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Comparative thermal ecology of copperheads (*Agkistrodon
contortrix*) and cottonmouths (*Agkistrodon piscivorus*)

Andy Mueller

Comparative thermal ecology of copperheads (*Agkistrodon contortrix*) and cottonmouths
(*Agkistrodon piscivorus*)

A Thesis

Presented to

The College of Graduate Studies

Austin Peay State University

In Partial Fulfillment

Of the Requirements for the Degree

M.S. Biology

Andrew T. Mueller

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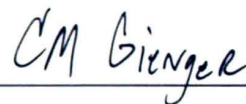
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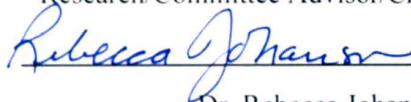
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DEDICATION

I dedicate this work to all of my friends and family that have supported me through this ever-enduring process.

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ABSTRACT

Comparative thermal ecology of copperheads (*Agkistrodon contortrix*) and cottonmouths (*Agkistrodon piscivorus*)

Body temperature is directly related to the physiology and behavior of ectotherms and the ability to thermoregulate is crucial for the survival and development of the organism. *Agkistrodon contortrix* (copperhead snakes) and *Agkistrodon piscivorus* (cottonmouth snakes) are relatively common, wide-ranging viperids, and their sit-and-wait ambush foraging strategy suggests that they are more likely to be passive thermoconformers within their thermal environment than active thermoregulators. Evaluating the thermal ecology of these species requires knowing the body temperature of the snakes (T_b), the operative temperatures available to snakes in their environment (T_e), and the preferred body temperature range of the species (T_{set}). We calculated effectiveness of thermoregulation index (E) and thermal exploitation index (Ex) to compare the degree to which snakes actively thermoregulate in their differing habitats. The T_{set} for both species was nearly identical at 24.9-27.8°C for copperheads and 24.9-27.9°C for cottonmouths. Cottonmouths had a significantly higher E index for the months of May, June, and July indicating that they are more effective thermoregulators than copperheads during mid-active season. Although it does appear that cottonmouths also have a higher Ex across the active season, it was not significantly different than the Ex copperheads.

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Chapter I

Introduction

Many organisms thermoregulate in some fashion, but the ways in which they accomplish thermoregulation differ. Endotherms are able to maintain their body temperature (T_b) physiologically over a wide variety of external temperatures; (Bennett and Ruben 1979); however, ectotherms typically take advantage of variation in environmental temperatures to regulate their T_b through behavioral thermoregulation. Thermoregulation is important because T_b influences nearly all physiological processes including locomotion, prey acquisition, egg production, immune response, predator avoidance, digestion, and growth (Tait 1969, Kaufmann and Bennett 1989, Van Der Have and De Jong 1996). The intensity of behavioral thermoregulation is often considered a continuum of strategies that range from complete thermoconformity, where individuals passively accept the thermal conditions of the environment, to active thermoregulation in which body temperatures are tightly regulated, usually at a level different from the average environmental temperature (Hertz et al. 1993, Angilletta 2009). The degree to which ectotherms regulate their body temperature is further influenced by the costs and benefits of thermoregulation (Huey and Slatkin 1976), which are determined by the availability of temperatures in the environment that permit optimal function of physiological processes (Huey and Stevenson 1979). High cost thermal environments may increase mortality risk, energy expended to thermoregulate, and missed opportunities of reproduction or food acquisition (Angilletta 2009). Some ectotherms have a wide thermal performance breadth (eurythermic), where physiological processes

are near optimal over a wide range of body temperatures while others have a narrow thermal breadth (stenothermic) of optimized physiological processes, behaviors, and performance (Huey and Stevenson 1979, Blouin-Demers et al. 2003). These thermal performance breadths influence the degree to which ectotherms thermoregulate leading to differing thermoregulation strategies (Huey and Stevenson 1979).

Thermoconformity is a viable behavioral strategy when the physiological disadvantages of conformity are low (Ruibal 1961). Physiological processes such as food assimilation (Du et al. 2007), heart rate (Licht 1965), and locomotor performance (Kaufmann and Bennett 1989) can have low or negligible costs when body temperature (T_b) can be maintained near the preferred body temperature range (T_{set}), negating the need for active thermoregulation (Blouin-Demers and Weatherhead 2001). Conformity may also be the preferred strategy when costs of active thermoregulation are high relative to available resources or predation risk (Huey and Slatkin 1976). Alternatively, some ectotherms invest extensive time and energy into precise thermoregulation. This strategy most often occurs with organisms in thermally heterogeneous environments where achieving preferred body temperatures does not have high costs due to lower energy expenditure for thermoregulation and reduced risk of mortality from shuttling over long distances (Huey and Slatkin 1976, Blouin-Demers and Nadeau 2005, Angilletta 2009).

Given the importance of thermoregulation in ectotherms, we examined the thermal ecology of two closely related viperids from the genus *Agkistrodon* (Gloyd and Conant 1990). Copperheads (*Agkistrodon contortrix*) and cottonmouths (*Agkistrodon piscivorus*) have a common evolutionary history (Burbrink and Guiher 2015), but the species differ considerably in habitat use and are typically locally parapatric in

distribution. Copperheads are typically found in deciduous hardwood forests with high levels of vegetative cover, brush piles, large logs, scattered rocks, and moist leaf litter (Fitch 1960, Ernst and Ernst 2003). They are often found near water but rarely observed in it (Fitch 1960, Niemiller et al. 2013), and tend to be hidden under cover of leaf litter where they can remain cryptic while waiting to ambush prey (Bechtel 1978). Conversely, cottonmouths are almost exclusively associated with aquatic habitats and slow-moving bodies of water, from brackish marshes to muddy swamps and sloughs with patchy vegetation and canopy cover (Ernst and Ernst 2003, Powell et al. 2016). Cottonmouths are frequently observed conspicuously basking on vegetation mats, logs, and hummocks exposed from the water (Burkett 1966) and they may aggregate at remaining waterholes during times of drought (Ernst 1992).

The objective of this study was to compare the thermal biology of these two closely related, but somewhat ecologically and behaviorally dissimilar species. Because they differ markedly in habitat use, occupying sites with potentially dissimilar thermal environments, we test the hypothesis that habitat use can influence the ways in which the species interact with their thermal environments (thermoregulation).

Chapter II

Materials and Methods

Locality

The study site for copperheads was located at Land Between the Lakes National Recreation Area (LBL) in Trigg county Kentucky. The landscape is dominated by secondary oak-hickory forest along the steep, dry ridges and mesophytic communities in the cooler, moist ravines (Close et al. 2002). Cottonmouths were captured from a site adjacent to the Cumberland River and backwater sloughs of Sycamore Creek, Cheatham County Tennessee near Cumberland River Bicentennial Trail (CRBT). The area is comprised of a large palustrine scrub-shrub wetland (Tiner Jr 1984) with adjacent agriculture fields and mixed hardwood forest. Snakes at both sites were collected opportunistically during the active seasons (April-September) and capture locations were recorded using a handheld GPS (Garmin GPSmap 60Sx). Sex was determined in the field via cloacal probing and only male snakes were used in this study because of potential differences in thermal ecology between the sexes (Charland and Gregory 1990, Graves and Duvall 1993, Gardner-Santana and Beaupre 2009). Individuals were assigned to one of two experimental groups: telemetered snakes to carry T_b recording dataloggers in the field, or laboratory gradient snakes to carry dataloggers in a lab experiment used to determine the preferred T_b range.

Laboratory Thermal Gradient and Preferred Body Temperature

A laboratory thermal gradient was used to estimate individual's preferred body temperature range (T_{set}). The gradient provides an environment that is free of ecological

costs and constraints that could potentially influence thermoregulation (Hertz et al. 1993) such as shuttle distance between sun and shade (Withers and Campbell 1985), low ambient temperature, radiation, wind and refugia access (Porter and Gates 1969). We used three identical thermal gradients and each was comprised of a large commercial snake cage (Vision cage V632, 183 x 91 cm) cooled at one end to $\sim 16^{\circ}\text{C}$ using a copper coil placed underneath the cage circulating water through a Fischer Scientific chiller (model 9010). Adjacent to the cooling coil we used eight 15 cm wide flexwatt heat strips (12 watts/ft) placed side-by side and individually connected to temperature controllers (Omega CSC32) with type-K thermocouples reading the surface temperatures on the bottom of the gradient. This design provided a linear thermal gradient of available temperatures between 16°C and 34°C on the interior floor of the cage (changing 2.0°C per 15cm). Lighting in the gradient was provided by fluorescent fixtures in the room set to a 12:12 h light:dark photoperiod. Snakes were given $\sim 5\text{cm}$ of leaf litter (native oaks) as substrate and water was available at three locations across the gradient (provided in small bowls) to reduce the likelihood that their location within the gradient was based on resources other than temperature.

To determine the preferred body temperature range (T_{set}), male snakes were anesthetized with isoflurane and surgically implanted with a Maxim iButton[®] DS1922L temperature data logger weighing no more than 5% of the snake's body mass. Loggers were coated in biologically inert rubber (Plasti Dip International, St. Louis Park, MN) and inserted into the coelomic cavity following the protocols of Reinert and Cundall (1982). Snakes were then allowed to recover for 24 hours before being placed in the thermal gradient and given 24 hours to acclimate before the trial began. After the

acclimation period, snakes remained in the gradient for 72 hours with data loggers recording body temperatures every 10 minutes. Snakes were then removed from the gradient and the data loggers were retrieved using the same surgical procedures as above. The bounds of the central 50% of T_{bs} during the 72 hours test period were considered the T_{set} for each individual (Hertz et al. 1993, Christian and Weavers 1996).

Telemetry

Snakes collected for telemetry had a radio transmitter (SI-2, Holohil Systems Ltd., Carp, ON, Canada) implanted in the left side of the coelomic cavity approximately one-third of the body length anteriorly to the cloaca following the methods of Reinert and Cundall (1982). These snakes were also implanted with an iButton® DS1922L data logger programmed to record body temperatures (T_b) every 20 minutes for the length of the active season. The combined mass of the radio transmitter and datalogger did not comprise more than 7% of the total body mass. After surgery, snakes were given 24-48 hours to recover in the lab and were then released at the point of capture. Snakes were relocated with telemetry (Advanced Telemetry Systems R410 receiver and Telonics RA-23 antenna) at least once per week to monitor general location and coordinates for each relocation were recorded as Universal Transverse Mercator units (UTM) with an accuracy of ≤ 3 meters.

Operative Temperatures

To estimate the distribution of body temperatures that snakes could potentially attain at the study sites, hollow copper models were used to estimate environmental operative temperatures (T_e ; Bakken 1992, Peterson et al. 1993, Christian et al. 2016). Models were 30 cm long and 1.9 cm in diameter with caps secured on each end.

Temperature data loggers (Maxim iButton® DS1922L) were placed inside each model and recorded operative temperature every 20 minutes, coinciding with recording of snake T_{bs} . Data loggers were first coated in rubber (Plasti Dip International, St. Louis Park, MN) for weatherproofing and secured with zip ties along perpendicular axes of the logger. The ties kept the datalogger in the center of the model, reducing conductive heat exchange with the sides of the model (Bakken 1992). Copper models were designed to be of a similar size, shape, and radiative properties of copperheads or cottonmouths and were painted to approximate the average reflectance of the dorsal surface of the snakes (Peterson et al. 1993).

We deployed 24 operative models at each site, dispersed in a manner to represent as closely as possible the different thermal regimes (thermal microhabitats) available to snakes while they are engaged in above-ground activities (i.e. moving or resting in ambush foraging posture). We placed models in open canopy tree-fall gaps, closed-canopy forests, under cover at the bases of fallen trees, along ecotone edges, and (for cottonmouth sites) in shallow-water areas of the swamp.

Analyses

To quantify the thermal properties of the habitats available to snakes, we used several commonly applied indices of operative temperatures and of thermoregulation (Hertz et al. 1993, Christian et al. 2016). To assess thermal quality of the habitats we used the d_e index (Hertz et al. 1993, Blouin-Demers and Weatherhead 2001) calculated as the mean deviations of T_{es} from the T_{set} range. If T_e is below T_{set} , d_e is measured as the difference between the lower bound of T_{set} and T_e and vice versa for T_{es} above T_{set} . We also measured the accuracy of thermoregulation, d_b , (Blouin-Demers and Weatherhead

2002) as the mean absolute value of deviations of T_{bs} from T_{set} (Hertz et al. 1993). An index of thermoregulatory effectiveness (E) was determined from the d_e and d_b values, defined as $E = 1 - (\bar{d}_b / \bar{d}_e)$ and generally ranges from 0 (no thermoregulation, strict thermoconformity) to 1 (very precise thermoregulation; Hertz et al. 1993). To further compare the effectiveness of thermoregulation between copperheads and cottonmouths we also used Blouin-Demers and Weatherhead's index of effectiveness ($d_e - d_b$; 2001). Their index ($d_e - d_b$) removes the ratio that is found in Hertz et al. (1993), allowing us to compare species by looking at the magnitude of the difference between d_e and d_b and not a ratio that could be potentially skewed by snakes having different thermal environments and strategies of thermoregulation, but in a similar proportion (Blouin-Demers and Weatherhead 2001). Both indices of effectiveness are considered here for comparison with other studies using only the Hertz et al. (1993) index. We calculated exploitation of the thermal environment (Ex) for each individual, defined as the time in which T_{bs} are within T_{set} divided by the time available for T_{bs} to be within T_{set} (Christian and Weavers 1996).

Data analysis was conducted using JMP Pro 10 (SAS Institute Inc., Cary, NC). All data analyses for the thermoregulatory indices were averaged for each individual snake and each operative model over the course of a month. Monthly means were used in mixed-model repeated measures analysis of variance (ANOVA) to determine differences between species and sites, among months, and for month*site interactions. Species, site, and month were all fixed effects in the model with either individual snake or individual model being considered a random effect (depending whether considering T_b or T_e). Post

hoc comparisons of species by month were conducted using Tukey HSD tests.

Comparisons were considered significant if statistical test results yielded $P \leq 0.05$.

Chapter III

Results

We recorded T_{bs} for 13 cottonmouths for a total of 215,756 T_{bs} (April 2012-September 2013) and 149,047 T_{bs} of 15 copperheads (April 2015 to September 2016). We collected 224,029 T_{es} for cottonmouth habitats and 575,808 T_{es} for copperhead habitats. Temperatures were combined to generate monthly means for calculation of indices of thermoregulation.

Thermal Preference (Laboratory)

Thirty-five male copperheads and 19 male cottonmouths were used to determine preferred T_b range in laboratory thermal gradient trials. Copperheads had a mean T_b of 26.4°C and mean 75% and mean 25% quartiles of 27.8°C and 24.9°C and cottonmouths were nearly identical, having a mean T_b of 26.1°C with 75% and 25% quartiles of 27.9°C and 24.9°C, respectively (Table 1). There was not a significant difference between the two species for any of these parameters (mean T_b , $F_{1,53} = 0.44$, $P > 0.51$; 75% quartile, $F_{1,53} = 0.0006$, $P > 0.98$; 25% quartile, $F_{1,53} = 0.1$, $P > 0.75$).

Thermal Quality of the Environment

Grand mean T_{es} for each month increased from April to July, peaking in July for both sites, and decreased through September (Table 2, Fig. 1). Mean T_e was significantly different among months ($F_{5,191} = 695.71$, $P < 0.0001$) but not between sites or among month*site interactions ($F_{1,206} = 1.66$, $P = 0.1994$; $F_{5,191} = 2.09$, $P = 0.0688$; Fig 1). A Tukey HSD shows that all months were significantly different (pairwise between sites) except June and August. Mean minimum temperatures differed significantly among

months and among month*site interactions but not between sites ($F_{5,190} = 307.41, P < 0.0001$; $F_{5,190} = 4.53, P = 0.0006$; $F_{1,212} = 0.06, P = 0.8049$). Mean maximum temperature was significantly different among months, between sites and among month*site interactions (Table 2; $F_{5,190} = 4.28, P = 0.001$; $F_{1,207} = 20.81, P < 0.0001$; $F_{5,190} = 4.07, P = 0.0016$). Mean monthly temperatures at both sites reached the T_{set} for each species in only July; however, mean maximum temperatures were above the upper bounds of T_{set} in each month of the active season indicating that microhabitats were available to allow snakes to reach their T_{set} .

Operative temperatures (T_e) indicate that habitats occupied by the species differed significantly in thermal quality (d_e). However, these results may be driven by sample size rather than biological differences, and for every month mean T_e s and mean d_e s were less than 1°C different between the two sites. However, month, site, and the interaction between month and site were all significantly different for mean d_e s ($F_{5,190} = 641.71, P < 0.0001$; $F_{1,215} = 7.35, P = 0.0073$; $F_{5,190} = 11.27, P < 0.0001$) indicating thermal quality is different between habitats among the months of the active season (Table 2). Post-hoc Tukey HSD tests indicates that LBL had a significantly lower d_e than CRBT for June and July. May was the only month where CRBT had a significantly lower d_e than LBL and the sites are not significantly different in August and September. The two sites were also different in max d_e among months, between sites, and among month by site interactions ($F_{5,190} = 6.92, P < 0.0001$; $F_{1,209} = 11.68, P = 0.0008$; $F_{5,190} = 6.44, P < 0.0001$). Tukey HSD indicates that the differences in d_e between sites occur in June and July with LBL having a lower mean maximum d_e .

Body Temperatures

Across the active season body temperatures (T_b) were significantly different among months, between species, and among month*species interactions ($F_{5,94} = 232.82$, $P < 0.0001$; $F_{1,22} = 9.48$, $P = 0.0055$; $F_{5,94} = 3.80$, $P = 0.0035$) with a Tukey HSD post hoc test indicating significantly different T_b s in May (19.1 ± 0.3 and 21.4 ± 0.4) and June (23.2 ± 0.4 and 24.6 ± 0.4) with cottonmouths having a higher T_b than copperheads. Both species follow the trend of having the lowest T_b s in April with increasing T_b until July and then decreasing again through September (Fig 2 and 3). Similarly the two species differ in their deviations from the set-point range (d_b) among months between species and among month*site interactions ($F_{5,91} = 267.37$, $P < 0.0001$; $F_{1,17} = 11.11$, $P = 0.0039$; $F_{5,91} = 5.17$, $P = 0.0003$) with a post hoc Tukey HSD test indicating that cottonmouths have a significantly lower d_b in May ($4.4 \pm 0.1^\circ\text{C}$) than copperheads ($6.3 \pm 0.1^\circ\text{C}$).

Thermoregulation Indices

We used multiple indices to compare copperhead and cottonmouth thermoregulation during the active season. Effectiveness of thermoregulation, (E ; Hertz et al. 1993), was significantly different between the two species ($F_{1,24} = 29.96$, $P < 0.0001$), among the months of the active season ($F_{5,102} = 16.48$, $P < 0.0001$), and among the species*month interaction (Table 3; $F_{5,102} = 17.47$, $P < 0.0001$). Significant differences between species occurred in May ($E = 0.33 \pm 0.06$ and 0.12 ± 0.02), June ($E = 0.51 \pm 0.03$ and 0.20 ± 0.003), and July ($E = 0.59 \pm 0.02$ and 0.15 ± 0.04) with cottonmouths having a higher E (thermoregulating more precisely) than copperheads in each of those months (Fig. 4a; Tukey HSD < 0.05 for each comparison). Significant differences in thermoregulation are apparent when examining d_e - d_b index (Blouin-

Demers and Weatherhead 2001). There was a significant difference between species ($F_{1,25} = 23.15$, $P < 0.0001$), among months ($F_{5,101} = 2.79$, $P < 0.0212$), and among month*species interactions ($F_{5,101} = 11.2$, $P < 0.0001$) across the active season with cottonmouths thermoregulating more precisely than copperheads in May (Fig 4b; 2.14 ± 0.40 vs. 0.90 ± 0.14), June (2.00 ± 0.12 vs. 0.58 ± 0.08), and July (1.74 ± 0.16 vs. 0.22 ± 0.06 ; Tukey HSD < 0.05 for all).

The index of thermal exploitation (Ex) was significantly different between species overall ($F_{1,25} = 5.49$, $P = 0.03$) and among months ($F_{5,96} = 23.0$, $P < 0.0001$) but not significant in the interaction of month*species (Fig. 4c; $F_{5,96} = 1.7$, $P = 0.14$). These results indicate that copperheads and cottonmouths exploit their thermal environments in a similar manner each month where the lower bounds of T_{set} are attainable. Cottonmouths consistently maintained a higher Ex throughout the active season (4 of 6 months) although differences were small in July (52.3 ± 3.36 and 51.39 ± 3.22) and August (54.95 ± 3.46 and 54.77 ± 3.33).

Chapter IV

Discussion

Overall, copperheads and cottonmouths exhibited remarkably similar patterns in monthly body temperatures (T_{bs}) and thermoregulation across much of the active season. Despite being different structurally, thermal habitats for the two species were also remarkably similar. This suggests that the two species have similar thermal challenges and interact with their thermal environments in a similar manner, overall. However, cottonmouths generally tend to thermoregulate more effectively, especially in late summer when their habitats offer higher maximal temperatures, and also tend to have a higher degree from conformity than copperheads. In May, June, and July cottonmouths maintained a higher effectiveness than copperheads, which tend to be closer to thermoconformity more passively enduring operative temperatures. Both species appear to exploit their thermal environments similarly, keeping their T_{bs} within T_{set} when T_{set} is available just over 50% of the time at max. Most of the active season, neither species seem to utilize the hotter microhabitats available. This may be due to costs that were not measured, such as predation.

Similar patterns of thermoregulation have been found in closely-related *Anolis sagrei* and *A. distichus* in Florida, with *A. sagrei* having higher T_{bs} in closed canopy habitats (Lee 1980). Some desert insects also exhibit trends in differing behavioral thermoregulation by using thermal microhabitats in different ways. In *Hyles lineata* and *Manduca sexta*, *H. lineata* is able to maintain a more constant T_b over a wide range of temperatures by adjusting its orientation to solar radiation and microsite location on

vegetation while *M. sexta* maintains a T_b that is near air temperature and lacks the overt thermoregulatory postures found in *H. lineata* (Casey 1976).

Thermoregulation can be a costly endeavor for ectotherms. This is especially true when habitats are not spatially or temporally thermally heterogeneous (Huey and Slatkin 1976). It may mean that the organism has to move great distances to find suitable temperatures, which can be costly (Huey and Slatkin 1976). The Cumberland River Bicentennial area is smaller than Land Between the Lakes National Recreation Area with more evenly distributed edge habitat potentially offering cottonmouths more thermal heterogeneity overall, permitting them to thermoregulate more efficiently with less need for movement and energy expenditure (Huey 1974, Sears et al. 2016).

While seeking suitable environmental temperatures for thermoregulation, individuals may also be increasingly exposed to predators. Adult cottonmouths are considerably larger than adult copperheads. Large adult size may allow cottonmouths the opportunity to spend more time exposed while searching for suitable temperatures because they have fewer predators relative to smaller copperheads of the same age (Mushinsky and Miller 1993, Ernst and Ernst 2003). This is supported by observations of adult cottonmouths occurring farther from the water's edge than juvenile cottonmouths while foraging, which is potentially driven by a higher predation risk for juveniles (Eskew et al. 2009). Higher predation risk may outweigh the benefits that copperheads receive when leaving refugia to seek favorable thermal environment. Remaining in the cooler environments may also reduce the energy costs of copperheads which decreases its foraging demands (Brown and Weatherhead 2000) and risk of predation.

Behavioral differences may account for some of the variation in thermoregulation between species. At our sites cottonmouths emerge from hibernation in limestone bluffs and disperse through a small hardwood corridor to a buttonbush swamp where they spend the majority of their active season. Copperheads, however, typically hibernate in small mammal burrows in closed canopy forests until spring emergence. They do not appear to show dispersion behavior away from hibernacula like cottonmouths. Cottonmouths may be dispersing to suitable thermal microhabitats, which allow them to thermoregulate more efficiently than copperheads. Similar results have been found in black ratsnakes and northern watersnakes that have overlapping ranges and a similar preferred temperature range (T_{set}). Black ratsnakes have lower T_{bs} in the field than northern watersnakes likely a result of a wider thermal performance breadth in black ratsnakes allowing them to perform adequately at these lower temperatures (Brown and Weatherhead 2000, Blouin-Demers and Weatherhead 2001, Blouin-Demers et al. 2003).

On the ambush predator foraging continuum, copperheads are thought to be a more active forager than cottonmouths, although both undergoing an ontogenetic shift from sit-and-wait predators as neonates to more active ambush predator as adults (Beaupre and Montgomery 2007, Eskew et al. 2009). The higher movement rates of the copperhead may produce a behavioral tradeoff between foraging and precise thermoregulation (Belluore et al. 1996). Christian and Weavers (1996) observed a similar pattern when comparing four species of varanid lizards in Australia, with *Varanus panoptes* being the most active species but thermoregulating with the least precision. In Asian monitor lizards, *Varanus bengalensis* and *V. salvator*, the species are sympatric with contrasting terrestrial (*V. bengalensis*) and semi-aquatic (*V. salvator*) habitat use.

Varanus salvator maintained lower T_b s with less variability than *V. bengalensis* (Wikramanayake and Dryden 1993) which is opposite of what we found with copperheads and cottonmouths as our semiaquatic species (cottonmouth) had a higher T_b than our terrestrial species although only significantly different in May. However, our results do support the anecdotal trend that Wikramanayake and Dryden (1993) found indicating that *V. salvator* likely had a lower T_b due to heavy habitat canopy cover (and presumably lower T_e s) near the riparian areas that *V. salvator* inhabited compared to inland areas that *V. bengalensis* prefer and this could help explain the slightly lower T_b found with copperheads in this study because they are in areas with higher canopy cover. Cottonmouths may also be using riparian vegetation to maintain a more consistent T_b than copperheads when air temperatures are not ideal, a similar behavior demonstrated by *V. salvator* (Wikramanayake and Dryden 1993). A better understanding of microhabitat use by both copperheads and cottonmouths may help us understand the interaction between habitat structure and behavioral thermoregulation by both species.

Cottonmouths are appreciably larger in adult body size than copperheads which may aid them in maintaining preferred body temperatures, even when conditions are not favorable (Shine and Madsen 1996). The average adult copperhead in our study was 746.9 mm SVL with an average mass of 285 g, whereas cottonmouths averaged more than twice that with a mean mass of 730 g and a mean SVL of 836.6 mm. Thermal inertia associated with additional mass may allow cottonmouths to maintain higher T_b s while traveling through thermally unfavorable habitats or while foraging in water (Bartholomew 1966). Australian tiger snakes maintain a higher overall T_b when limited to semiaquatic vs terrestrial activity and have increased performance in foraging and

predator escape (Aubret and Michniewicz 2010). Entering the water with a higher T_b may delay the drop in locomotor performance associated with a cooling body temperature and extend the time that an ectotherm can forage or evade a predator in the water (MacKinnon et al. 2006). Locomotor performance has been shown to decline for other species after entering cool water, causing them to go slightly hypothermic. Both the Australian water rat (*Hydromys chrysogaster*) and the *Triturus* newt had reduced locomotor performance after entering cooler water (Dawson and Fanning 1981, Gvozdik and Van Damme 2008). Since performance can be linked to fitness in many species (Angilletta et al. 2002), it is beneficial for ectotherms to maintain a T_b that promotes performance (Huey and Kingsolver 1989, Marvin 2003), which may help explain higher precision of thermoregulation in cottonmouths.

We estimated the T_{set} for copperheads to be 24.9-27.8°C and the T_{set} of cottonmouths to be 24.9-27.9°C. Other studies of these same species have shown wider preferred T_b ranges than the range that we estimated. Copperheads have been previously estimated to have a preferred T_b range of 23-30.5°C ($n = 20$; Sanders and Jacob 1981) encompassing our estimated range. Our calculated T_{set} range is likely more precise due to larger sample size. Cottonmouths in Texas were previously estimated to have a T_{set} of 22.6-29.2°C ($n = 8$; Keck 1998) and 23.5-29.5°C in Southwest Missouri ($n = 4$; Menzel 2008), which also encompasses our calculated set-point range but is likely also an artifact of smaller sample size. Copperheads and cottonmouths appear to have a lower T_{set} than other North American snakes. They have a lower T_{set} than massasauga rattlesnakes (*Sistrurus catenatus*) at 30.0-33.6°C (Harvey and Weatherhead 2010, 2011), milksnakes (*Lampropeltis triangulum*) at 29.0-31.0°C (Row 2005), and black ratsnakes

(*Pantherophis obsoletus*) at 26.5-29.8°C (Blouin-Demers and Weatherhead 2001). This suggests that copperheads and cottonmouths routinely prefer lower temperatures than other snakes, even those of higher latitudes, which are shown to have lower or broader T_{set} ranges than the same species at lower latitudes (Stevens 1989, Weatherhead et al. 2012).

Departure from thermoconformity (d_e-d_b) was also lower for copperheads (0.76 ± 0.1) and cottonmouths (1.6 ± 0.1) over the course of the active season than massasauga rattlesnakes (3.3 ± 0.1 ; Harvey and Weatherhead 2011) and black ratsnakes of Texas (3.24 ± 0.25), Illinois (3.08 ± 0.38), and Ontario (3.66 ± 0.29 ; Weatherhead et al. 2012). However, we had a higher d_e-d_b index for cottonmouths (1.6 ± 0.1) than a previous study of cottonmouths in Missouri (0.6934 ; Menzel 2008). We also had a higher exploitation (Ex) index for copperheads ($33.6\% \pm 2.9$) and cottonmouths ($44.9\% \pm 3.0$) than found previously for cottonmouths (35.9% ; Menzel 2008) and black ratsnakes of Texas ($23.9\% \pm 1.5$), Illinois ($26.7\% \pm 2.3$), and Ontario ($21.6\% \pm 1.5$; Weatherhead et al. 2012).

Effectiveness of thermoregulation (E) was higher for our copperheads (0.2 ± 0.02) and cottonmouths (0.43 ± 0.02) than previously estimated by Menzel (2008) for cottonmouths of Southwest Missouri (0.14). This suggests that copperheads and cottonmouths routinely thermoregulate less effectively than some other species; however, when the lower bounds of T_{set} are attainable, cottonmouths exploit their environment to a higher degree than previously reported and both species have a higher Ex than black ratsnakes. Overall this suggests that copperheads and cottonmouths perform more adequately at lower temperatures than some other North American snakes by tolerating

cooler temperatures but maintain T_b s in their T_{set} range more frequently when the environment allows.

Although both species have a similar T_{set} range, cottonmouths tend to thermoregulate more precisely than copperheads during the months of May, June, and July, and both species seem to regulate their T_b less efficiently than other snake species (Harvey and Weatherhead 2011, Weatherhead et al. 2012). This study gives us an overall view of how copperheads and cottonmouths thermoregulate over the course of the active season, but future studies may need to focus on thermoregulation at a finer scale. This is important to investigate if there are differences in diel cycles between the two species, which could potentially help explain the temporal differences in thermoregulation. It would also be advantageous to monitor the behavior and microhabitat use of each species concurrently with recording T_b . This information would allow for more inferences on the thermal ecology of both species, and may give more insight into the driving forces behind the differences in thermoregulation.

Chapter V

Tables and Figures

Table 1. Mean body temperatures (T_b in °C) selected by male *Agkistrodon sp.* in a laboratory thermal gradient with 75% and 25% quartiles of distributions represented. Means \pm 1 standard error with ranges in parentheses.

Gradient index	<i>A. contortrix</i> (N=35)	<i>A. piscivorus</i> (N=19)	df	<i>F</i>	<i>P</i>
25% quartile	24.9 \pm 0.5 (24.4-25.7)	24.9 \pm 0.8 (24.1-25.7)	1,53	0.100	>0.75
75% quartile	27.8 \pm 0.3 (27.5-28.1)	27.9 \pm 0.6 (27.3-28.5)	1,53	<0.001	>0.98
Mean	26.4 \pm 0.3 (26.1-26.7)	26.1 \pm 0.6 (25.5-26.7)	1,53	0.440	>0.51

Month	Mean Max T_e (°C)		Mean T_e (°C)		Mean Min T_e (°C)		Mean d_e (°C)		Max d_e (°C)		d_e (% = 0)	
	LBL	CRBT	LBL	CRBT	LBL	CRBT	LBL	CRBT	LBL	CRBT	LBL	CRBT
April	37.4 ± 2.6	42.7 ± 1.8	16.2 ± 0.3	15.7 ± 0.2	1.3 ± 0.5	0.2 ± 0.5	9.6 ± 0.1	10.4 ± 0.2	23.9 ± 0.7	24.7 ± 0.5	3.3 ± 0.005	5.3 ± 0.004
May	35.8 ± 2.5	36.3 ± 2.8	18.4 ± 0.3	19.0 ± 0.4	6.1 ± 0.5	7.6 ± 0.8	7.2 ± 0.1	6.4 ± 0.3	19.9 ± 0.9	18.1 ± 1.2	3.8 ± 0.007	7.3 ± 0.01
June	36.5 ± 2.1	45.6 ± 3.1	23.6 ± 0.3	23.7 ± 0.3	13.4 ± 0.3	14.2 ± 0.6	2.9 ± 0.1	3.7 ± 0.2	14.3 ± 1.4	19.1 ± 2.6	18.1 ± 0.016	13.5 ± 0.014
July	36.6 ± 2.1	47.0 ± 3.4	25.1 ± 0.2	25.3 ± 0.3	18.3 ± 0.3	16.5 ± 0.9	1.5 ± 0.1	2.5 ± 0.3	11.2 ± 1.7	19.4 ± 3.3	28.9 ± 0.021	23.2 ± 0.021
August	37.7 ± 2.3	43.5 ± 3.3	24.1 ± 0.3	24.2 ± 0.3	13.8 ± 0.4	14.1 ± 0.8	2.6 ± 0.2	2.8 ± 0.2	14.7 ± 1.6	18.0 ± 2.6	21.1 ± 0.015	19.0 ± 0.018
September	38.6 ± 2.4	39.8 ± 2.8	22.3 ± 0.3	22.4 ± 0.3	10.1 ± 0.4	10.4 ± 0.8	4.3 ± 0.2	4.0 ± 0.2	17.4 ± 1.4	17.5 ± 1.8	11.0 ± 0.008	11.9 ± 0.012

Table 2. Mean maximum, grand mean, and mean minimum environmental operative temperatures along with mean deviation, mean maximum deviation and percentage of deviations equal to T_{set} of environmental temperatures from T_{set} for Land Between the Lakes National Recreation Area (LBL) and Cumberland River Bicentennial Trail (CRBT) ± 1 standard error

Month	<i>A. contortrix</i>				<i>A. piscivorus</i>			
	n	<i>E</i>	d_e-d_b	<i>Ex</i>	n	<i>E</i>	d_e-d_b	<i>Ex</i>
April	10	0.08 ± 0.02	0.77 ± 0.17	2.0 ± 1.3	5	0.13 ± 0.02	1.40 ± 0.26	5.7 ± 5.7
May	11	0.12 ± 0.02	0.90 ± 0.14	16.5 ± 5.7	9	0.33 ± 0.19	2.14 ± 0.40	40.0 ± 10.0
June	12	0.20 ± 0.03	0.58 ± 0.08	42.2 ± 2.6	12	0.51 ± 0.03	2.00 ± 0.12	53.2 ± 5.8
July	14	0.15 ± 0.04	0.23 ± 0.06	51.4 ± 3.2	13	0.59 ± 0.02	1.74 ± 0.16	52.3 ± 3.4
August	12	0.34 ± 0.04	1.04 ± 0.17	54.8 ± 3.3	13	0.46 ± 0.03	1.46 ± 0.13	54.9 ± 3.5
September	9	0.28 ± 0.06	1.30 ± 0.34	22.2 ± 8.6	9	0.10 ± 0.05	0.41 ± 0.21	35.6 ± 8.4

Table 3. Mean values (± 1 SE) of effectiveness of thermoregulation (*E*), departure from thermoconformity (d_e-d_b), and thermal exploitation (*Ex*) for copperheads and cottonmouths each month of the active season

Figure 1. Mean minimum, grand mean, and mean maximum operative environmental temperatures for each month of the active season at Land Between the Lakes National Recreation Area (LBL) and Cumberland River Bicentennial Trail (CRBT; \pm standard error bars). Horizontal lines denote the preferred body temperature ranges for copperheads and cottonmouths.

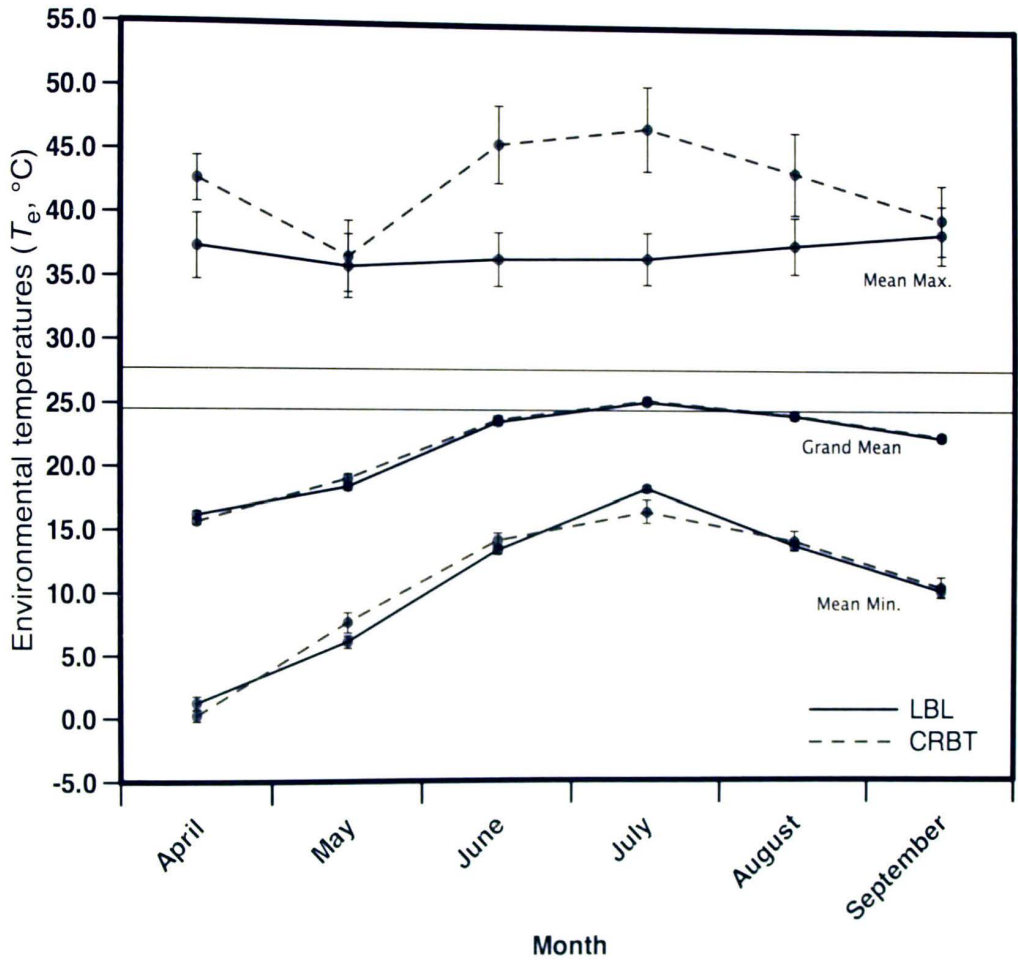


Figure 2A. The gray-shaded bar is the preferred body temperature range of copperheads (T_{set}). The solid line represents the mean monthly body temperature (T_b). Bars represent the mean deviations in body temperature from the set-point range (d_b). Error bars are ± 1 standard error. **Fig 2B.** Percentage of observations in which copperheads are above, below, or within their preferred body temperature range (T_{set}).

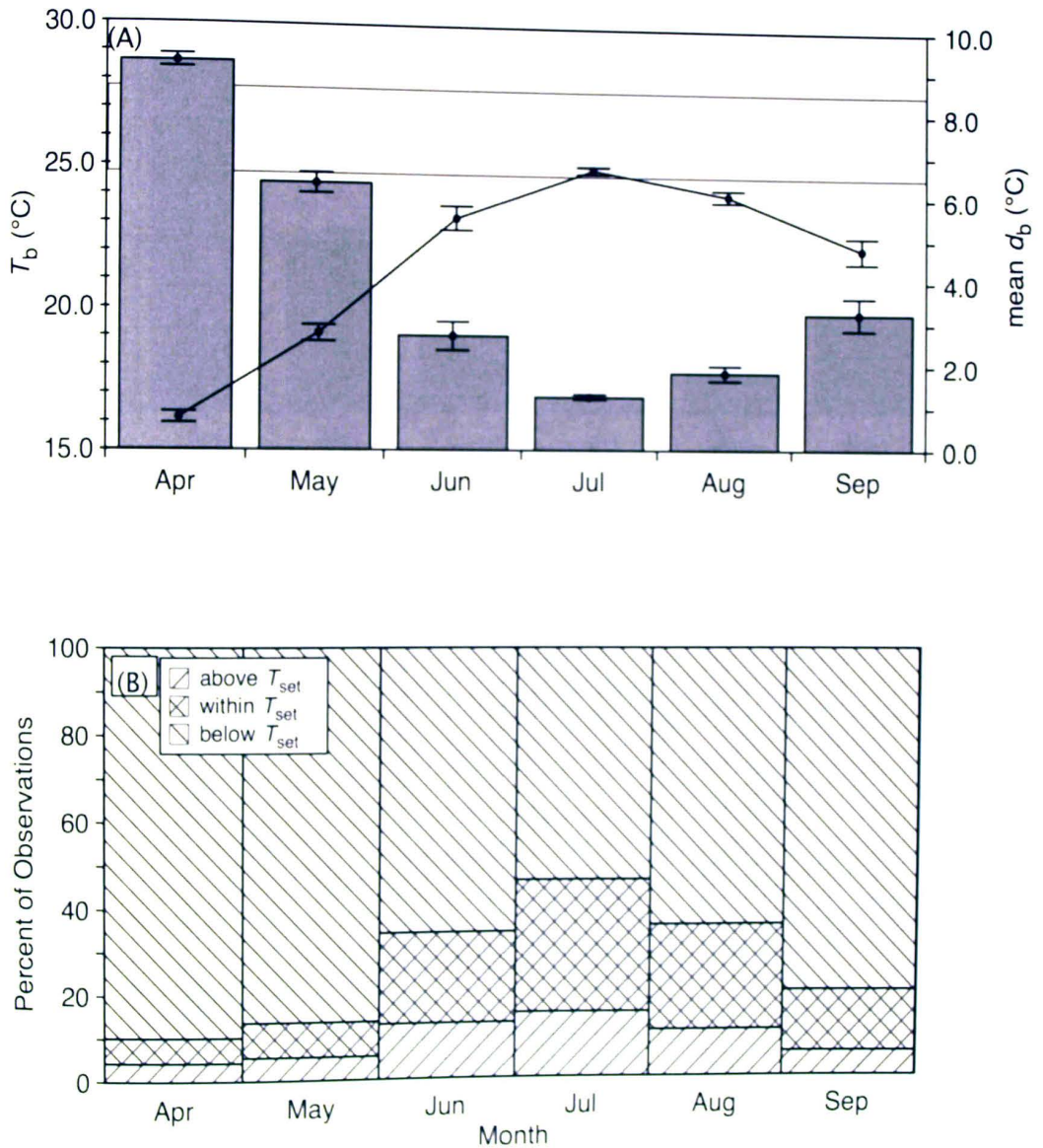


Figure 3A. The gray-shaded bar is the preferred body temperature range of cottonmouths (T_{set}). The solid line represents the mean monthly body temperature (T_b). Bars represent the mean deviations in body temperature from the set-point range (d_b). Error bars are ± 1 standard error. **Fig 3B.** Percentage of observations in which cottonmouths are above, within, or below their preferred body temperature range (T_{set}).

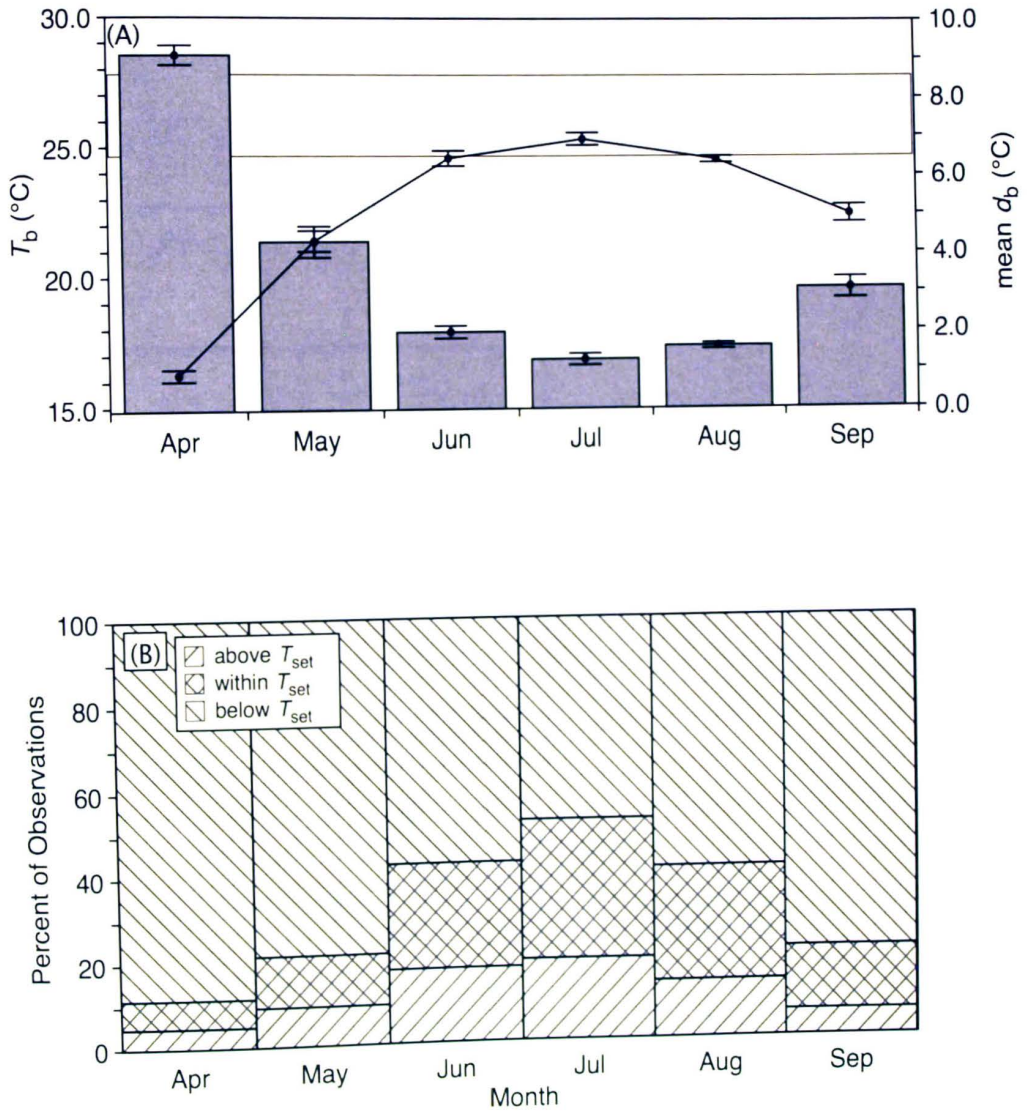
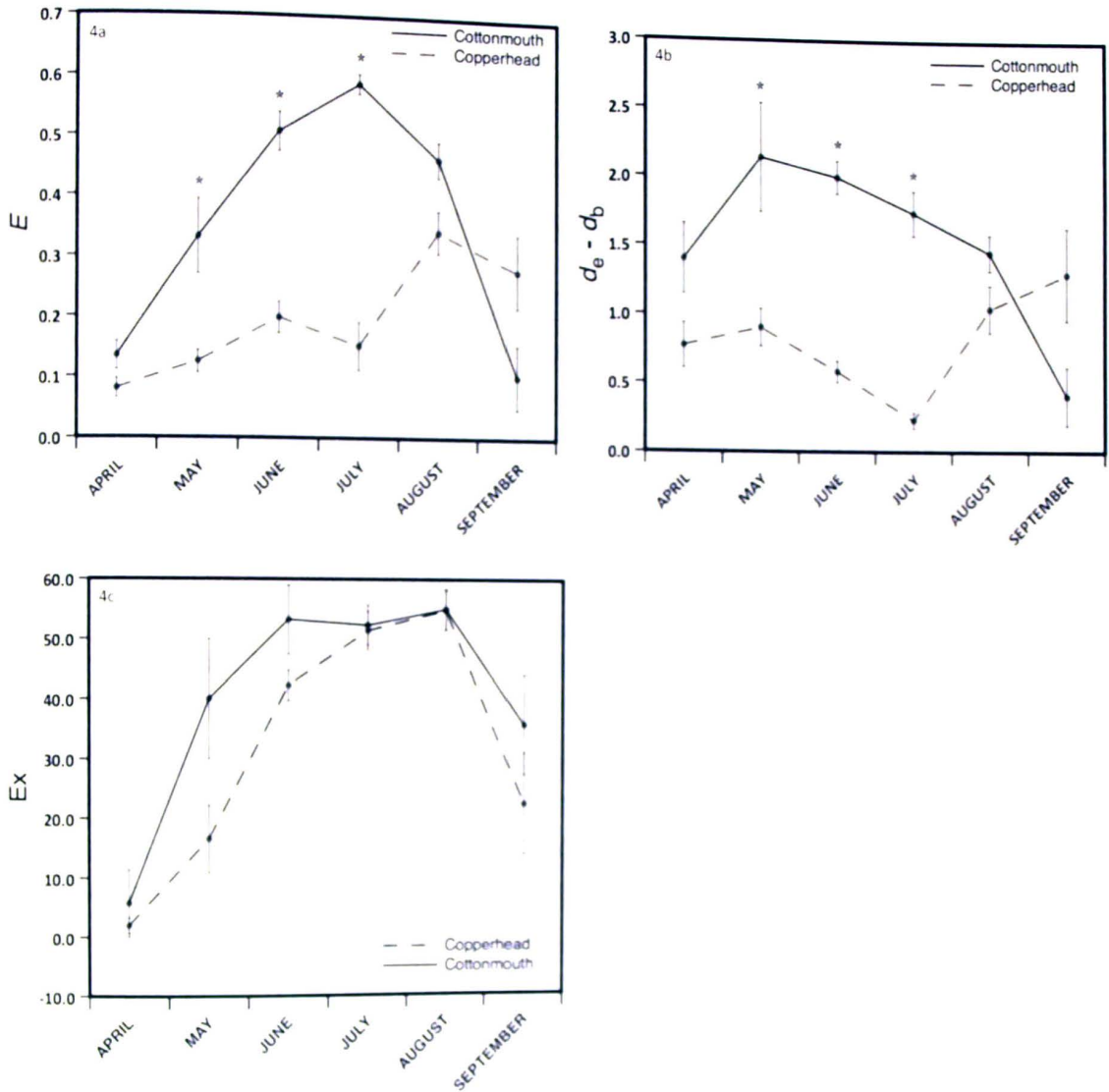


Figure 4a. Mean effectiveness of thermoregulation (E) over the active season **4b.** Mean $d_e - d_b$ for each month of the active season **4c.** Mean thermal exploitation (Ex) for each month of the active season. Asterisks indicate significance with a post hoc Tukey HSD



Chapter VI

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