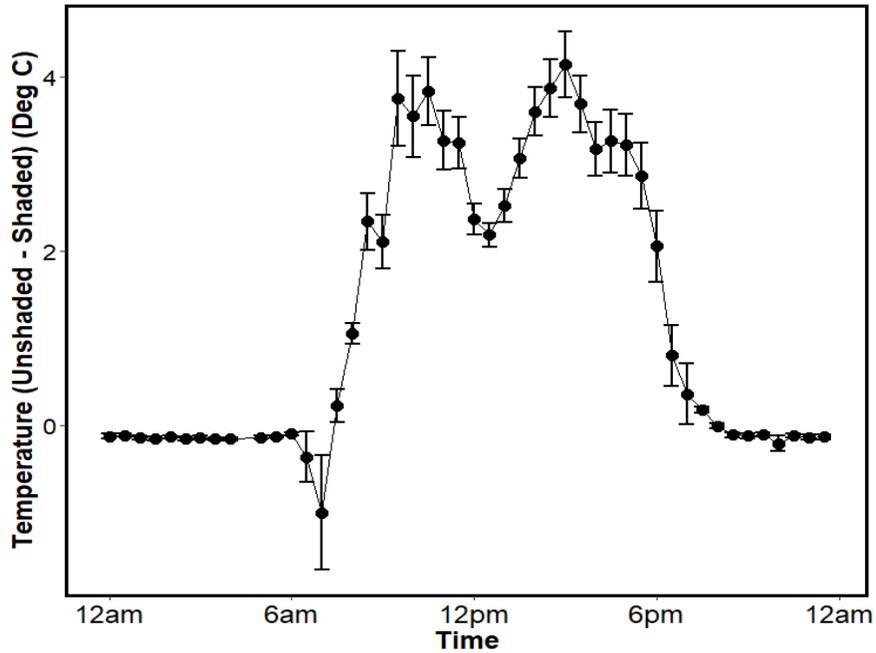


Figure A.5 Difference in ambient temperature between the shaded and unshaded feeder in the individual experiment

I suspended temperature data loggers (Onset Hobo, Bourne, MA, USA) 1 m from the top of each feeder in the individual experiment. I recorded temperature at 30 min intervals at each feeder over the duration of the group experiment. I calculated the difference in temperature as the temperature at the unshaded feeder minus the temperature at the shaded feeder and measure it by hour for the 24-hour day. Error bars are  $\pm 1$  SE.

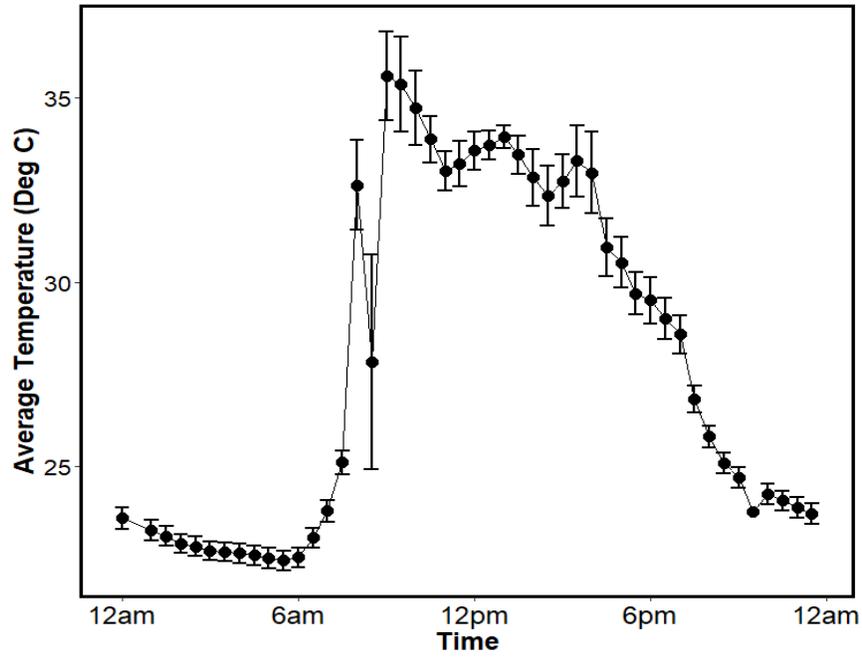


Figure A.6 Average temperature per hour at thermal refuge

I recorded temperature at 30 min intervals throughout the duration of the individual experiment. I average the temperature from the three loggers to estimate average ambient temperature at the refuge each hour of the 24-hour day. Error bars are  $\pm 1$  SE.

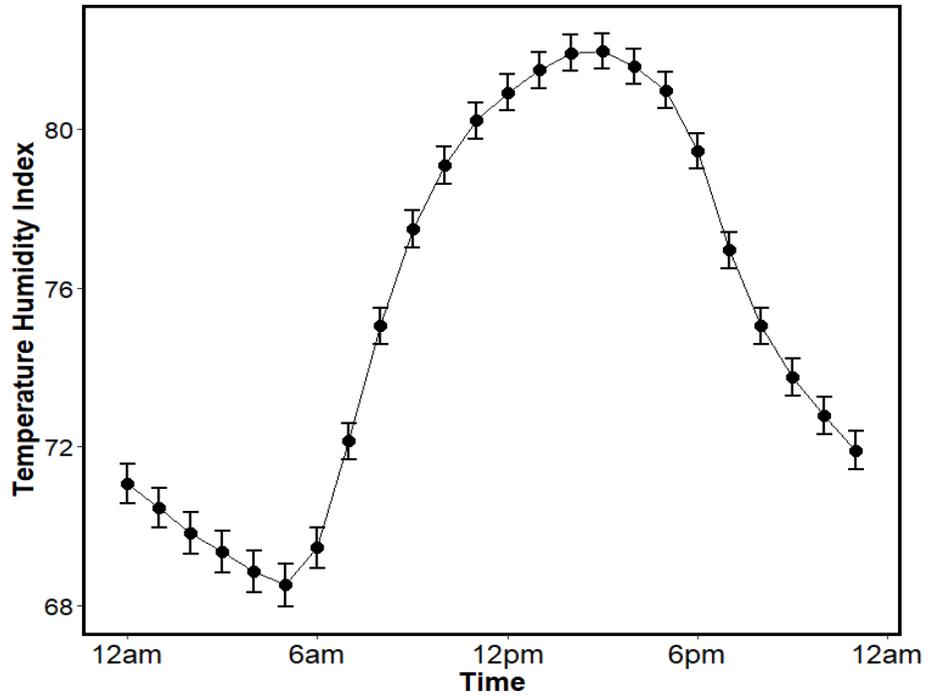


Figure A.7 Thermal Index by hour of the day throughout the 2017 Field Season

Hourly measurements of air temperature and relative humidity data from the local weather station were used to calculate a thermal index for the 2017 field season. I calculated the index according to Dikmen and Hansen (2009), for each hour of the day. Error bars are  $\pm 1$  SE.