

THERMAL AND TEMPORAL ASPECTS OF COLD-WATER FORAGING BY THE
NORTHERN WATER SNAKE (*NERODIA SIPEDON SIPEDON*)

Kerry A. Hansknecht

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science

Department of Biology
Central Michigan University
Mount Pleasant, Michigan
August, 2003

Accepted by the Faculty of the College of Graduate Studies,
Central Michigan University, in partial fulfillment of
the requirements for the Master's degree

Thesis Committee:

James C. Tillman Committee Chair
Charles E. Novitski Faculty Member
Thomas M. Gehring Faculty Member

Date: November 11, 2003

James H. Hageman Dean

College of Graduate Studies

Date: November 11, 2003

A narrow Fellow in the Grass
Occasionally rides—
You may have met Him—did you not
His notice sudden is—

The Grass divides as with a Comb—
A spotted shaft is seen—
And then it closes at your feet
And opens further on—

He likes a Boggy Acre
A Floor too cool for Corn—
Yet when a Boy, and Barefoot—
I more than once at Noon
Have passed, I thought, a Whip lash
Unbraiding in the Sun
When stooping to secure it
It wrinkled, and was gone—

Several of Nature's people
I know, and they know me—
I feel for them a transport
Of cordiality—

But never met this Fellow
Attended, or alone
Without a tighter breathing
And Zero at the Bone—

—Emily Dickinson

For Lisa, who makes my life whole

ACKNOWLEDGMENTS

No research endeavor is conducted without the assistance of others, but the level of support I received during my residency at CMU was greater than I have ever experienced. First, I wish to thank my advisor, Dr. James C. Gillingham. Never have I known a more resourceful individual, particularly one so generous with the fruits of such an asset. His knowledge, guidance, and enthusiasm were invaluable, and I cannot imagine having had a mentor better for me than he has been at this stage of my career. I am also grateful to my other committee members, Dr. Charles E. Novitsky and Dr. Thomas M. Gehring. Both were always eager to discuss my project, which has benefited greatly as a result of their expertise. Most important among those who have helped me here is Elizabeth McDonald. Lisa's companionship on both the personal and academic fronts has been the primary factor making my experience at CMU a joyful one. In the field, in the lab, and at home, she has been there to support me whenever possible, and I am a better person and scientist because of her.

Dr. John Rowe, Nancy Seefelt, Dr. Brad Swanson, and Dr. A. Scott McNaught frequently provided valuable input and insightful discussion regarding this project. Dr. Jungsywan Sepanski valiantly saved me from certain doom at the hands of statistics demons. Dan Benjamin generously made his land on Beaver Island available to me, but more important was his wonderfully positive attitude and the advice that stemmed from it; Dan was always a great source of inspiration. Seth Gallagher, Jennifer Moore (long

live the Clan of the Cave Salamander!), Mandy Deering, Beth Whately, and too many others to name here provided the friendship and commiseration necessary to survive graduate school. To my family I am thankful for their understanding, for because of my studies I have long been too distant or too busy to visit. I wish also to thank Ron and Bert McDonald, who have hospitably welcomed me into their home for the occasional, much-needed break from my stressful life. Additionally, the support staff at CMU helped me tremendously with nearly every aspect of my pursuit of this degree. Thank you, Jan, Kim, Brandy, Stephanie, Abbie, and Melanie. I am also grateful to Dr. John Scheide, the department chair, who more than once directed me toward sources of funding I had been unaware of. Thanks, too, to The Omega Concern.

For their aid in the field and laboratory, I wish to thank Jamie Pejza, Angie Pohlman, Theresa Barber, Adam Nelson, Amanda Weber, Catherine Peters, Amy Boetcher, Josh Picotte, Courtney Moore, and Rob Carmichael and his Lake Forest gang. For their great hospitality, I am grateful to the citizens of Beaver Island.

This research was made possible by the generosity of the CMU Biological Station on Beaver Island and by that of Saint James Township, who permitted me to conduct my research at Gull Harbor Natural Area. Funding and logistical support were provided by the CMU Biological Station (thanks for the great food, Carolyn!), the CMU College of Graduate Studies, the CMU Department of Biology, the Chicago Herpetological Society, and the Explorers Club.

ABSTRACT

THERMAL AND TEMPORAL ASPECTS OF COLD-WATER FORAGING BY THE NORTHERN WATER SNAKE (*NERODIA SIPEDON SIPEDON*)

by Kerry A. Hansknecht

The direct effects of environmental temperature on nearly all of their physiological processes make it of utmost importance in the lives of ectotherms. Reptiles exposed to conditions far cooler than their physiological optimum are therefore expected to somehow limit the potential negative impacts of this on their fitness. My goal was to discover behavioral mechanisms that permit northern water snakes, *Nerodia sipedon*, to forage in cold water on Beaver Island in northern Lake Michigan. Five snakes were fitted with temperature-sensitive radio transmitters and monitored daily during the summer of 2001 and the spring of 2002. Body temperatures (T_b) of the snakes and the environmental temperatures available to them were recorded at 15-minute intervals, with more frequent observation directed toward individuals in the lake. Snakes first entered Lake Michigan in late May, when courtship activity declined, operative temperature regularly exceeded 30°C, mean water temperature exceeded 14.5°C, and fishes apparently began to arrive at the study site. Which of these, if any, serve as annual cues for the snakes to begin foraging remains unknown. The snakes remained diurnal throughout the year and foraged mostly between 1000 h and 2000 h, with more snakes observed in the lake at 1500 h than during any other hour. The numbers of snakes

observed in the lake daily and hourly were significantly correlated with environmental temperatures. The duration of foraging excursions was significantly correlated with the amount of time since the most recent excursion but not with T_b . Snakes appeared to prolong foraging in cold water by making occasional visits to the shoreline, where they elevated T_b in warmer water. This occurred when T_b dropped to approximately 16°C. Snakes did not significantly elevate T_b before or after entire foraging periods. In a separate laboratory experiment, snakes from the same study site spent less time in cold water than in warmer water. Snakes thus used two strategies that enabled them to forage in cold water; they waited until the water was warm enough, and they shuttled between cold and warm water during foraging excursions. This information may better our understanding of semi-aquatic reptiles worldwide.

TABLE OF CONTENTS

LIST OF TABLES	x
LIST OF FIGURES	xi
CHAPTER	
I. INTRODUCTION	1
II. MATERIALS AND METHODS.....	10
Radio Telemetry.....	10
Environmental Temperatures.....	14
The Laboratory Study.....	15
Analyses	17
III. RESULTS.....	19
Seasonal Timing of Foraging.....	19
Daily Timing of Foraging.....	29
Duration and Frequency of Foraging	35
Temperature Profiles of Snakes in Lake Michigan.....	43
The Excursion T_b Threshold.....	51
Thermal Compensation	58
Excursion Duration versus T_b in the Laboratory	58
IV. DISCUSSION.....	62
LITERATURE CITED.....	70

LIST OF TABLES

TABLE	PAGE
1. Spearman's rank correlations (r_s) for numbers of snakes observed in Lake Michigan during each hour of the day and seasonal mean hourly operative temperature (SMHT _e) and seasonal mean hourly lake temperature (SMHT _w) for the 2001 and 2002 field seasons.....	34
2. Summary of body temperatures (in °C) of snakes in Lake Michigan. Lowest T _b refers to the lowest body temperature achieved during each foraging excursion	44
3. Mean frequency and duration (in minutes) of excursions made by northern water snakes into pools of water of different temperature during 48-hour trial periods.....	60

LIST OF FIGURES

FIGURE	PAGE
1. Ecologically important temperatures within the thermal profile of an ectotherm (adapted from Zug et al., 2001).....	2
2. Geographic distribution of <i>Nerodia sipedon</i> (adapted from Ernst & Barbour, 1989).....	5
3. The Beaver Archipelago and its location in northern Lake Michigan (source: Michigan Center for Geographic Information, Michigan Geographic Framework statewide and county layers, 2002)	6
4. Aerial view of Gull Harbor Natural Area, Beaver Island, MI, (source: 1998 Series USGS Digital Orthophoto Quadrangle) and features relevant to the study of northern water snakes there.....	11
5. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season.....	20
6. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season and the mean midday (1000–1600 h) operative temperature (T_e). Dotted line is seasonal T_e trend.....	21
7. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season and the mean afternoon (1200–1800 h) water temperature (T_w). Dotted line is seasonal T_w trend	22
8. Scatterplots of the numbers of snakes observed in Lake Michigan daily in 2001 and mean midday T_e (A) and mean afternoon T_w (B).....	23
9. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season.....	25
10. Scatterplots of the numbers of snakes observed in Lake Michigan daily in 2002 and mean midday T_e (A) and mean afternoon T_w (B).....	26

FIGURE	PAGE
11. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season and the mean midday (1000–1600 h) operative temperature (T_e). Dotted line is seasonal T_e trend.....	27
12. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season and the mean afternoon (1200–1800 h) water temperature (T_w). Dotted line is seasonal T_w trend	28
13. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2001 field season and the mean operative temperature (T_e) recorded during those hours averaged over the season	30
14. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2001 field season and the mean water temperature (T_w) recorded during those hours averaged over the season	31
15. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2002 field season and the mean operative temperature (T_e) recorded during those hours averaged over the season	32
16. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2002 field season and the mean water temperature (T_w) recorded during those hours averaged over the season	33
17. Durations of foraging excursions observed during the 2001 field season	36
18. Intervals, in days, between successive foraging excursions observed during the 2001 field season.....	37
19. Scatterplot of the durations of foraging excursions in 2001 and mean T_b s during them.....	38
20. Durations of foraging excursions observed during the 2002 field season	39
21. Intervals, in days, between successive foraging excursions observed during the 2002 field season.....	40

FIGURE	PAGE
22. Scatterplots of the durations of foraging excursions and the non-foraging intervals that preceded (A) and followed (B) during the 2002 field season.....	41
23. Scatterplot of durations of foraging excursions in 2002 and mean T_{bs} during them.....	42
24. Frequency histogram of all body temperatures experienced by radio-implanted snakes while in Lake Michigan in 2001	45
25. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 20 July 2001	46
26. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 26 July 2001	47
27. Body temperature profile of a northern water snake in Lake Michigan on 7–8 August 2001	48
28. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 11 August 2001.....	49
29. Frequency histogram of all body temperatures experienced by radio-implanted snakes while in Lake Michigan in 2002	50
30. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 31 May 2002.....	52
31. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 18 June 2002.....	53
32. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 30 May 2002.....	54
33. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 28 May 2002. Nearly all T_{bs} greater than 19°C occurred when the snake was observed at the shoreline	55

FIGURE	PAGE
34. Body temperature profiles of five northern water snakes, one of which remained in Lake Michigan until nightfall, on 18 June 2002.....	56
35. Body temperature profiles of five northern water snakes, one of which foraged late and remained in Lake Michigan all night, on 19–20 June 2002	57
36. Frequency histogram of the lowest body temperatures experienced by telemetered snakes in 2002.....	59

CHAPTER I

INTRODUCTION

The importance of temperature to reptiles, and to other ectotherms, can scarcely be overstated, as it affects nearly all aspects of their physiology and behavior (Cowles & Bogert, 1944; Huey, 1982; Lillywhite, 1987). Because of the effect of temperature on variables such as metabolic rate (Hailey & Davies, 1986) and locomotion (Heckrotte, 1967; Stevenson et al., 1985), there is a certain temperature range within which individuals of a given species can function. The upper and lower extremes of this range are lethal, and within these limits there exist several ecologically important temperatures (Figure 1) that also vary among species (Cowles & Bogert, 1944; Pough & Gans, 1982). The mean selected temperature (MST), often referred to as preferred body temperature (PBT), is the average of body temperatures selected by an individual when given a sufficiently wide range of temperatures from which to choose. By definition (Pough & Gans, 1982) MST is measured in a laboratory thermal gradient. A reptile will voluntarily remain active only while its body temperature is between a certain minimum and maximum, which fall on either side of its MST but within the lethal extremes. The temperature range bordered by the voluntary minimum and maximum of free-living animals is termed the activity temperature range (ATR; Pough & Gans, 1982). If necessary, an individual will regulate its temperature within its ATR, and within a narrower preferred range around its MST, by visiting microhabitats that have different thermal characteristics (Lillywhite, 1987). Temperatures outside of the voluntary limits are dangerous; locomotion is greatly hampered, increasing the likelihood that lethal

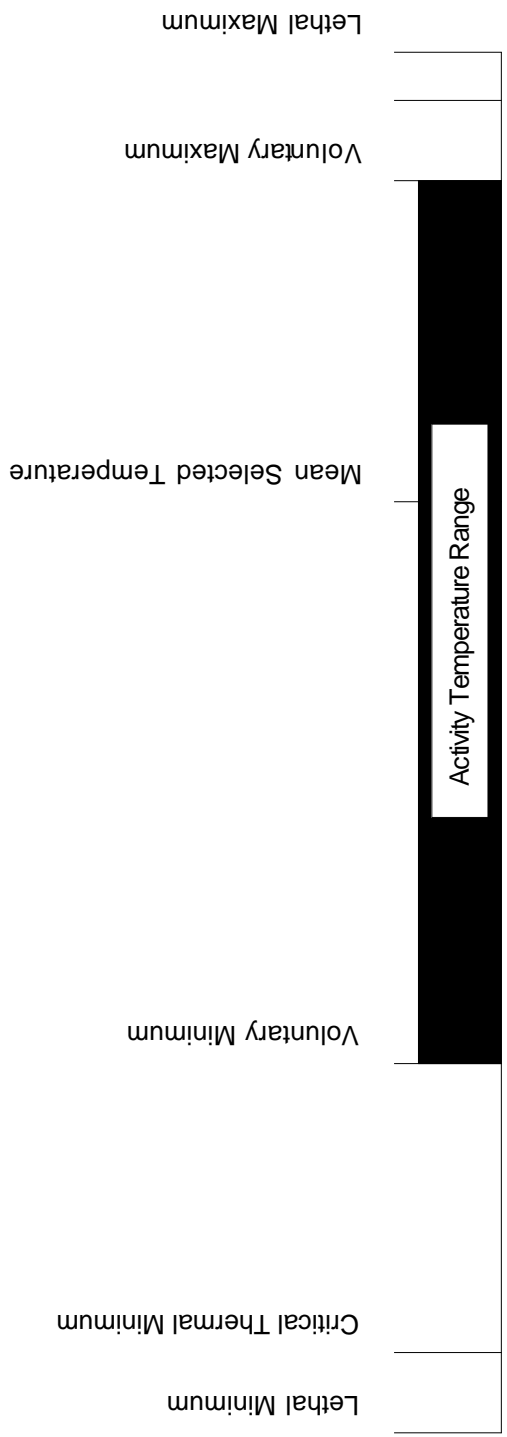


Figure 1. Ecologically important temperatures within the thermal profile of an ectotherm (adapted from Zug et al., 2001).

temperatures will be experienced before an adequate thermal source or sink can be reached. Additionally, individuals subjected to these critical temperatures may be more susceptible to predatory attacks due to their reduced ability to flee (Stevenson et al., 1985).

Generally, rates of metabolism (Huey, 1982), digestion (Greenwald & Kanter, 1979; Stevenson et al., 1985), and locomotion (Heckrotte, 1967; Weatherhead & Robertson, 1992; Scribner & Weatherhead, 1995; Finkler & Claussen, 1999) increase with temperature. This poses a particular problem for temperate-zone reptiles, which are often faced with unfavorably cold environments, even during their normal activity season (Gregory, 1982). During such times, they may experience lower digestive and metabolic rates than do reptiles in warmer regions. This can lead to reduced energy transduction (Bennett, 1982), and growth and reproductive output may therefore be inhibited. To avoid such losses in fitness, reptiles living in cooler regions must spend a considerable amount of time regulating their body temperature, and time spent thermoregulating is frequently time not spent conducting other activities such as foraging and searching for mates (Huey, 1982). In addition, animals that are active in the open, whether for foraging, mating, or thermoregulating, may be increasing their vulnerability to predators. Thus a greater need to thermoregulate, which often must be achieved in the open, can lead to greater risk of predation. In order to successfully grow and reproduce, then, temperate-zone reptiles must strike a particularly fine balance between searching for food, searching for mates during the appropriate season, maintaining a body temperature at which required physiological processes can take place, and limiting the amount of time they are exposed to potential predators.

The problem of managing the aforementioned demands can be especially complex for freshwater snakes worldwide, as many must forage in water that is far cooler than their preferred body temperature (Hailey & Davies, 1987; Manjarrez & Drummond, 1996; Nelson & Gregory, 2000). In North America, the wide-ranging (Figure 2) northern water snake, *Nerodia sipedon*, is one such species. Data from several studies indicate that *N. sipedon* are active mostly between 21°C and 35°C and have an MST of approximately 27.3°C (Kitchell, 1969; Lutterschmidt & Reinert, 1990; Robertson & Weatherhead, 1992; Brown & Weatherhead, 2000). However, northern water snakes that forage along the Lake Michigan shores of the Beaver Archipelago (Figure 3) may be confronted with water temperatures well below this throughout their activity season. Carbone (1993) collected lake temperatures three times daily in June, July, and August 1990 at a Beaver Island site heavily used by water snakes, and these averaged 17.5°C and ranged from 8–25°C. At the same location on 11 July 1987, Meyer (1992) observed a radio-implanted water snake whose temperature dropped 10°C while it foraged briefly in Lake Michigan.

Such a situation might influence foraging and thermoregulatory schedules in several ways. Snakes may simply forego foraging until water temperature increases to a tolerable threshold (Manjarrez & Drummond, 1996), determined by factors discussed below. This would be similar to the practice of many reptiles that exhibit given behaviors only after a particular body temperature has been attained (Cowles & Bogert, 1944; Hailey & Davies, 1987; Passek & Gillingham, 1997). Rather than waiting until an ideal body temperature can be reached, however, the snakes may wait until water temperature is high enough to allow them to maintain their temperature above a certain point. Strict

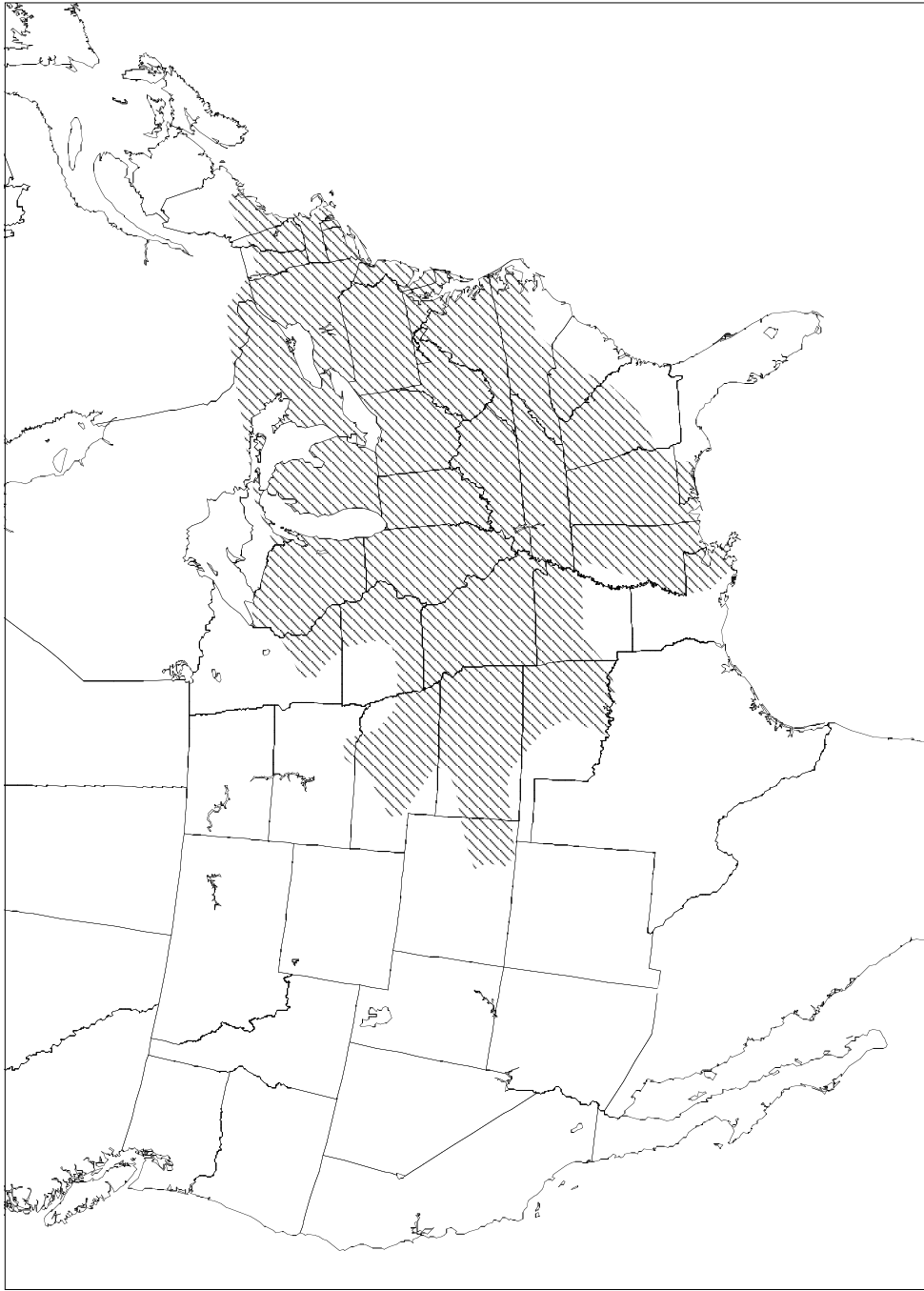


Figure 2. Geographic distribution of *Nerodia sipedon* (adapted from Ernst & Barbour, 1989).



Figure 3. The Beaver Archipelago and its location in northern Lake Michigan (source: Michigan Center for Geographic Information, Michigan Geographic Framework statewide and county layers, 2002).

adherence to this strategy could severely limit daily or seasonal activity periods to the degree that temporal and energetic needs related to reproduction would not be met at all. Alternatively, peaks in prey abundance might not be exploited and fitness thus merely reduced. Clearly, too, there may be localities where water temperatures never reach the necessary threshold, and an alternative strategy is necessary for residents.

Another solution may be to forage in the cold waters only until body temperature has decreased to a given minimum, which would be dictated by any of several factors. Very low body temperatures can directly inhibit via reduced agility a snake's ability to capture prey (Greenwald, 1974), so foraging in the lake might cease at a body temperature below which capture rates are severely limited. Also, the risk of capture by predators increases as a snake's temperature is lowered and its locomotive ability accordingly reduced (Stevenson et al., 1985; Scribner & Weatherhead, 1995). The need to avoid potential predators, such as herons and gulls, while in the water may thus require snakes to keep body temperatures from getting too low while foraging. In addition, Scribner and Weatherhead (1995) found that northern water snakes crawl on land more slowly than they swim in the water, and temperature has a greater effect on the crawling speed than on the swimming speed of, at least, garter snakes (Stevenson et al., 1985). Therefore, the performance of snakes on land after foraging excursions might ultimately determine the temperature at which they leave the water. Travel from the shoreline to suitable refugia or thermoregulatory sites after foraging in cold water may be one of the more hazardous activities undertaken by water snakes. As a consequence, they might benefit from leaving the water before their body reaches a temperature at which they could not crawl quickly enough to evade terrestrial predators.

One problem that may be associated with exiting the water at a certain low body-temperature threshold is the strict limit such behavior would place on the amount of time one could forage during each excursion. Given the findings of Weatherhead and Robertson (1992), an average-sized *N. sipedon* foraging in water as cold as that along the Lake Michigan shoreline (Carbone, 1993) may have only 6 minutes before its body reaches the voluntary minimum temperature of approximately 16°C suggested by Brown (1940) and Brattstrom (1965). As water snakes tend to take frequent, small meals (Brown, 1958; King, 1986; Bowen, 2002), this may be enough time to allow them to obtain their normal ration of fish without putting themselves in excessive danger as they leave the water. Carbone (1993) found that shoreline-foraging *N. sipedon* followed the shifts of sculpin patches as they moved to different locations within his study site, and foraging always took place within 10 m of the shore. Such knowledge of close, highly profitable prey localities may permit snakes to minimize the time required to capture the typical number of fish prey, thus allowing them to leave the water before their body temperatures are reduced to dangerous levels.

In the absence of knowledge of close prey patches, however, snakes foraging in cold water may be forced to cease doing so before prey can be found. In locations where water temperature remains low for much of the day or activity season, cessation of foraging is not an option, and another strategy is needed. It is conceivable that snakes could forage for extended periods in the cold waters to ensure sufficient prey are captured and to compensate for the long periods at sub-optimal temperatures by thermoregulating at above-normal temperatures. Such compensation could be restricted to periods immediately before or after foraging excursions.

The goal of this research is to shed light on the relationship between water temperature and the timing, frequency, and duration of foraging by *Nerodia sipedon sipedon*. Such knowledge is of value worldwide, as many species of semi-aquatic snakes utilize, at least occasionally, cold water bodies to obtain food (Hailey & Davies, 1987; Manjarrez & Drummond, 1996; Nelson & Gregory, 2000). Specific questions that are addressed here include: Do water snakes foraging in cold water cease to do so when their body temperature reaches a certain lower threshold (excursion T_b threshold)? Do they avoid entering the water until it has reached a certain temperature? Do these snakes achieve above-normal temperatures prior to entering or after leaving cold water? Do they spend less time in water that is cold than in water that is warm?

CHAPTER II

MATERIALS AND METHODS

Radio Telemetry

This research comprised two separate but related components: a field study, which involved radio telemetry; and a laboratory study, which did not. The field component was conducted during the summer of 2001 and spring of 2002 at Gull Harbor Natural Area (GHNA; Figure 4), a newly protected site on the Lake Michigan shoreline at the northeastern corner of Beaver Island, Charlevoix County, Michigan. *Nerodia sipedon* there frequent an area of approximately 1 ha immediately inland of a road that passes through the site, and they cross the road and an adjacent cobble field in order to forage for sculpin in Lake Michigan. Five water snakes from GHNA were fitted with surgically implanted (Reinert & Cundall, 1982) SI-2T temperature-sensitive radio transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada) weighing 9 g and having a battery life of 12 months at 35°C. Transmitters weighed no more than 5% of the body mass of snakes in which they were implanted (Hardy & Greene, 1999), and the snakes were released at GHNA after a 48-hour post-operative recovery period.

Prior to radio implantation, I established calibration equations for the conversion of pulse-interval data into temperature data. To achieve this, transmitters were placed in water baths at 15 temperatures approximately 2.5°C apart between 1.3°C and 37.5°C, as indicated by a laboratory mercury thermometer. At each temperature, I determined the pulse interval of each transmitter by using a stopwatch to measure the amount of time, in milliseconds, between each pulse. This was achieved by timing 11 pulses, which



Figure 4. Aerial view of Gull Harbor Natural Area, Beaver Island, MI, (source: 1998 Series USGS Digital Orthophoto Quadrangle) and features relevant to the study of northern water snakes there.

included the "start" pulse, and dividing the result by 10, which was the number of intervals timed. For each transmitter, I used the average of three pulse-interval measurements at each temperature for computation of a fifth-order polynomial regression equation.

Only female snakes were implanted with radio transmitters. Male northern water snakes often curtail activity, including foraging, after the spring mating season (J. Gillingham, pers. comm.; Feaver, 1977; Brown & Weatherhead, 2000); thus the number of foraging excursions observed may have been severely limited had I chosen males for this component. Furthermore, females that are pregnant have been shown to thermoregulate more precisely and have higher MSTs than non-pregnant females (Tu & Hutchison, 1994; Charland, 1995; Brown & Weatherhead, 2000), and because their energy needs are greater, they may need to feed more often than other snakes (Birchard et al., 1984). Given this, pregnant females foraging in cold water may either leave the water at a higher threshold or wait for the water to reach a higher temperature. With the expectation that relatively high feeding frequencies would lead to a more robust data set and that a slightly warmer thermal threshold might itself be more evident relative to the lake water temperature, only females who were deemed pregnant at the beginning of the study were fitted with transmitters.

In the attempt to obtain foraging frequency and duration data on as many snakes as possible, all adult and sub-adult *N. sipedon* captured at the study site were measured, weighed, and marked uniquely by scale clipping (modified from Brown & Parker, 1976). Measurements of snout-vent length (SVL) and total body length (TBL) were made using either a meter stick or tailor's tape in 2001; in 2002, a squeeze box (Quinn & Jones, 1974)

was used in conjunction with a cartometer. Body mass was measured with Pesola™ spring scales. Remote identification of all study subjects, both telemetered and non-telemetered, was made possible by marking them with unique tricolor bands of enamel spray paint. Meyer (1992) used a similar method and found no evidence that it increased the probability of predation. Because very small snakes were unlikely to be remotely observable, however, and because they are presumably more susceptible to predation than are larger snakes, yearling and juvenile snakes were not paint marked and were left relatively undisturbed.

Observations were made from the ground and from 4.5 m above ground atop a portable tripod platform placed amid the cobble field adjacent to the lake. Use of the elevated platform increased transmitter signal reception and, coupled with the use of binoculars, enabled me to see and identify snakes as far away as 350 m and 150 m, respectively. By recording pulse intervals of implanted transmitters in the field, deep body temperatures (T_b ; Pough & Gans, 1982) of the five free-ranging telemetry subjects were obtained at intervals of 15 minutes or less. Snakes were observed daily, usually between sunrise and sunset, and I would occasionally extend this to before and after these times. Observation periods lasted as long as 27 hours, and the 15-minute schedule was interrupted occasionally during the longer field days.

Snakes were monitored most closely before, during, and after visits into Lake Michigan. During these times, I attempted to record pulse intervals approximately every 2 minutes, maintaining visual contact as much as possible. This was to allow determination with reasonable precision the time and temperature at which snakes entered and left the water and the lowest body temperature experienced by foraging

snakes. Occasionally, particularly when more than two telemetered snakes were in the lake, I was unable to record pulse intervals every two minutes. During such times, I recorded measurements as often as possible, usually more frequently than every 10 minutes. Because visual contact was impossible to maintain while making written notation of pulse-interval data, I dictated into a voice-activated micro-cassette recorder from the time a transmittered snake was found approaching or swimming in the water until it had left the water and clearly ceased foraging for the day.

Environmental Temperatures

A snake model (Peterson, 1987) equipped with a temperature data logger was placed in an open area at the study site to evaluate the temperature regime available to the snakes there. The operative temperatures (T_e) provided by this model permitted identification of time periods when the snakes were capable of experiencing body temperatures at least as high as the MST reported for *N. sipedon*. The model was constructed of copper tubing 4 cm in diameter and painted with gray primer. A Stowaway® TidbiT® data logger (Onset Computer Corp., Bourne, MA, USA) was sealed inside using rubber stoppers. Four Stowaway® TidbiT® temperature loggers also were placed in Lake Michigan at depths of 10, 30, 50, and 70 cm in or near areas where snakes were seen foraging. Mean water temperatures were calculated by averaging the data from all four depths. The five Stowaway® TidbiT® loggers were calibrated using the same methods and the same mercury thermometer used to create the calibration equations for the radio transmitters implanted in snakes. All data loggers recorded

temperature every 15 minutes, on the hour and every quarter hour. These times coincided with the times that pulse interval data were collected from telemetered snakes.

The Laboratory Study

The laboratory component was designed to complement the field study by providing further comparative data regarding the effects of water temperature on the duration of aquatic excursions. The experiment was conducted at the Central Michigan University Biological Station (CMUBS) on Beaver Island during July and August 2002. In a large indoor facility, three arenas were constructed in identical fashion. Each consisted of a circular plastic container 20 cm deep by 100 cm in diameter and a perimeter wall 70 cm tall made from two 375 cm lengths of aluminum flashing riveted together lengthwise. A pile of large rocks covering approximately one eighth of the pool area was built near the edge of each arena, and a 100 W red outdoor floodlight was placed 45 cm above it. A 40 cm length of 5 cm diameter gray PVC conduit was lain atop the rocks and slanted such that one end was slightly submerged to provide access from the water. Snakes were thus provided with a dry land area upon which to thermoregulate or hide as well as an area where they could hide while partly or completely in the water under the rocks. The status of hidden snakes was easily determined by their actions before and after disappearance. Only snakes within the PVC tube could be hidden while on land, thus any hidden snake not seen entering the tube was clearly in the water and hiding under rocks.

A floor of cobble covered the rest of the pool, which was filled with tap water to achieve a depth of 15 cm. This provided the aquatic setting. Separate heating and

cooling devices regulated water temperature in each of the three arenas; submersible electric aquarium heaters provided heat, while groundwater fed through a horizontal coil of copper tubing beneath the cobble floor provided cooling. The groundwater was chilled by first running it through spiral coils of copper tubing that were enclosed in electric freezers. Thermostatically controlled solenoid valves modulated the flow of cold water through the pool coils, and aquarium power heads provided circulation and aeration of water. The temperature of the water in each arena was set using the same mercury thermometer used in all other calibrations.

Three *N. s. sipedon*, one individual per arena, were tested during each of three separate trial periods (a total of nine snakes was tested) in a randomized complete block design (Quinn & Keough, 2002). For each trial period, snakes and arenas were randomly assigned one of three water temperatures such that one snake would encounter water that was 16–17°C, one would have water that was 20–21°C, and another would have water that was 26–27°C. Male snakes were used for the laboratory study because, at its inception, most of the non-radioed females at Gull Harbor had relocated to temporarily unknown locations. Snakes were brought to CMUBS from GHNA and fasted for 5 days prior to testing. After the snakes had experienced an initial 24-hour acclimatization period within their arenas, one temperature-acclimated mottled sculpin (*Cottus bairdi*) from GHNA was introduced to each pool. Two more *C. bairdi* were introduced after another 24 hours.

Arenas were separately and continuously video taped for the entire 72-hour duration of each trial period, but the 24-hour acclimatization periods were not included in the analysis. From the videotapes, I determined the duration of all excursions into the

water. A snake was considered to be in the water when more than $\frac{1}{2}$ of its body had entered it. Excursions into and departures from the water that lasted less than 1 minute were considered exploratory rather than thermoregulatory and were ignored.

Analyses

I used Spearman's rank correlation procedure (Quinn & Keough, 2002) in SPSS version 10.1 to examine relationships between the following: environmental temperatures and numbers of snakes observed in Lake Michigan on different days and at different hours, snake body temperatures and duration of excursions into the lake, and duration of excursions and the non-foraging intervals that preceded and followed them.

In an attempt to find an excursion T_b threshold that might be generally applicable to *Nerodia sipedon*, I examined inter-individual variation in the lowest T_b experienced during all foraging excursions by the telemetered subjects. I conducted a variance components analysis (J. Sepanski, pers. comm.; Quinn & Keough, 2002) using a mixed-effects repeated-measures model in SAS version 8.0, with mean water temperature (average of all four loggers at the time of the T_b measurement) as a covariate. The difference of the $-2 \log$ likelihoods produced by the model with and without each random effect (subject or occasion) yielded a χ^2 statistic with 1 degree of freedom. I used this procedure, rather than the more straightforward repeated-measures ANOVA, because the data were considerably unbalanced; some snakes foraged much more often than others.

To test whether or not snakes elevated T_b to above-normal levels during the hours prior to or after foraging, as well as on the preceding and following day, I used paired-samples t -tests (Zar, 1999) in SPSS to compare the mean T_b s of each snake during such

times to the mean T_b exhibited by each snake throughout the season. To calculate these means, I used only those body temperatures that were achieved when T_e exceeded 30°C.

For the laboratory study, I separately compared each of three different response variables (total time spent in water, \log_{10} [mean duration of excursions], and \log_{10} [number of excursions]) among the three temperature-treatment levels in a mixed model two-factor ANOVA (Zar, 1999). I conducted the analysis in SPSS using the GLM Repeated Measures procedure (Zar, 1999; Quinn & Keough, 2002), and I used planned Helmert contrasts to compare the means of the lowest- and higher-temperature treatments as well as between the two higher-temperature treatments.

For all of these analyses, except where Dunn-Sidak adjustments for multiple comparisons were necessary, $\alpha = 0.05$. When data did not meet the assumption of normality, I either \log_{10} transformed the data and re-tested for normality before using a parametric test or used a non-parametric equivalent. When the assumption of sphericity was not met by data from the laboratory study, the Greenhouse-Geisser approximation was used from the GLM Repeated Measures procedure in SPSS (Zar, 1999).

CHAPTER III

RESULTS

Seasonal Timing of Foraging

The 2001 field season ran from 28 June through 27 October. During this time, I recorded 4,326 body temperatures of the 5 radio-implanted snakes. Of these, 1,186 were obtained while the snakes were in Lake Michigan. Throughout the season, I observed as many as 28 different snakes in the lake, but because I could not positively identify every snake and may have unknowingly seen some individuals on multiple occasions, the latter number is a maximum estimate. Snakes were seen in the lake 41 times, all between 28 June and 14 August (Figure 5). Full-time dedication to field work in 2001 began on 16 July and ended on 13 August, with brief visits to the site every 2–3 days prior to this; thus, the gap in observations between 30 June and 16 July (Figure 5) is due to limited time in the field rather than snake inactivity. The snake model was in place by 1100 h on 16 July, and water temperature (T_w) loggers were in place by 1130 h on 17 July.

From 17 July until 13 August, lake temperature at GHNA never dipped below 18.1°C, and mean daytime (0900–2000 h) T_w averaged 24.4°C, well within the ATR (16–33°C; Brown, 1940; Brown & Weatherhead, 2000) of *Nerodia sipedon*. By 16 July, use of the lake by snakes had already begun at the study site and at other sites on Beaver Island, and mean midday (1000–1600 h) T_e and mean afternoon (1200–1800 h) T_w were near their annual maxima (Figures 6–7). No significant correlation existed between the number of snakes observed in the lake on a given day and either mean midday T_e ($r_s = 0.120$, $P = 0.544$, $n = 28$) or mean afternoon T_w ($r_s = -0.010$, $P = 0.960$, $n = 27$; Figure 8).

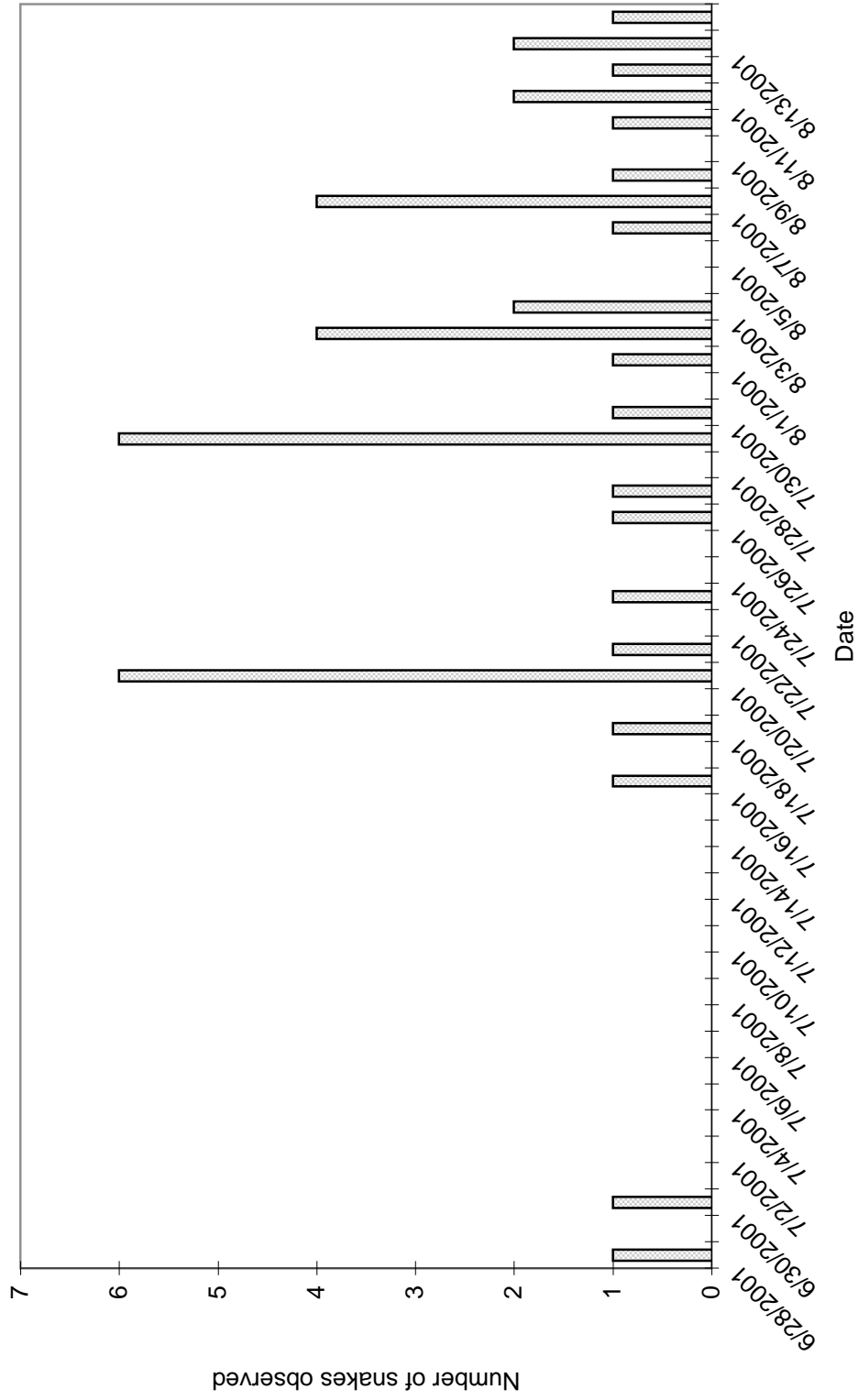


Figure 5. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season.

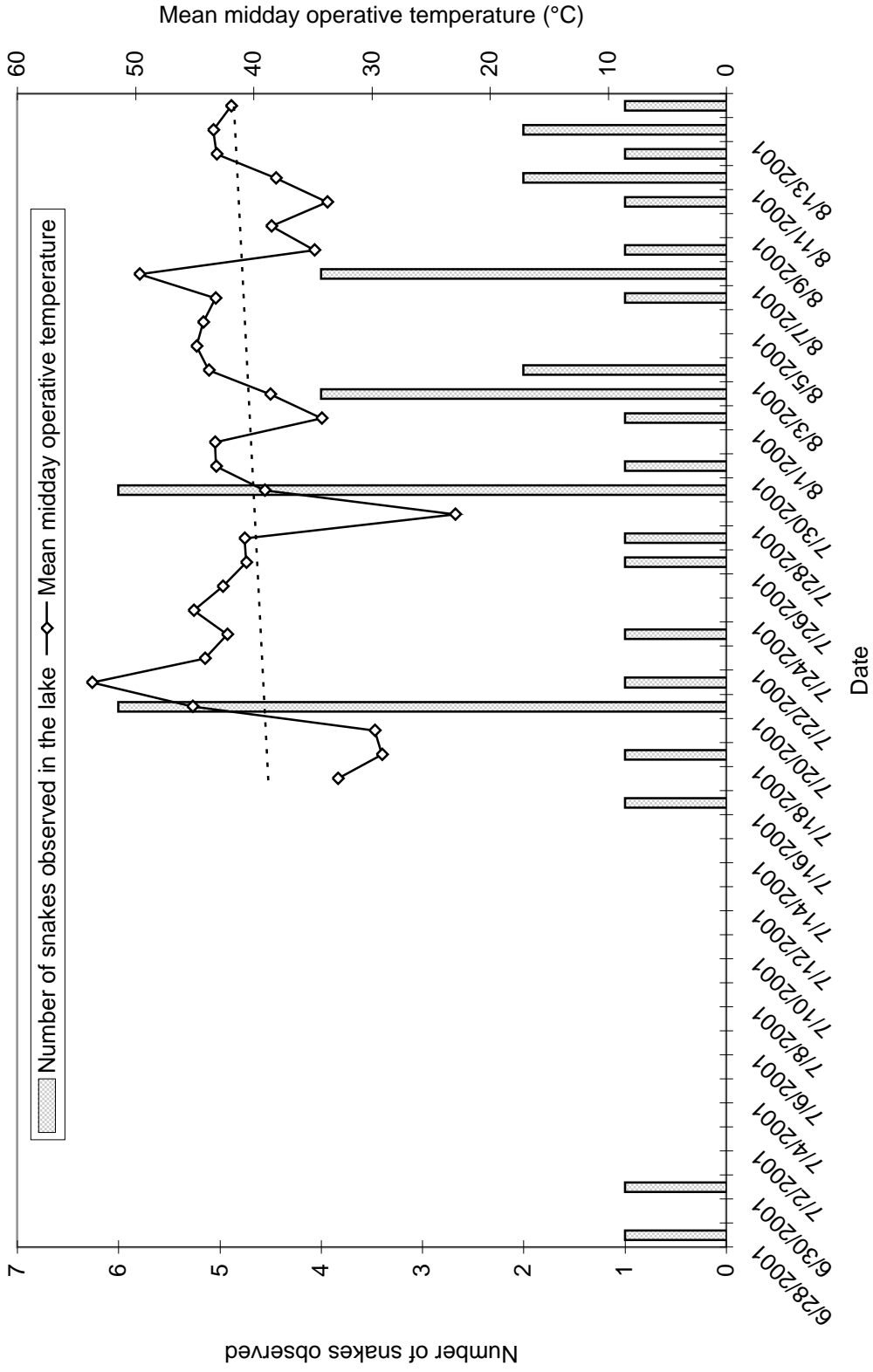


Figure 6. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season and the mean midday (1000–1600 h) operative temperature (T_e). Dotted line is seasonal T_e trend.

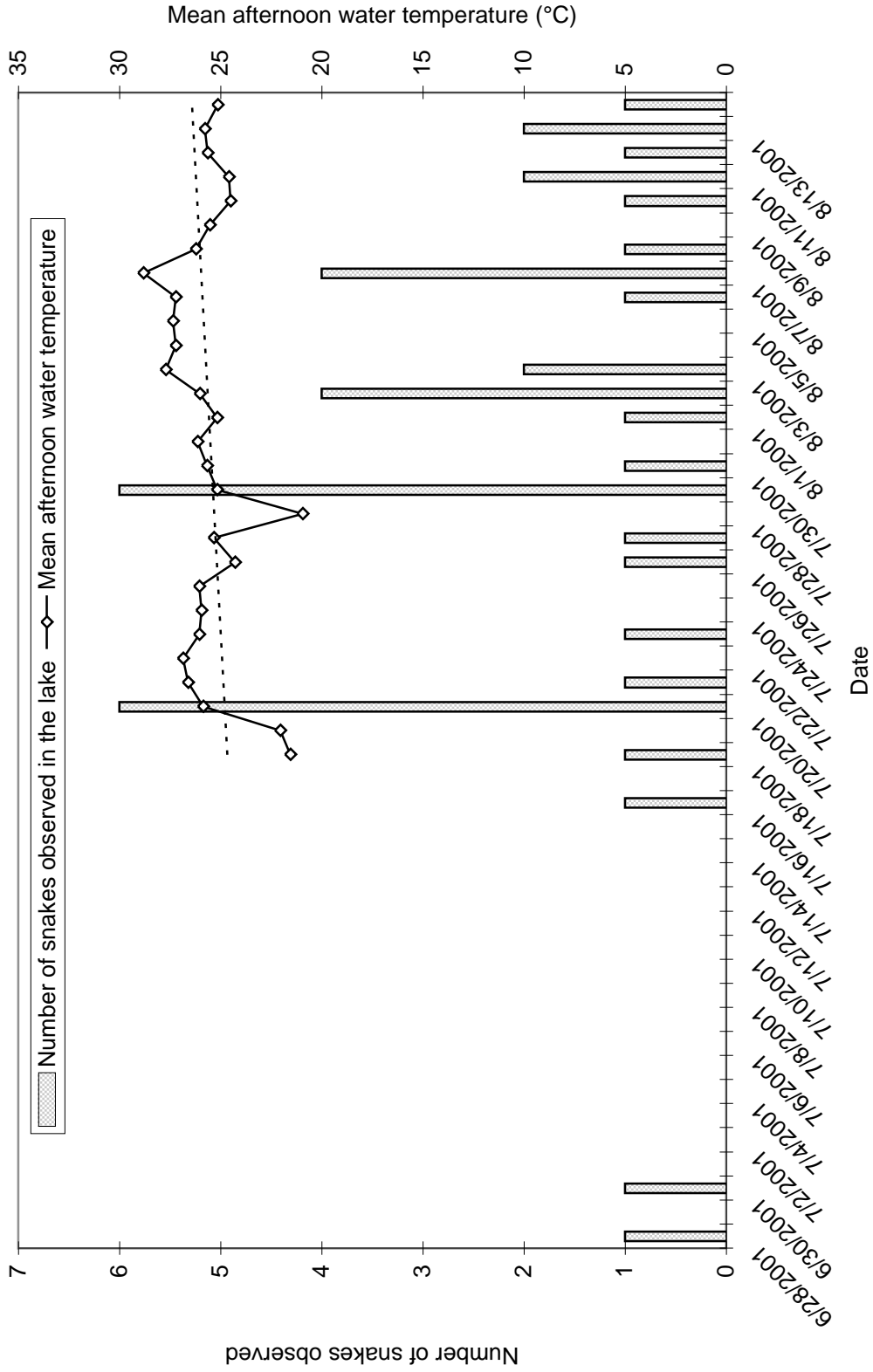


Figure 7. Numbers of snakes observed in Lake Michigan on different days throughout the 2001 field season and the mean afternoon (1200–1800 h) water temperature (T_w). Dotted line is seasonal T_w trend.

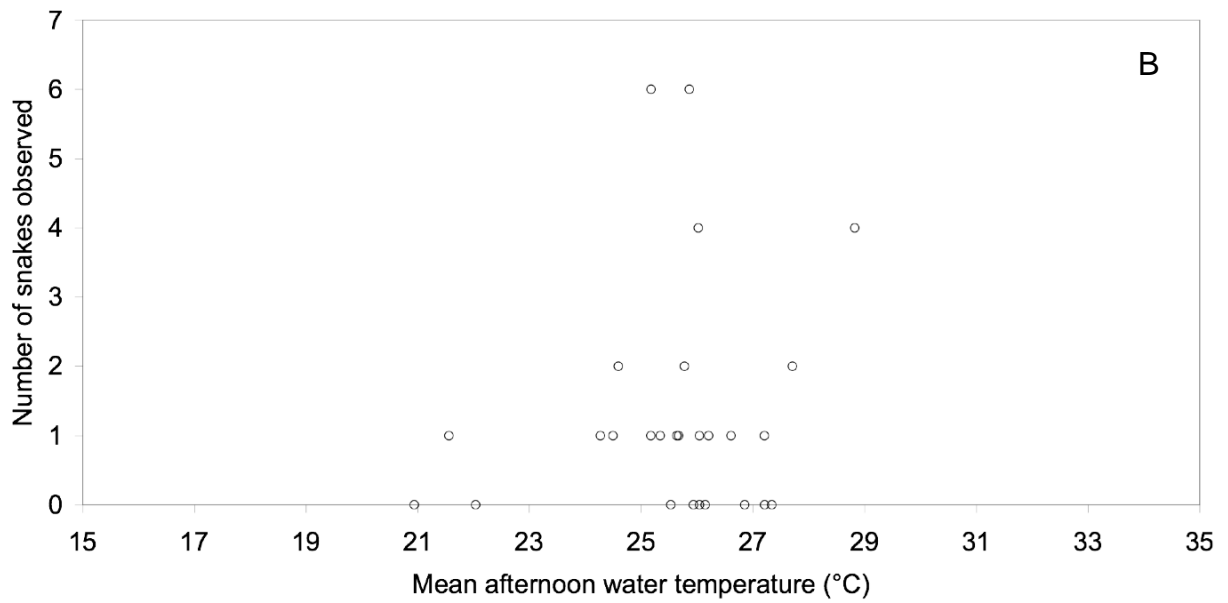
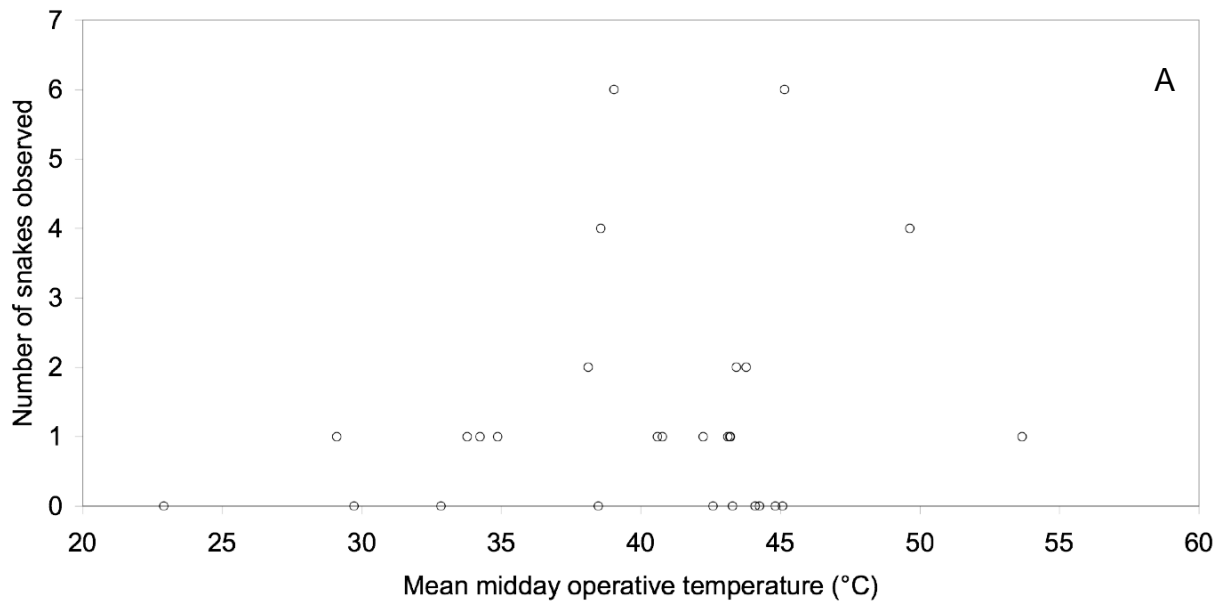


Figure 8. Scatterplots of the numbers of snakes observed in Lake Michigan daily in 2001 and mean midday T_e (A) and mean afternoon T_w (B)

The 2002 field season included observations between 23 February and 25 June. I recorded 6,374 body temperatures of the same 5 snakes during this time, and of these, 1,911 were of the snakes while in Lake Michigan. During 2002, I observed as many as 45 different snakes in the lake, with all 71 sightings taking place between 28 May and 25 June (Figure 9). Full-time dedication to field work in 2002 began on 21 May and ended on 23 June, with brief visits to the site every one to two days beginning May 7. The snake model and water temperature loggers were in place on 13 May. The earliest observation of a snake in Lake Michigan in 2002 occurred on 28 May, and such activity increased sharply thereafter. The number of snakes observed in the lake each day was significantly correlated with both mean midday T_e ($r_s = 0.512$, $P = 0.002$, $n = 34$) and mean afternoon T_w ($r_s = 0.533$, $P = 0.001$, $n = 34$; Figure 10).

The beginning of snake activity in the lake in 2002 coincided with a number of events. Mean midday T_e regularly exceeded 30°C (Figure 11), and mean afternoon T_w began to exceed 14.5°C (Figure 12). Courtship behavior was observed for the last time on 28 May, and while some courtship likely continued unnoticed after this date, the majority of such behavior had apparently ceased. On 17 May, while snorkeling along the shoreline typically explored by the snakes at GHNA, I found only a single sculpin (*Cottus* sp.). On 29 May, seven sculpin were found along the same stretch of shoreline. Also, the arrival of hundreds of carp (*Cyprinus carpio*) to the area for spawning was first noted on 30 May. Odor from the carp was easily discerned by me, so it is very likely the snakes, being more sensitive to chemical cues than I, also were able to detect their presence (Drummond, 1979).

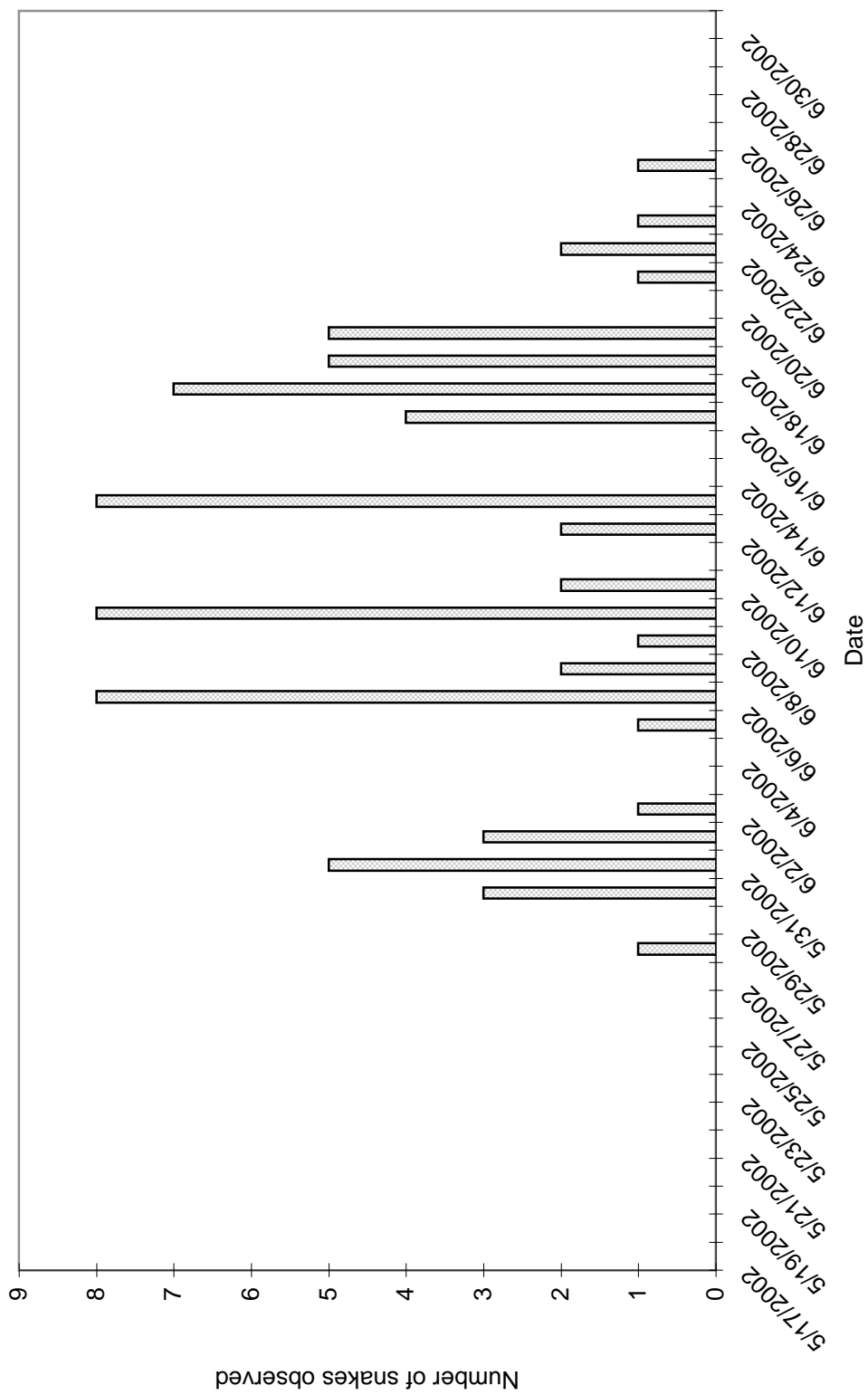


Figure 9. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season.

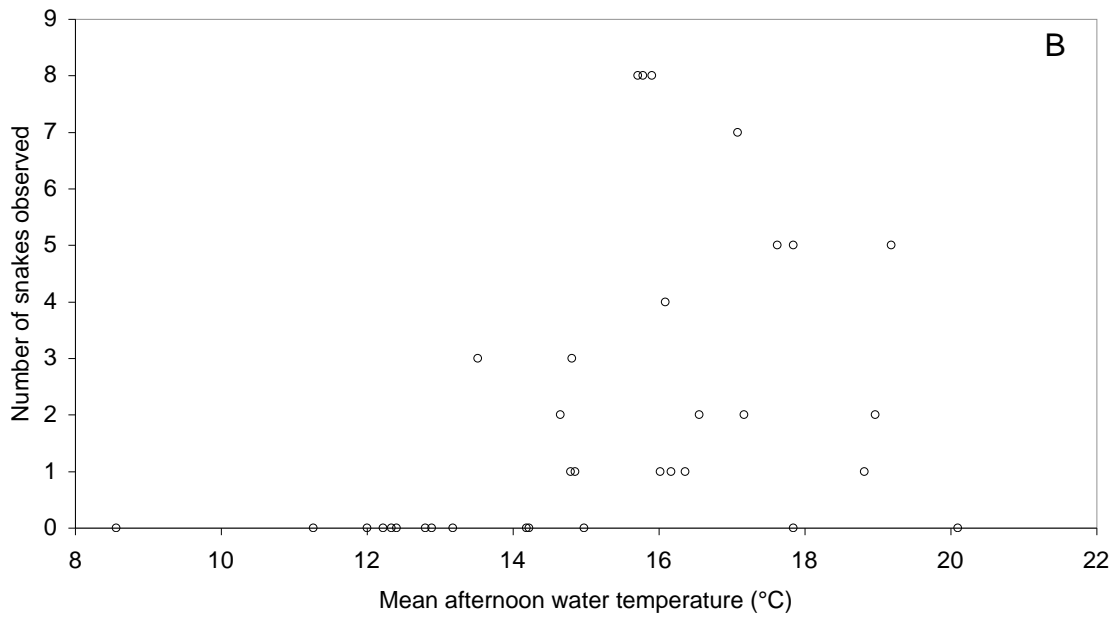
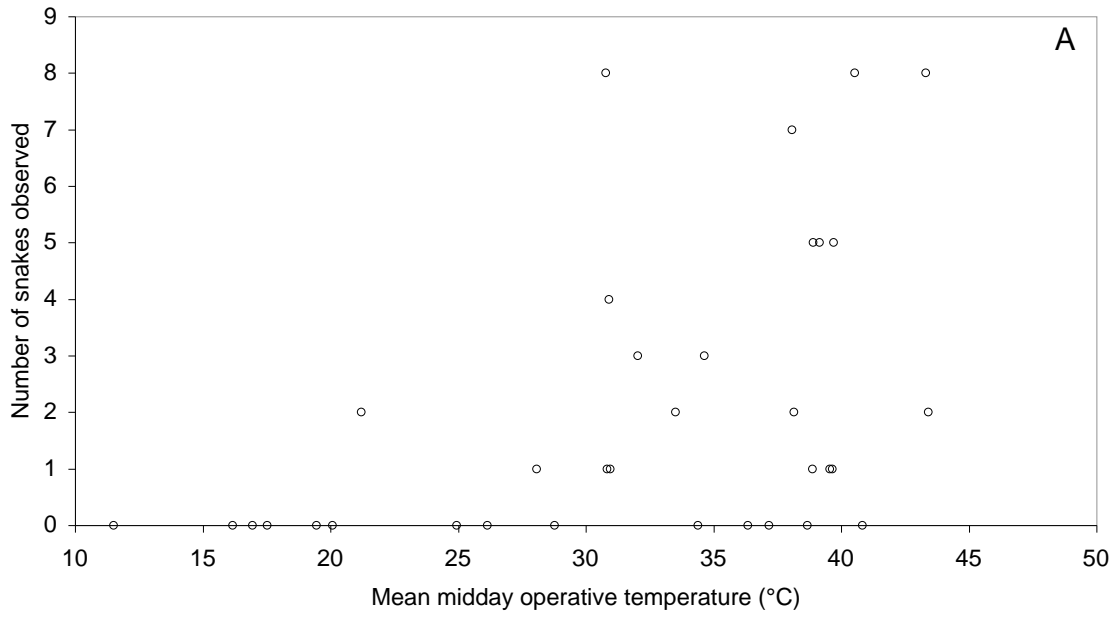


Figure 10. Scatterplots of the numbers of snakes observed in Lake Michigan daily in 2002 and mean midday T_e (A) and mean afternoon T_w (B).

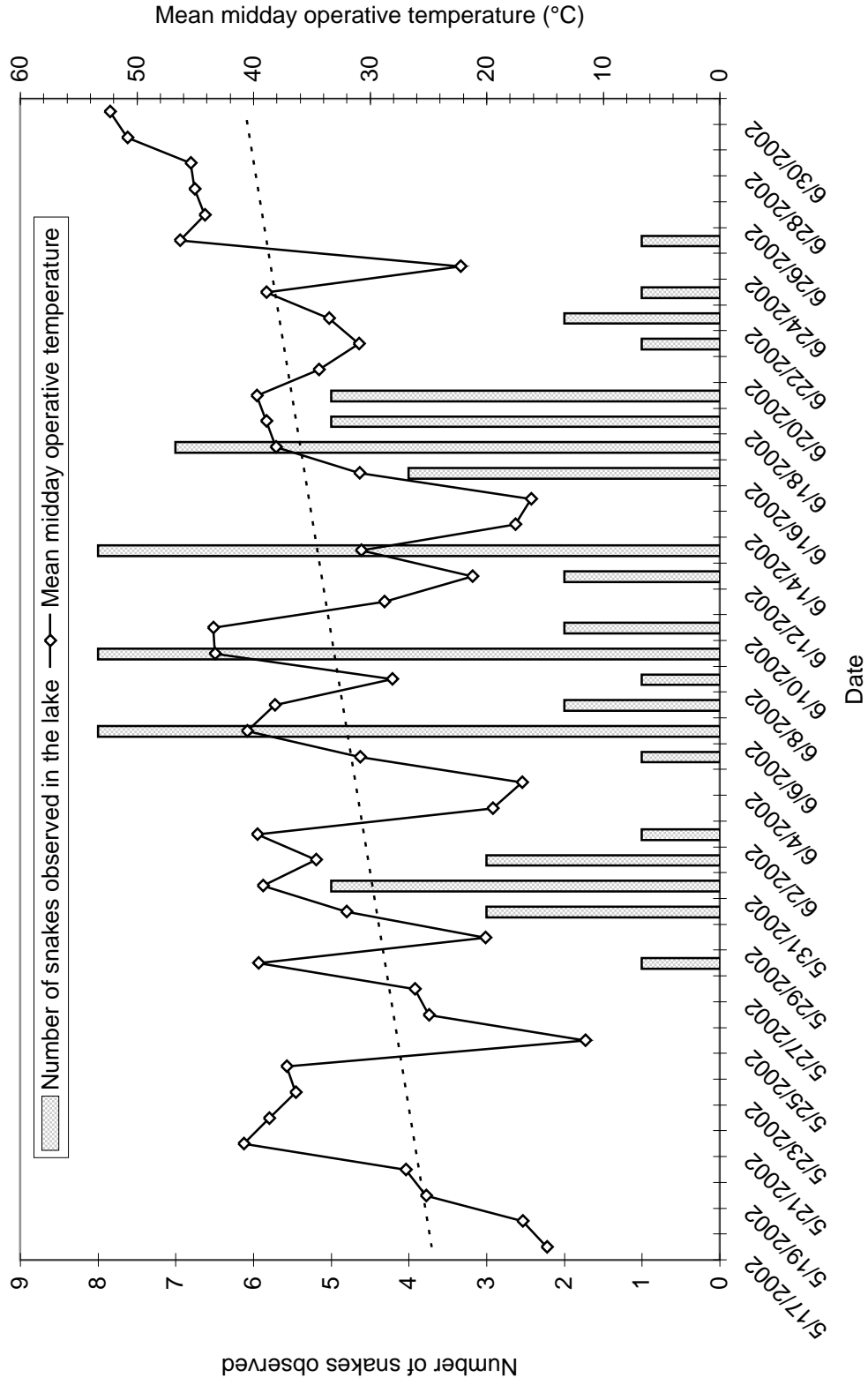


Figure 11. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season and the mean midday (1000–1600 h) operative temperature (T_e). Dotted line is seasonal T_e trend.

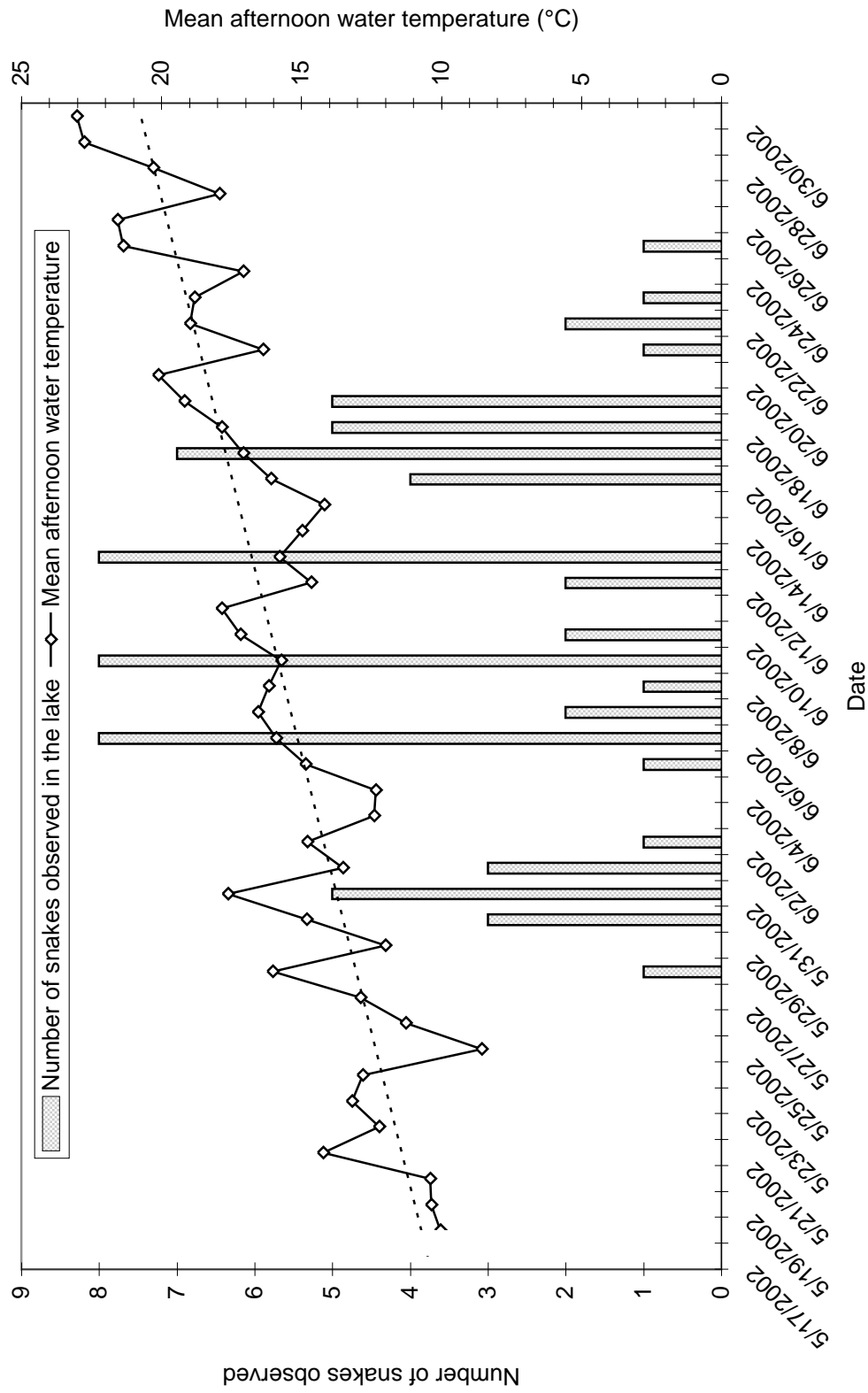


Figure 12. Numbers of snakes observed in Lake Michigan on different days throughout the 2002 field season and the mean afternoon (1200–1800 h) water temperature (T_w). Dotted line is seasonal T_w trend.

Daily Timing of Foraging

During both 2001 and 2002, nearly all snake activity observed in the lake occurred during daylight hours, began as T_e neared 30°C , and peaked at 1500 h (Figures 13–16). The number of snakes observed in the lake throughout the season at the half-hour mark of each hour of the day was significantly correlated with both the seasonal mean hourly T_e and the seasonal mean hourly T_w in both years (Table 1). For this analysis, a snake was considered to be in the lake during a given hour only if it was in at the half-hour mark because environmental temperatures were averaged over entire hours (30 minutes on either side of the half-hour mark) rather than over the two half-hours surrounding the top of the hour. Snakes that were seen in the lake during only one hour, but not necessarily on the half-hour mark, were considered to be in the lake during that hour. The presence of an individual in the lake at any one half-hour mark was considered independent of its presence in the lake at any other half-hour mark because some excursions lasted less than 1 hour. Also, had a snake been in the lake from 1350–1510 h and considered to be in the lake during 1300, 1400, and 1500 h, the assumption of independence would clearly have been violated.

While snake activity in the lake occurred primarily during the day, two snakes, one with a transmitter and one without, spent the night in Lake Michigan on a total of three occasions in 2001. One radio-implanted snake spent the night in the lake once during 2002. All of these snakes had initially entered the lake well before sunset. In fact, I did not see any snake begin an excursion after 1900 h. While it is quite possible that limited foraging by the aforementioned snakes occurred during the night, no such behavior was observed after dark.

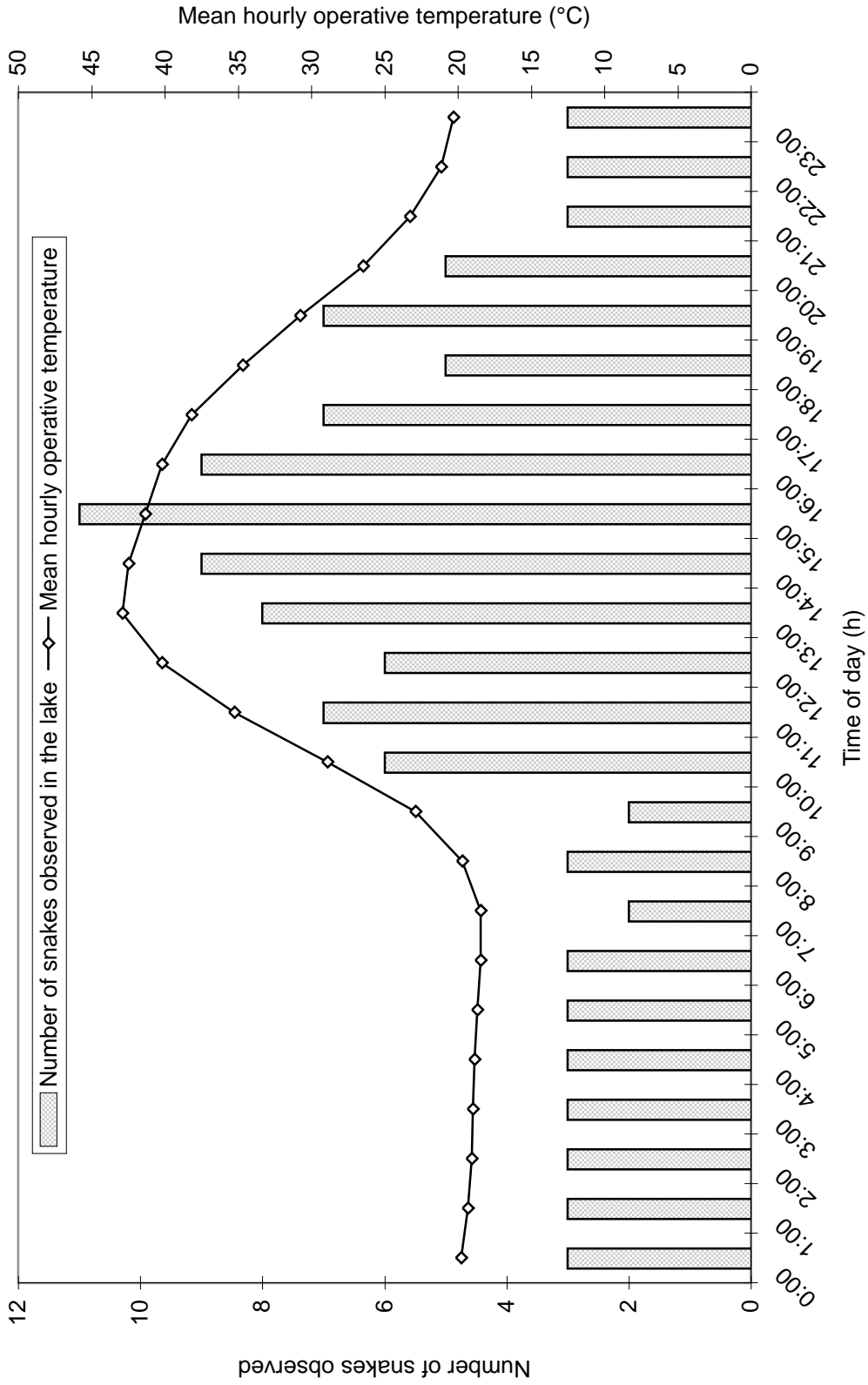


Figure 13. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2001 field season and the mean operative temperature (T_o) recorded during those hours averaged over the season.

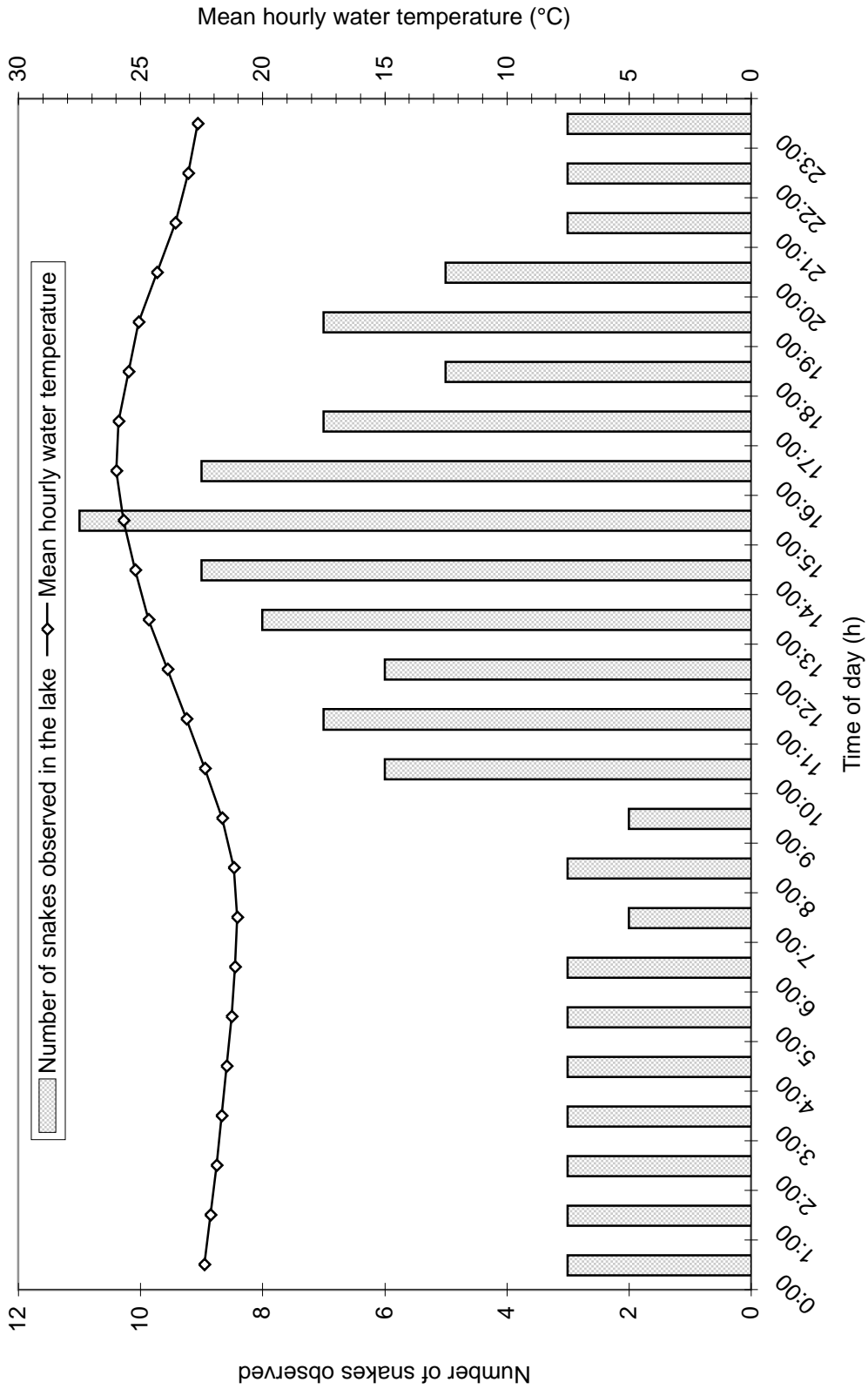


Figure 14. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2001 field season and the mean water temperature (T_w) recorded during those hours averaged over the season.

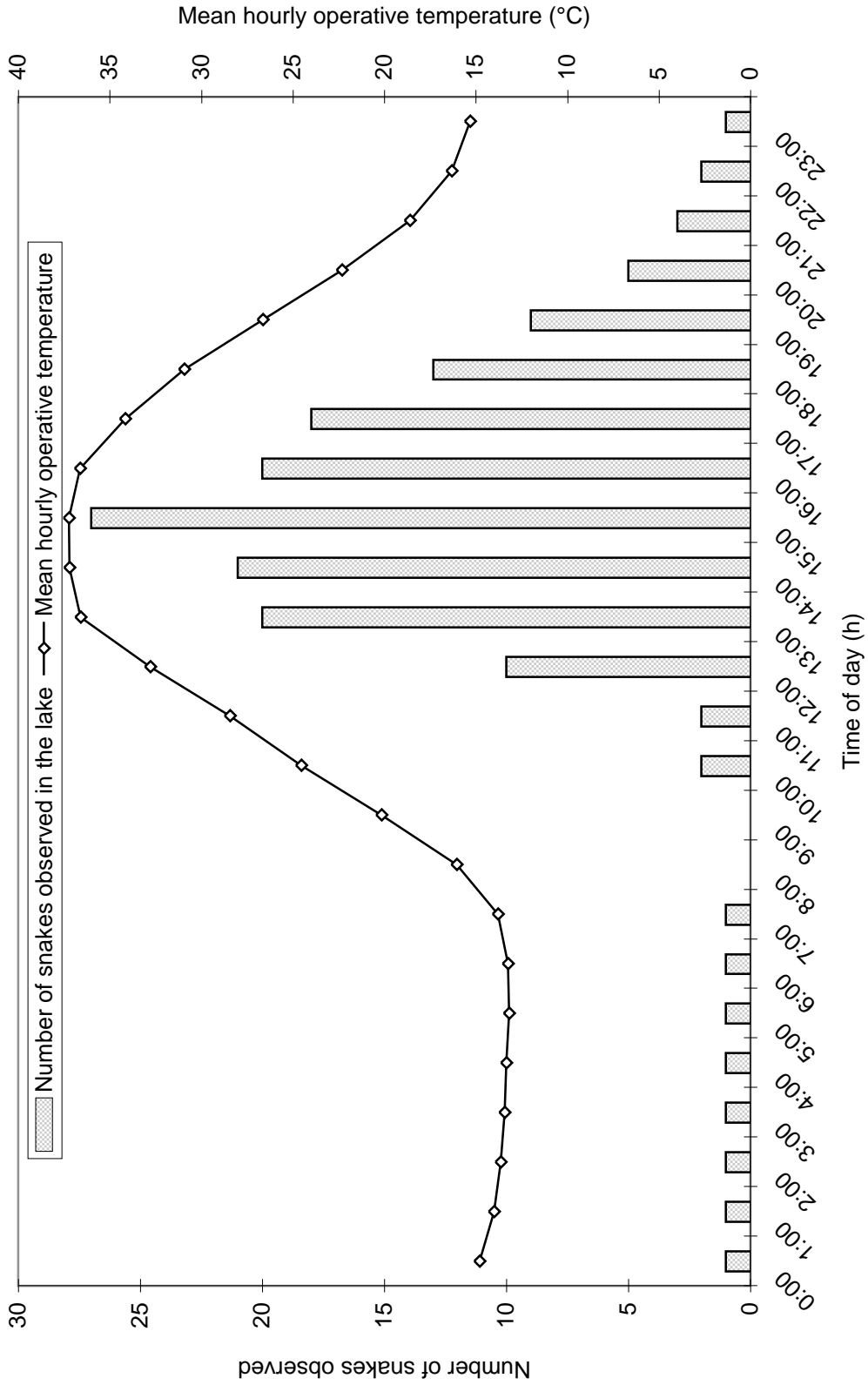


Figure 15. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2002 field season and the mean operative temperature (T_o) recorded during those hours averaged over the season.

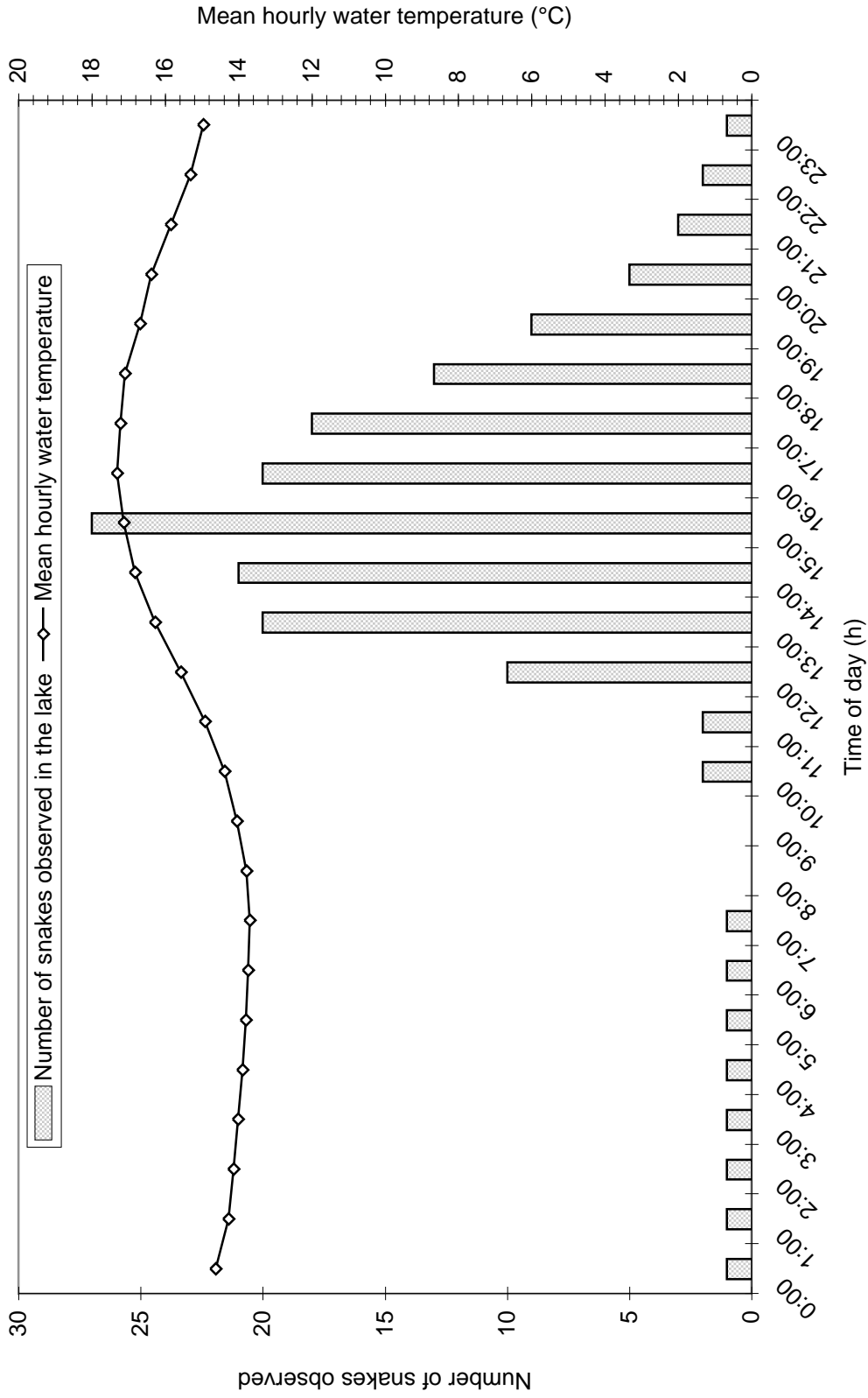


Figure 16. Numbers of snakes observed in Lake Michigan during different hours of the day throughout the 2002 field season and the mean water temperature (T_w) recorded during those hours averaged over the season.

Table 1. Spearman's rank correlations (r_s) for numbers of snakes observed in Lake Michigan during each hour of the day and seasonal mean hourly operative temperature (SMHT_e) and seasonal mean hourly lake temperature (SMHT_w) for the 2001 and 2002 field seasons.

	2001			2002		
	r_s	P	n	r_s	P	n
SMHT _e	0.864*	< 0.000	24	0.848*	< 0.000	24
SMHT _w	0.836*	< 0.000	24	0.890*	< 0.000	24

Note: Asterisks indicate significance after Dunn-Sidak adjustment for two comparisons ($\alpha' = 0.025$).

Duration and Frequency of Foraging

During 2001, the duration of foraging excursions averaged 6.29 ± 8.82 hours (mean ± 1 SD). This was measurable on six occasions involving only three snakes (Figure 17). Inclusion of additional, underestimated data for excursions not observed from beginning to end did not appreciably alter the mean (6.24 ± 8.36 h). The interval between foraging excursions in 2001 averaged 3.57 ± 0.53 days and was measurable on 7 occasions involving the same 3 snakes (Figure 18). Too few adjacent excursion durations and intervals were known from 2001 to examine possible correlation between the two. No significant correlation existed between the duration of foraging excursions in 2001 and the mean T_b of snakes during them ($r_s = -0.257$, $P = 0.623$, $n = 6$; Figure 19).

During 2002, the duration of foraging excursions averaged 4.77 ± 3.24 hours. This was measurable on 21 occasions involving the 5 telemetered individuals (Figure 20). The interval between foraging excursions averaged 3.54 ± 1.91 days and was measurable on 24 occasions involving 9 snakes (Figure 21). In 2002, there was a significant positive correlation between the duration of foraging excursions and the preceding non-foraging interval ($r_s = 0.802$, $P = 0.003$, $n = 11$), but no such relationship existed between the duration of foraging excursions and the non-foraging interval that followed ($r_s = -0.356$, $P = 0.313$, $n = 10$; Figure 22). There was no significant correlation between the duration of excursions in 2002 and the mean T_b of snakes during them ($r_s = 0.317$, $P = 0.200$, $n = 18$; Figure 23). I considered the durations of and intervals between multiple foraging excursions made by the same individual snakes to be independent of each other because all interval-duration-interval triplets used in the analysis were separated by at least one unknown or unused duration; no duration or interval value was used more than once.

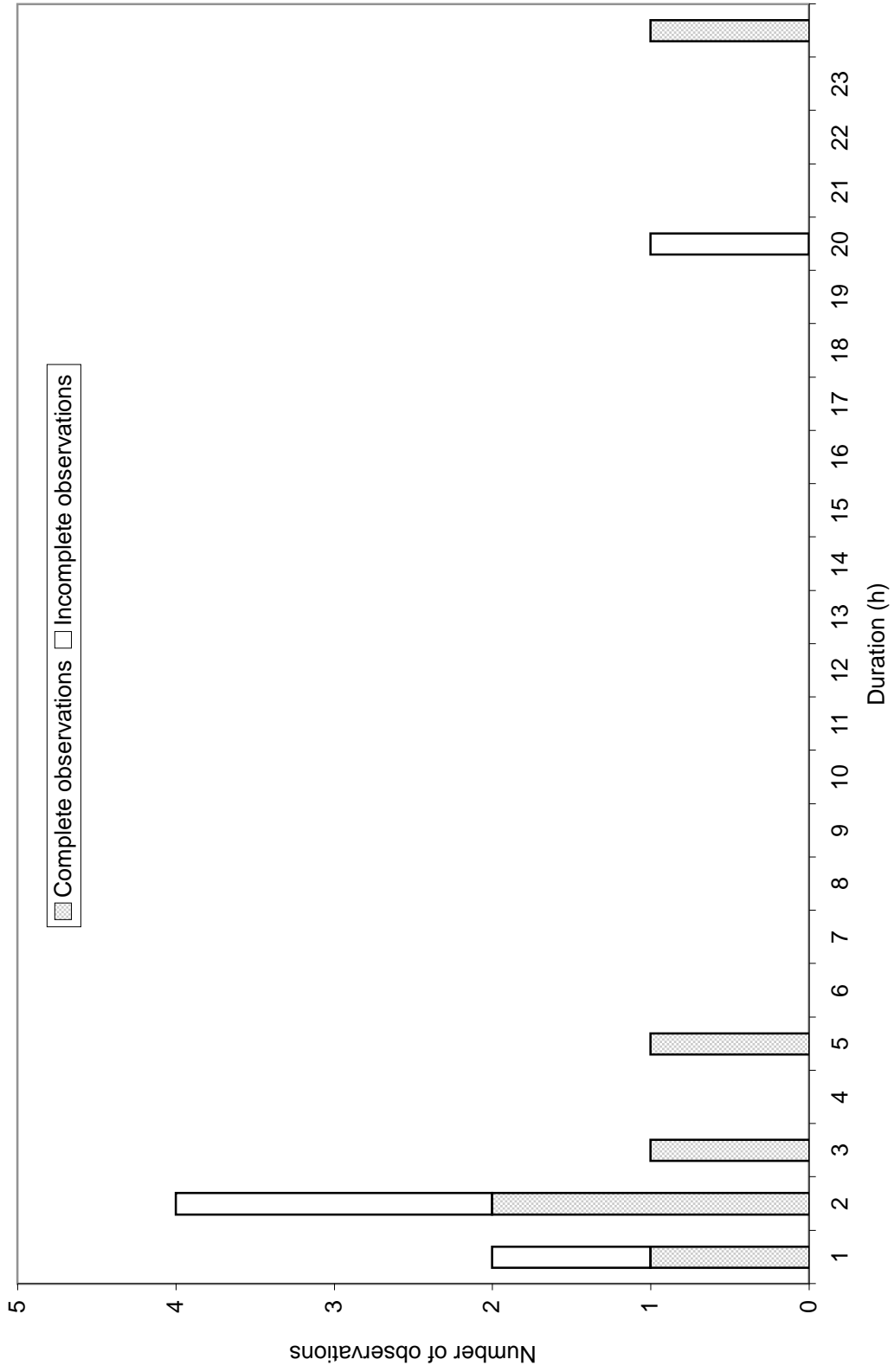


Figure 17. Durations of foraging excursions observed during the 2001 field season.

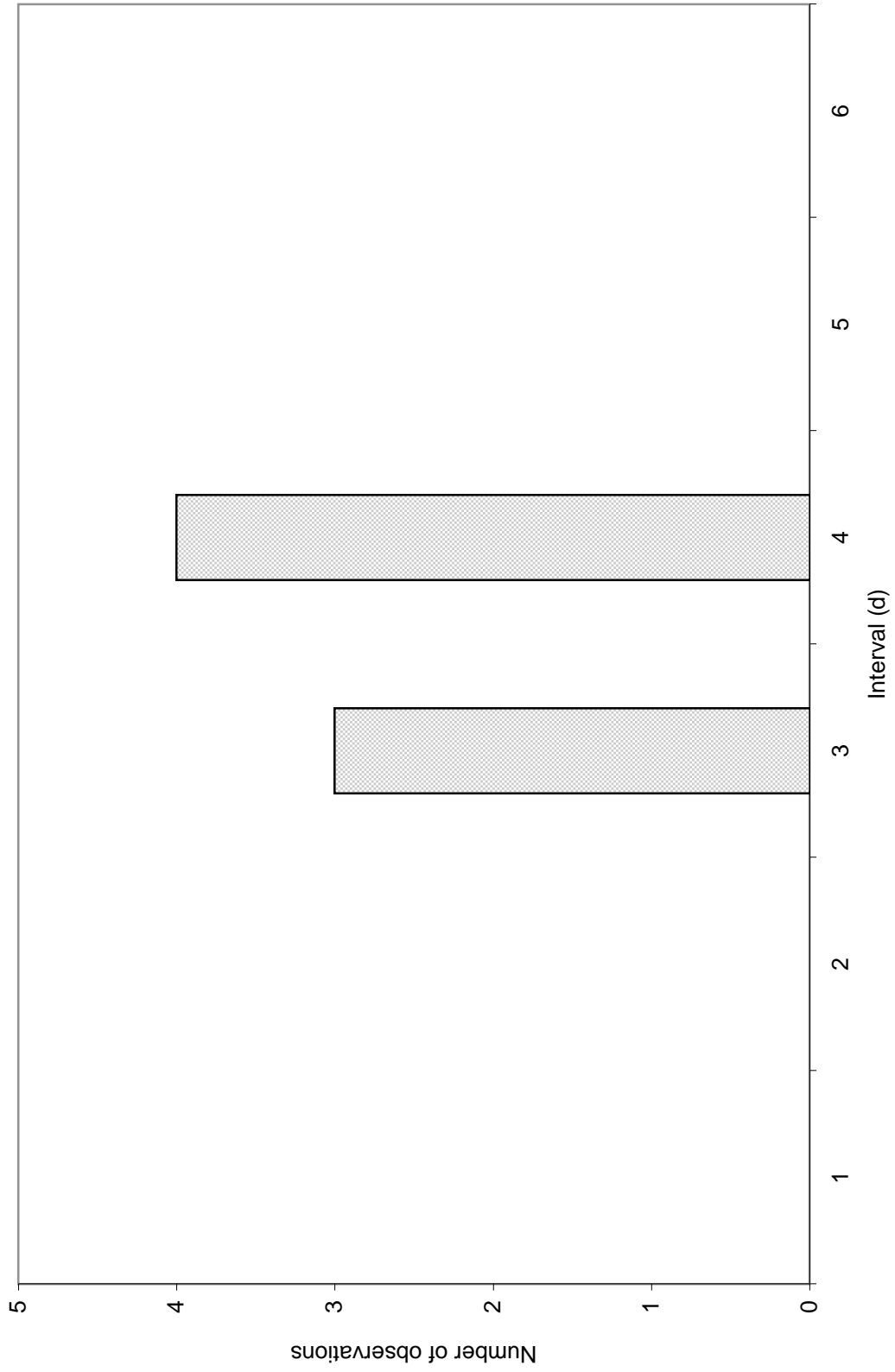


Figure 18. Intervals, in days, between successive foraging excursions observed during the 2001 field season.

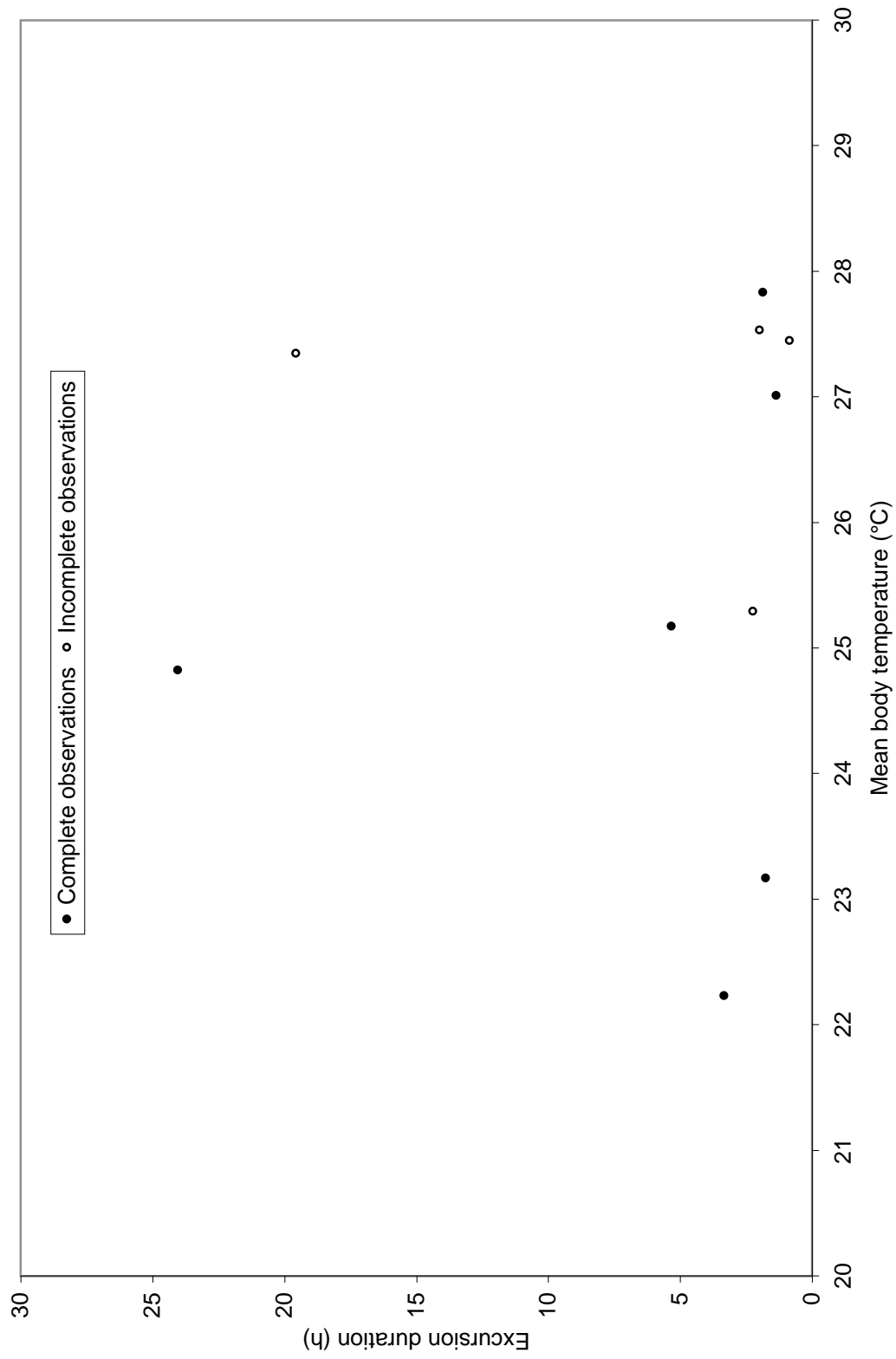


Figure 19. Scatterplot of the durations of foraging excursions in 2001 and mean $T_{b,s}$ during them.

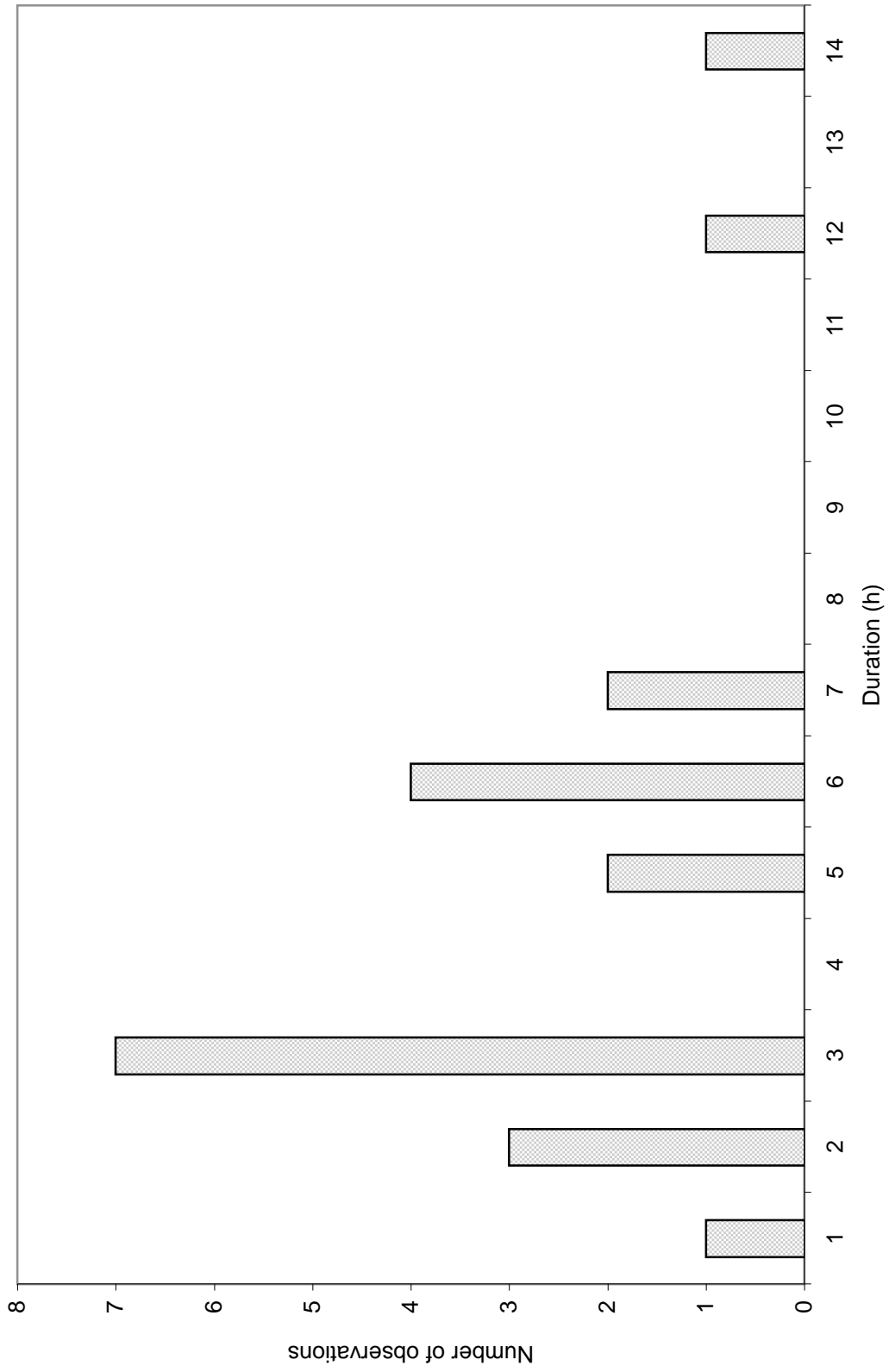


Figure 20. Durations of foraging excursions observed during the 2002 field season.

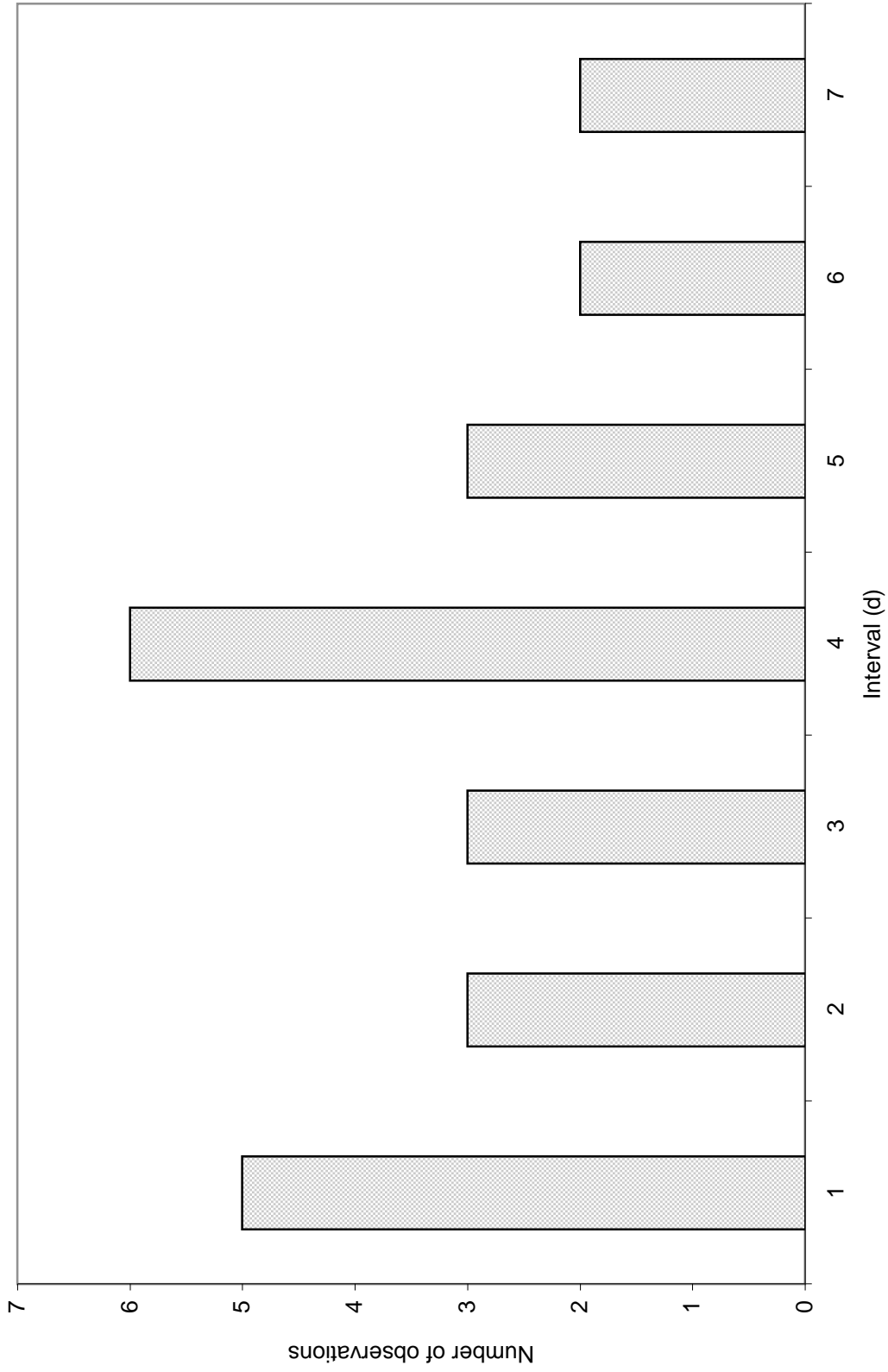


Figure 21. Intervals, in days, between successive foraging excursions observed during the 2002 field season.

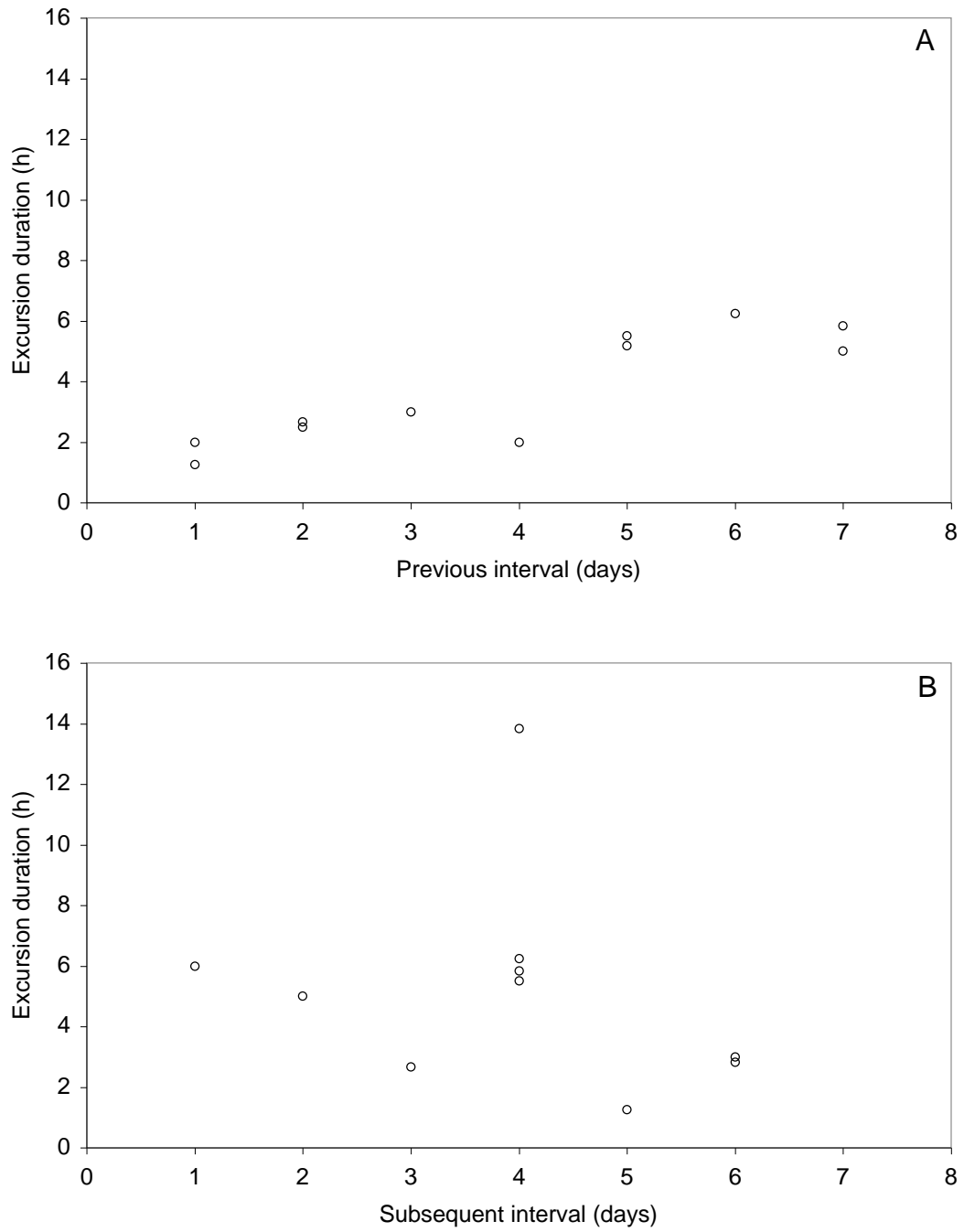


Figure 22. Scatterplots of the durations of foraging excursions and the non-foraging intervals that preceded (A) and followed (B) during the 2002 field season.

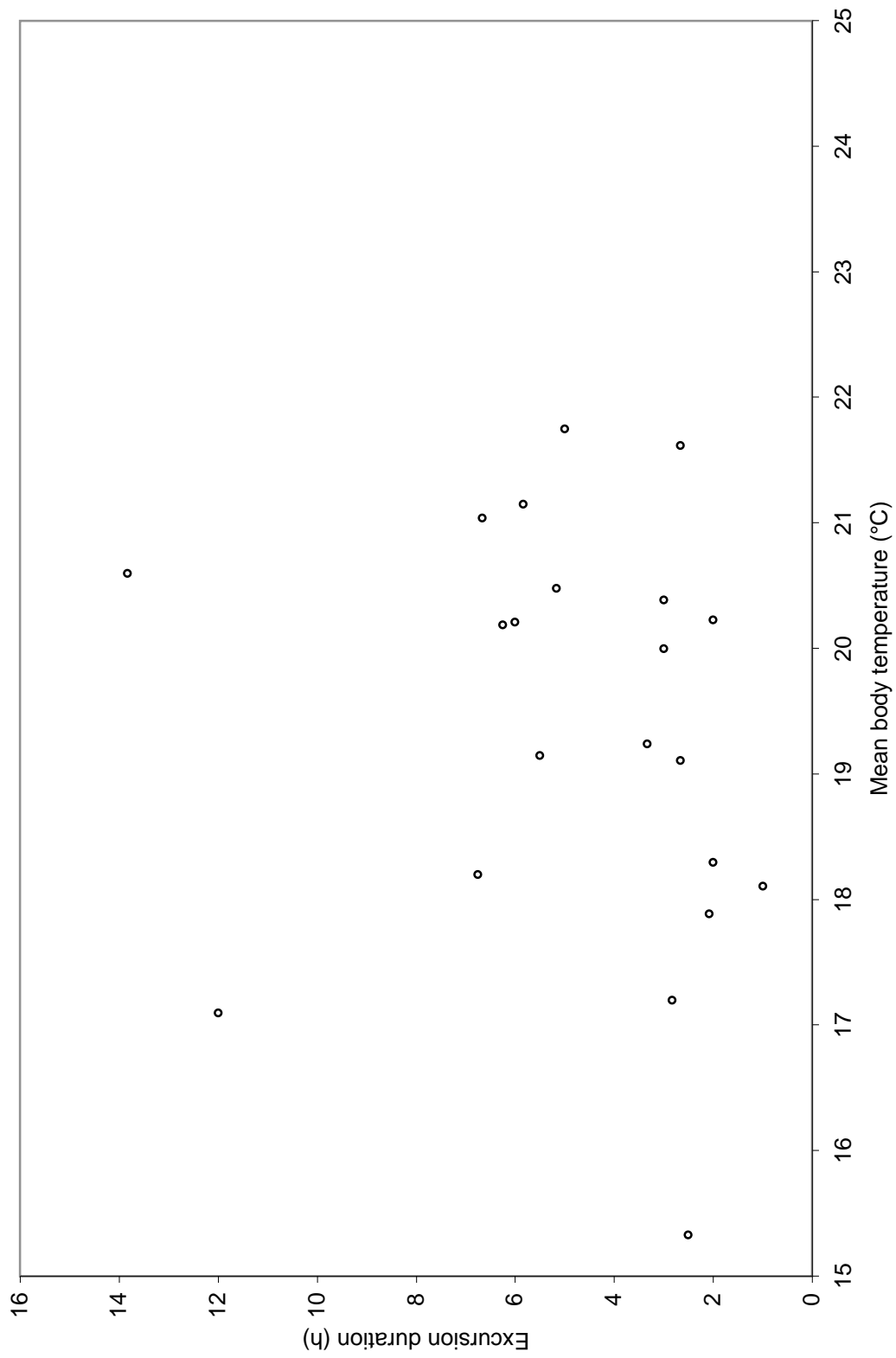


Figure 23. Scatterplot of durations of foraging excursions in 2002 and mean $T_{b,s}$ during them.

Three cases were excluded from the analysis to achieve independence between interval-duration-interval triplets; one of these was the only possible choice of three adjacent cases, while two were chosen randomly as a pair from four adjacent cases. For the analysis of excursion duration and T_b , durations of excursions made by the same individuals were considered independent if separated by more than one day; to achieve this, I randomly eliminated from the analysis three duration values, each being one of a pair of excursions that snakes made on adjacent days. Dunn-Sidak adjustment ($\alpha' = 0.0170$) was made for the three comparisons involving excursion duration.

Temperature Profiles of Snakes in Lake Michigan

While foraging in Lake Michigan, radio-implanted snakes experienced body temperatures as cold as 12.9°C (6/2/02) and as warm as 32.7°C (7/23/01). Table 2 summarizes the body temperatures of the snakes in both seasons. Temperatures of telemetered snakes in the lake in 2001 never went below 20.4°C (Figure 24), and their thermal profiles while in the water were rather simple. Body temperature quickly fell toward that of the water and fluctuated relatively little during most excursions (Figures 25–27). Many changes in T_b clearly resulted from snakes visiting offshore sites of different temperatures. However, snakes would occasionally come ashore, sometimes when attempting to swallow prey backwards, and these shoreline visits were commonly associated with notable T_b increases (Figure 28).

In the early part of their activity season, represented by data from 2002, snakes encountered lake temperatures that were much lower than those of the latter part of the previous activity season (Figure 29), resulting in noticeably different T_b profiles. Body

Table 2. Summary of body temperatures (in °C) of snakes in Lake Michigan. Lowest T_b refers to the lowest body temperature achieved during each foraging excursion.

	2001		2002	
	Lowest T _b	All T _b	Lowest T _b	All T _b
Mean	22.9	25.4	16.4	19.6
Minimum	20.4	20.4	12.9	12.9
Maximum	25.2	32.7	19.3	28.8
SD	1.37	2.59	1.52	2.57
SE Mean	0.395	0.752	0.31	0.589
<i>n</i>	12	1186	24	1911

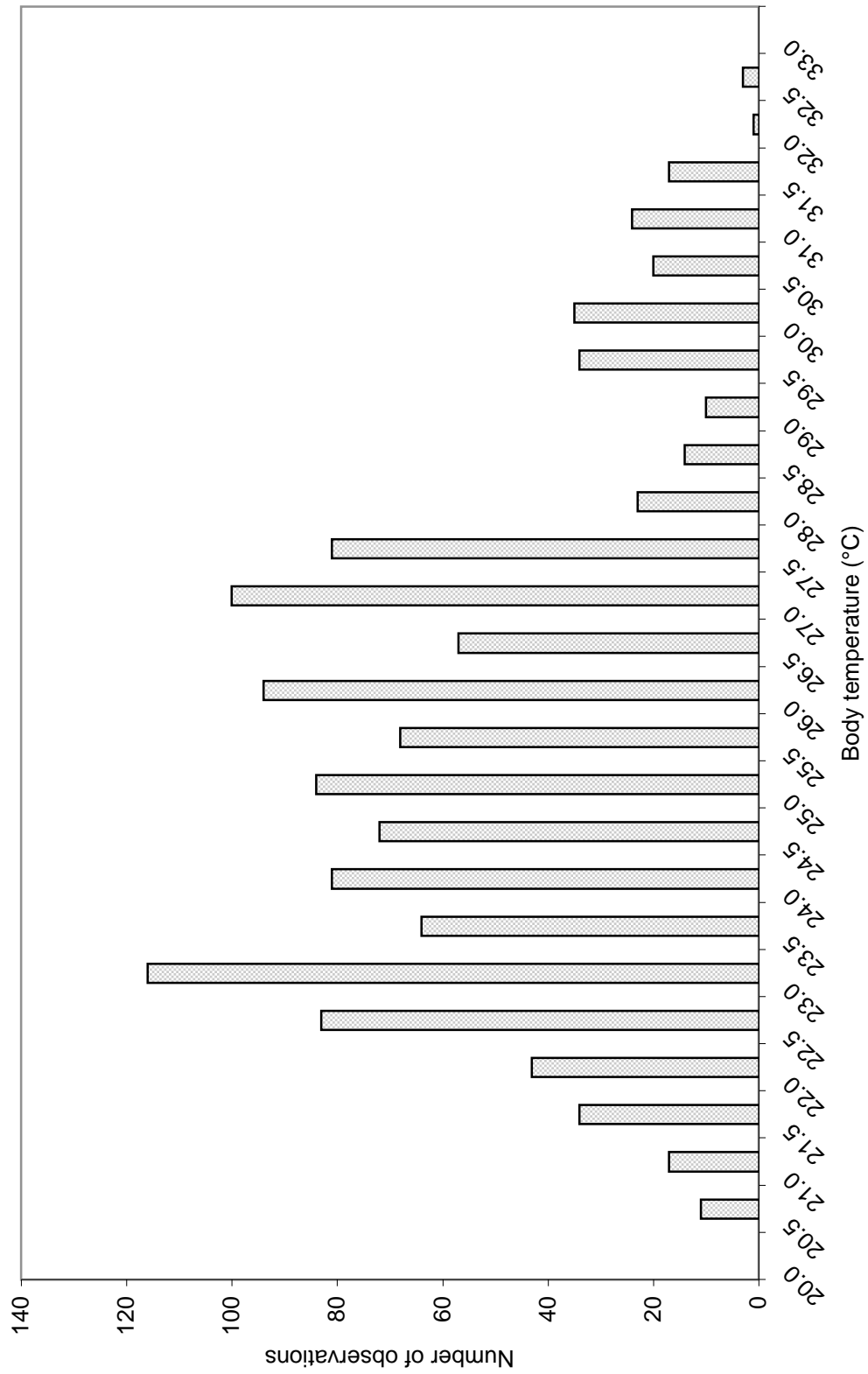


Figure 24. Frequency histogram of all body temperatures experienced by radio-implanted snakes while in Lake Michigan in 2001.

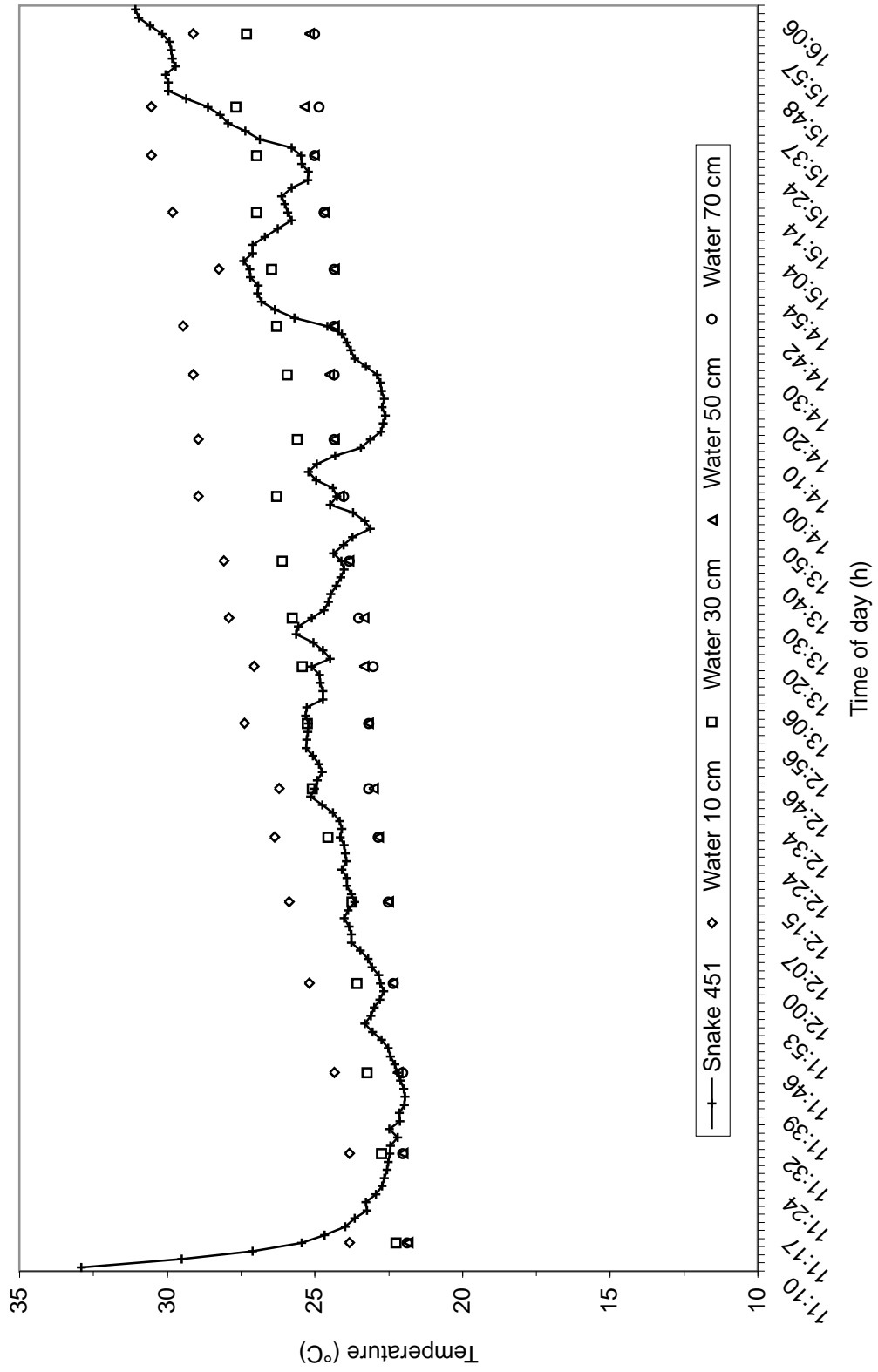


Figure 25. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 20 July 2001.

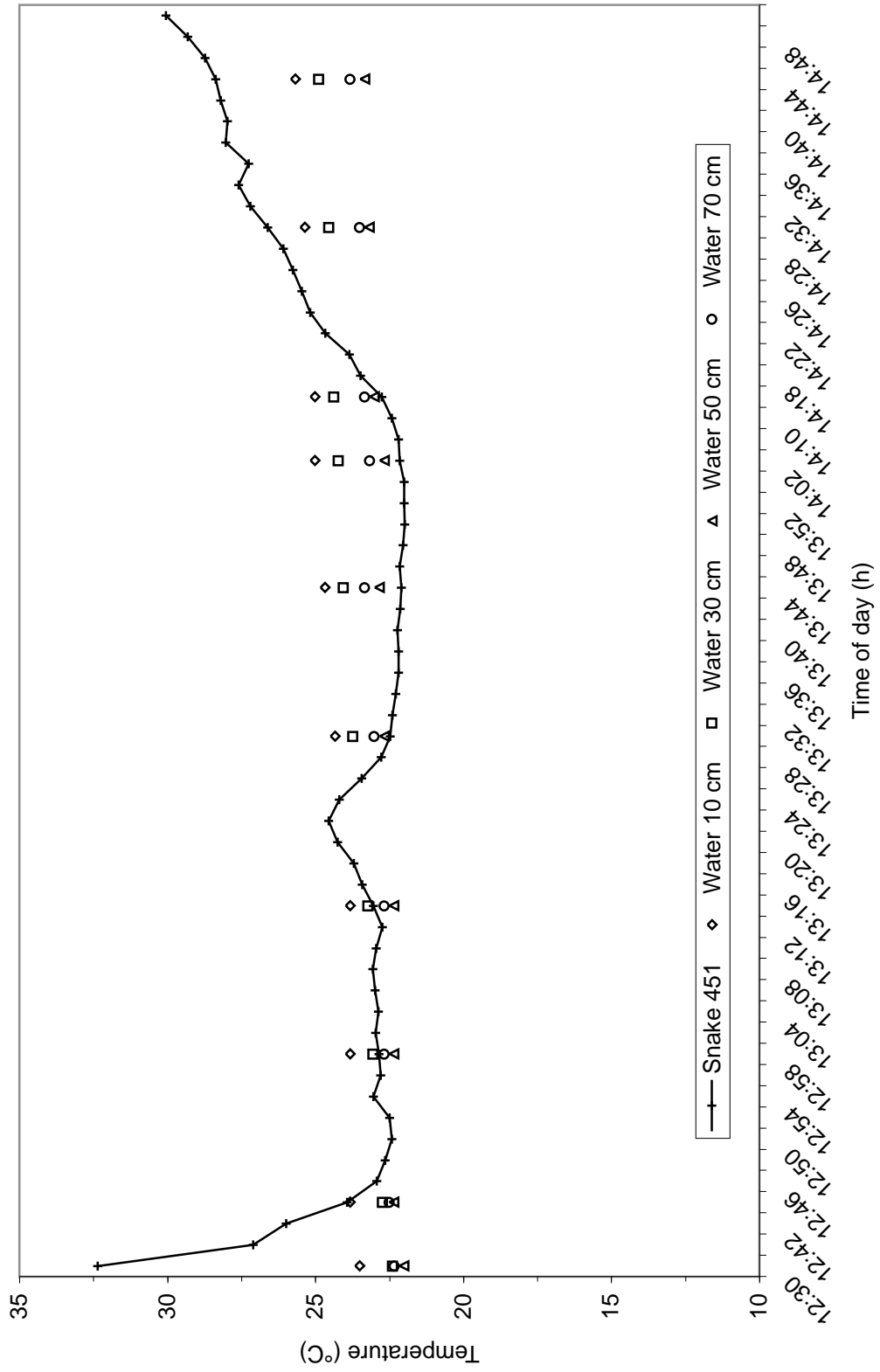


Figure 26. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 26 July 2001.

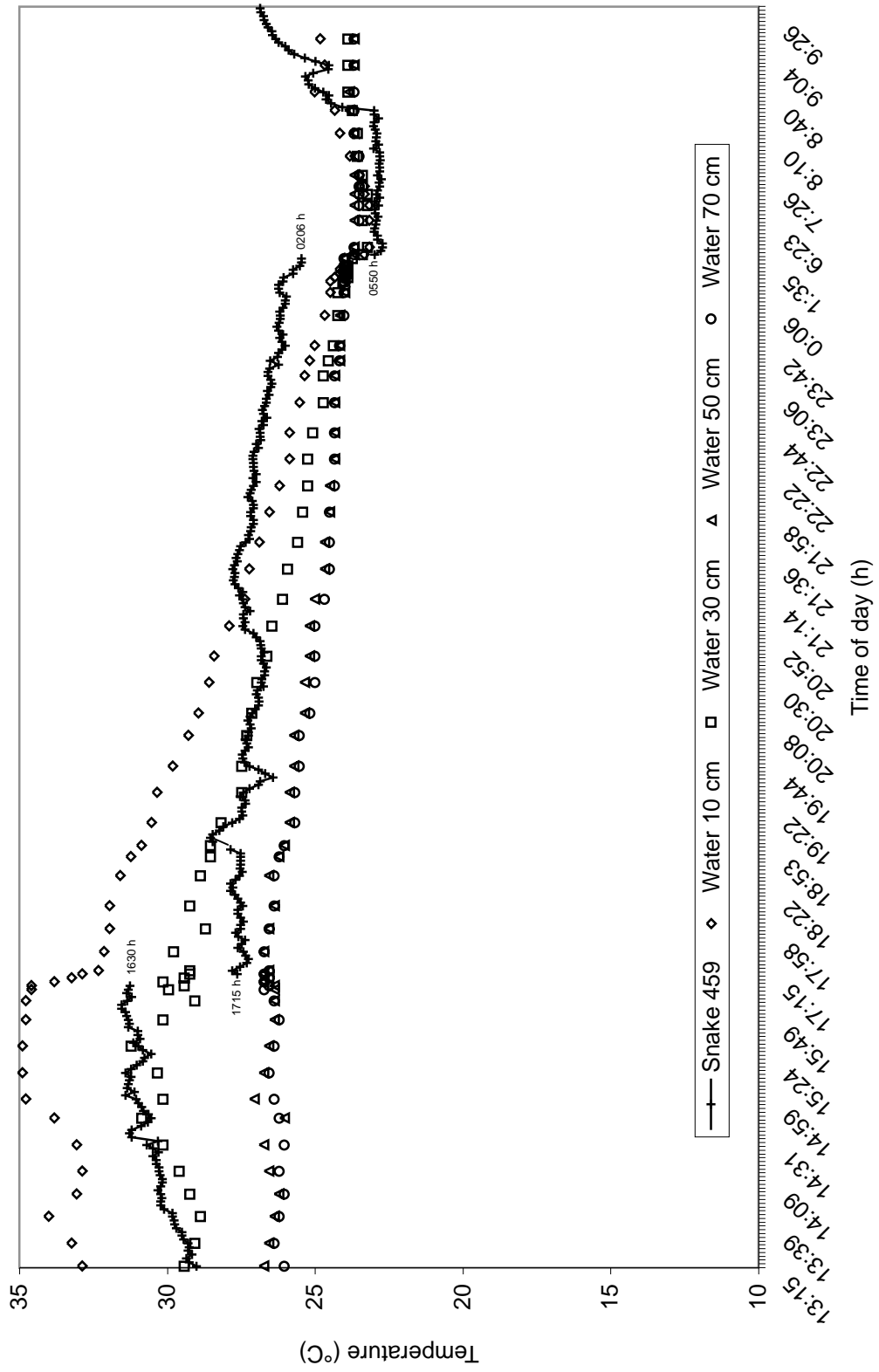


Figure 27. Body temperature profile of a northern water snake in Lake Michigan on 7–8 August 2001.

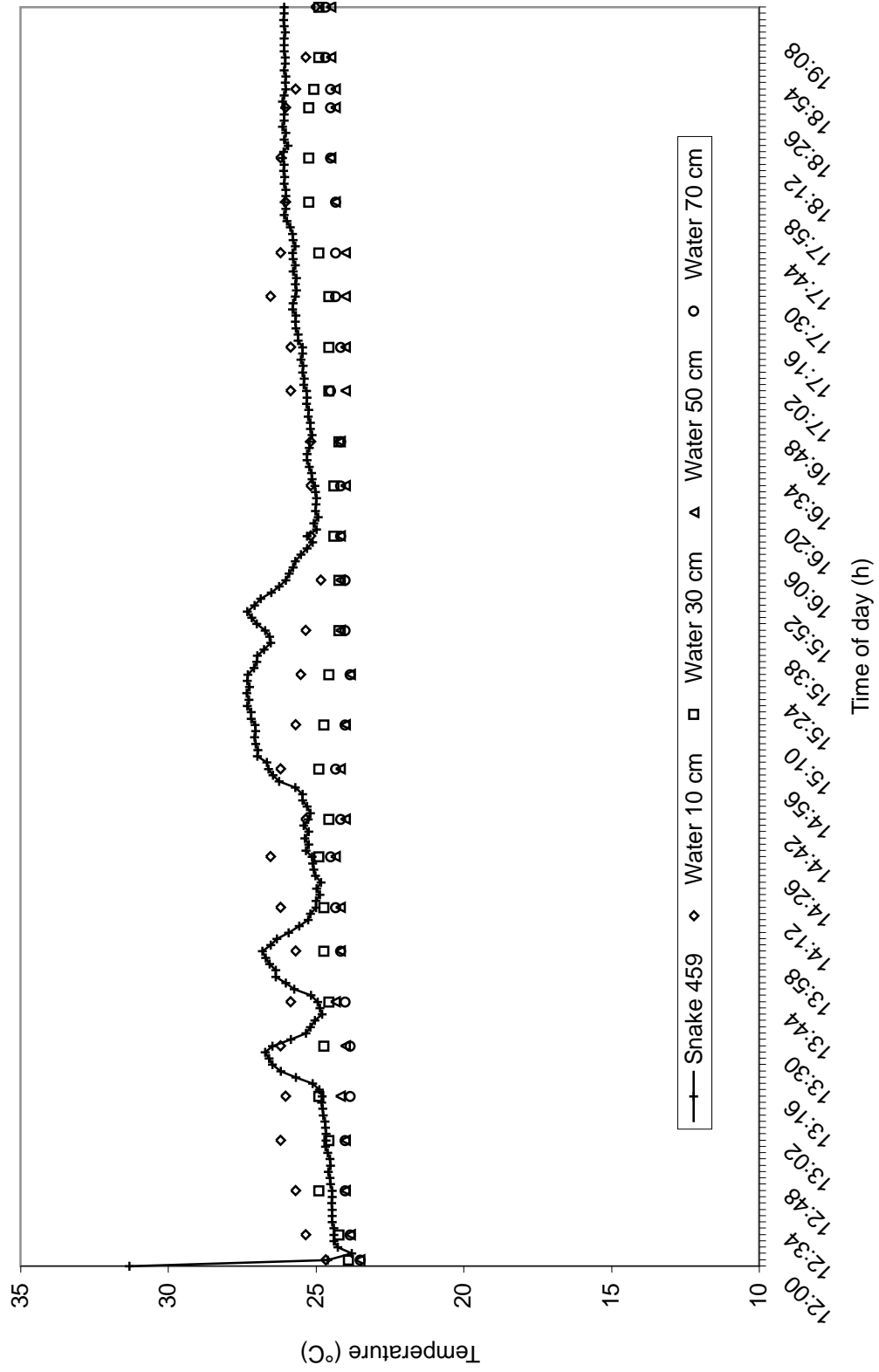


Figure 28. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 11 August 2001.

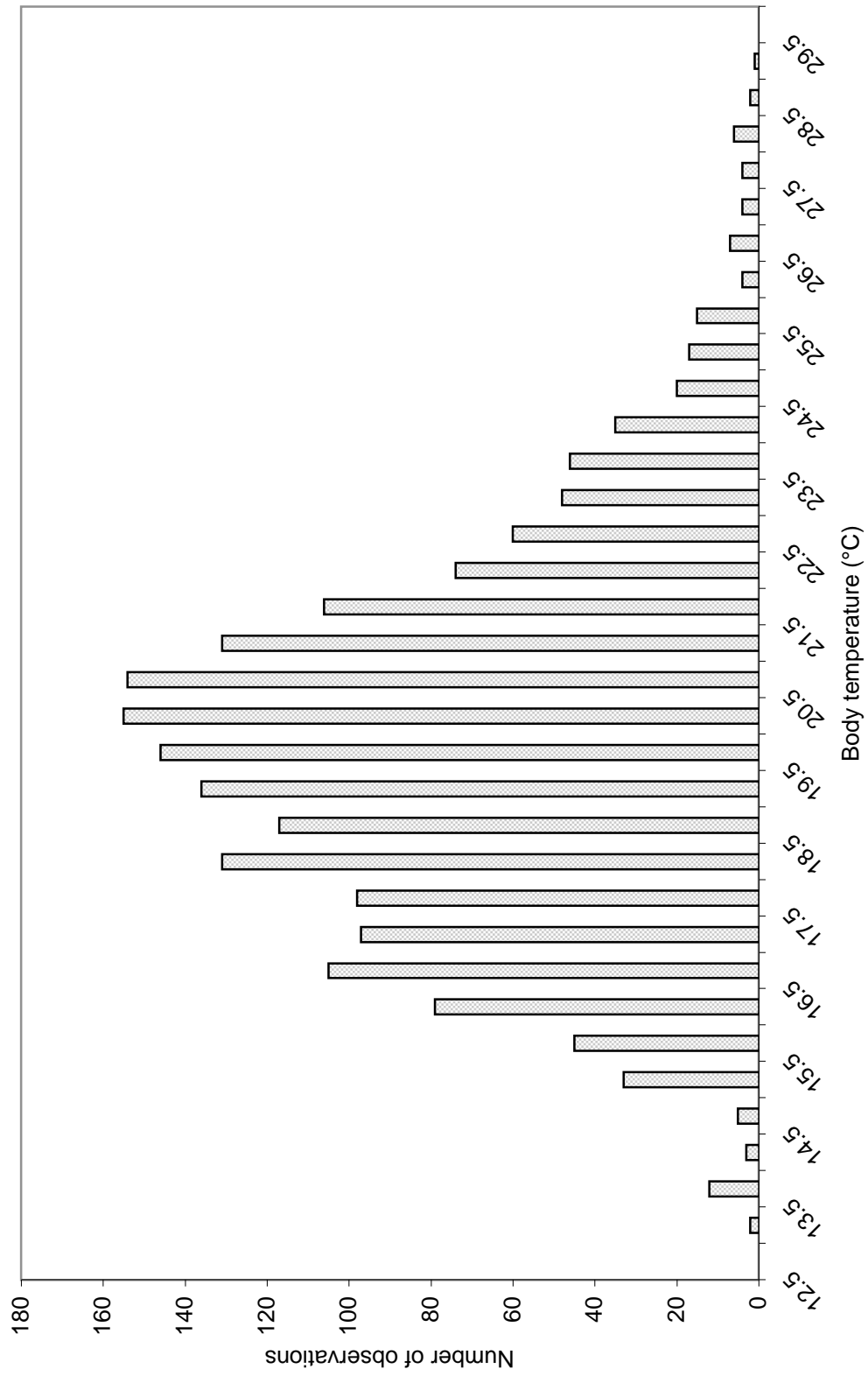


Figure 29. Frequency histogram of all body temperatures experienced by radio-implanted snakes while in Lake Michigan in 2002.

temperature fluctuated frequently and considerably during most foraging excursions (Figures 30–31), and snakes in the lake typically experienced their lowest T_b only briefly before warming again. This was not always the case, however, particularly when snakes foraged during inclement weather (Figure 32). As in 2001, snakes occasionally came very near the shore during excursions, but these shoreline visits appeared to occur more frequently in 2002 (Figure 33). Increases in T_b that were associated with trips to the shore were more pronounced, as well. Visits to the lake surface between dives did not appear to result in noticeable T_b changes. For example, snake 469 made three foraging dives between 1511 h and 1518 h on 31 May 2002 (Figure 30) and her T_b changed less than 0.1°C during this entire span of time.

Snakes that did not exit the lake at a “normal” time exhibited interesting T_b patterns. A snake that foraged until dark, and left the water long after T_e had dropped considerably, experienced body temperatures from $5\text{--}10^\circ\text{C}$ below the mean T_b achieved by the other telemetered snakes for at least an hour (Figure 34). A snake that began foraging late and remained in the lake all night experienced body temperatures that, from the time it ceased foraging at 2130 h until it left the lake at 0720 h, averaged 5°C below the mean T_b of the other radioed snakes (Figure 35).

The Excursion T_b Threshold

Presumably, if a low-temperature threshold exists for these snakes, then the lowest T_b s experienced by them while foraging in cold water should all be roughly the same. This is of course provided water temperatures are as low as or lower than the threshold. The lowest body temperatures experienced by the 5 radio-implanted snakes

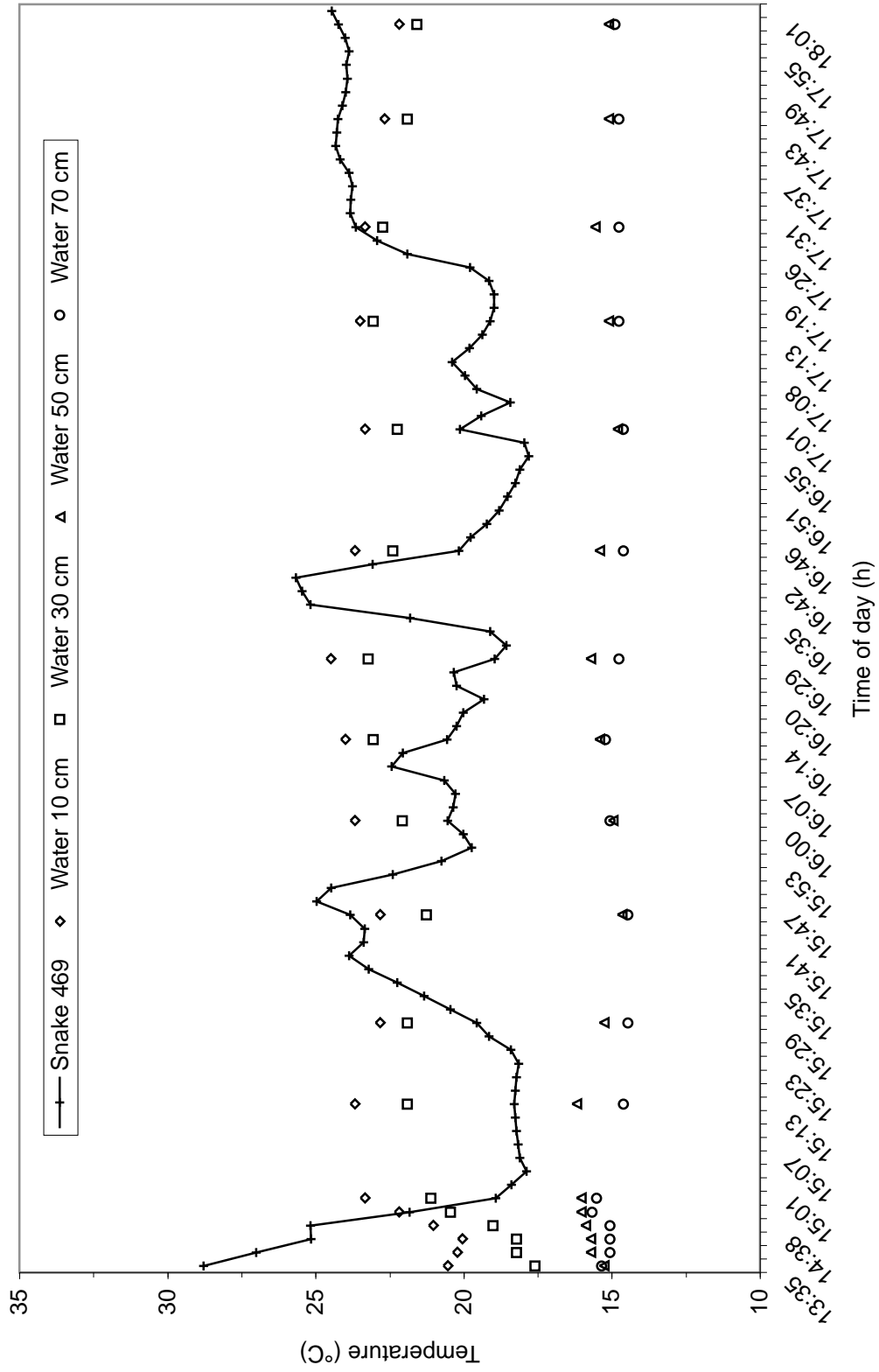


Figure 30. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 31 May 2002.

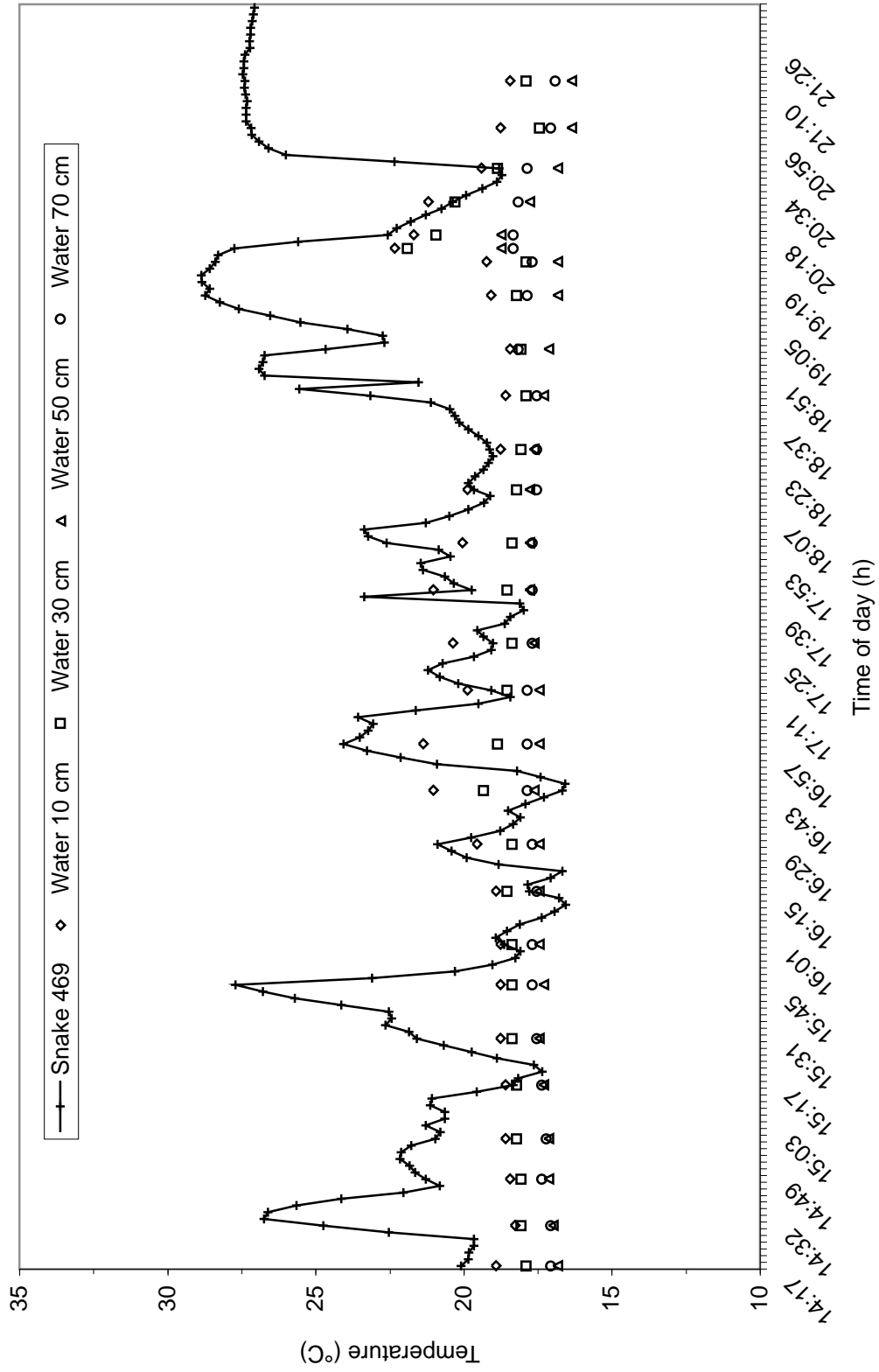


Figure 31. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 18 June 2002.

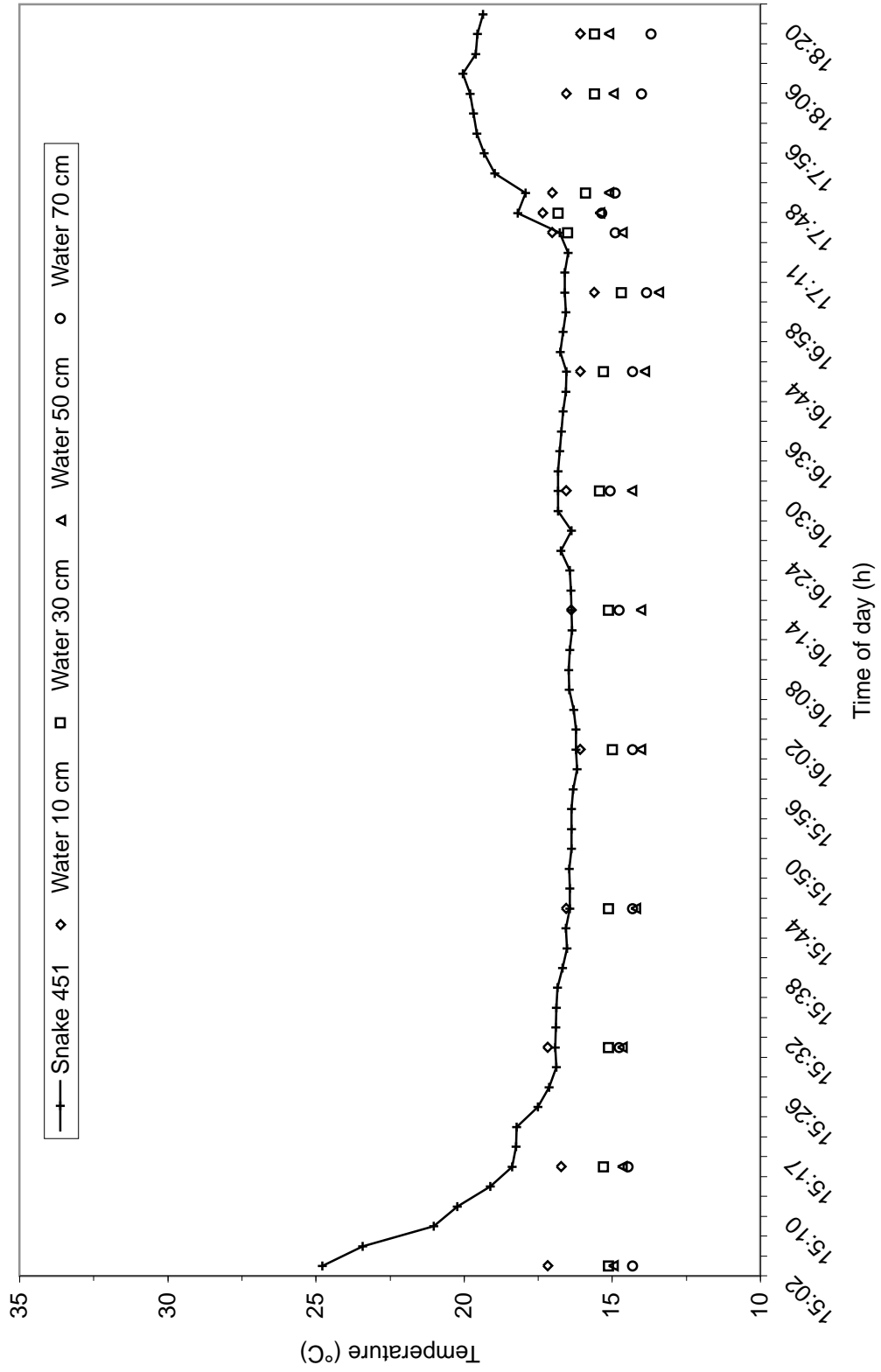


Figure 32. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 30 May 2002.

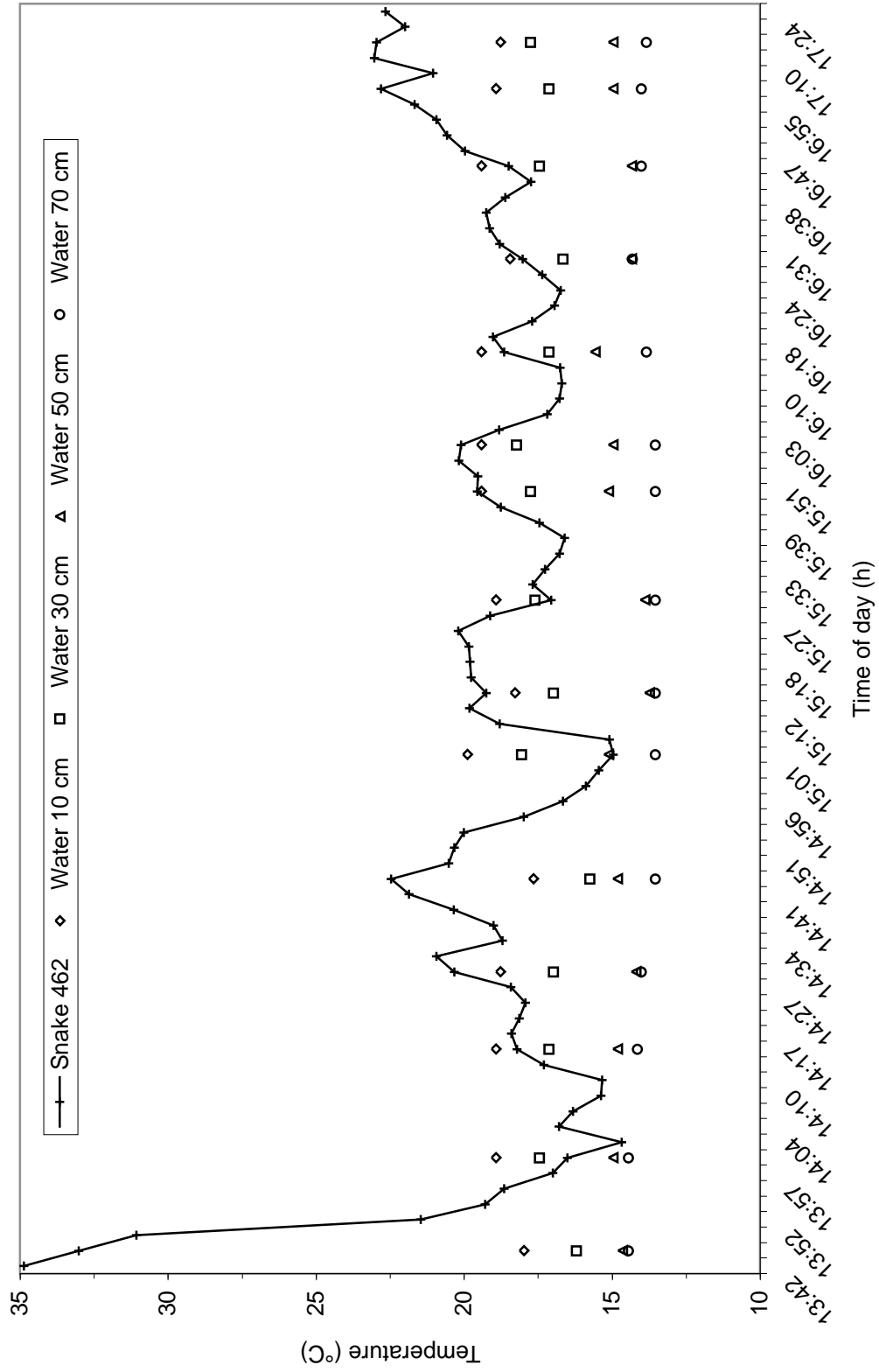


Figure 33. Body temperature profile of a northern water snake while it foraged in Lake Michigan on 28 May 2002.

Nearly all $T_{b,s}$ greater than 19°C occurred when the snake was observed at the shoreline.

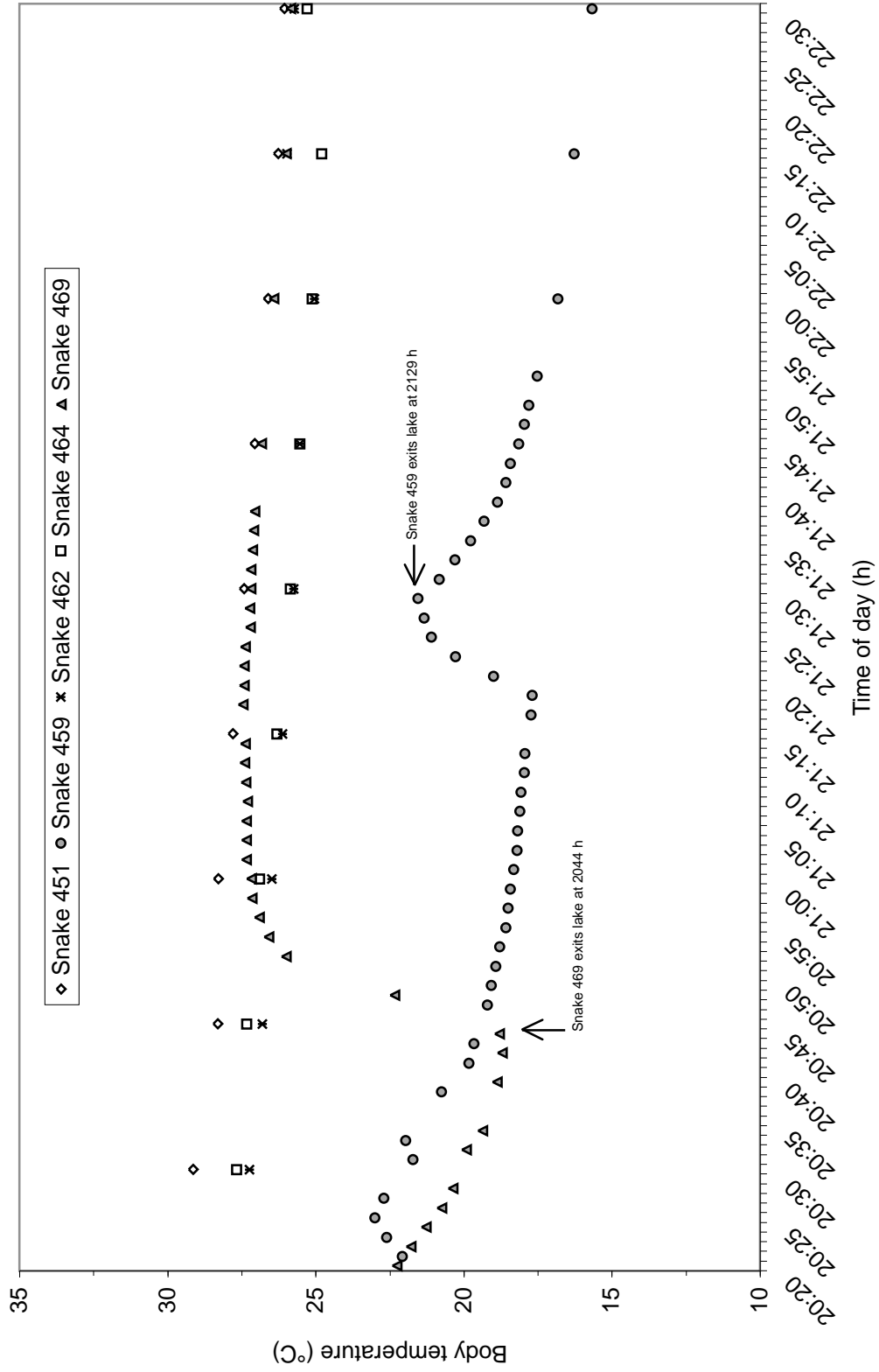


Figure 34. Body temperature profiles of five northern water snakes, one of which remained in Lake Michigan until nightfall, on 18 June 2002.

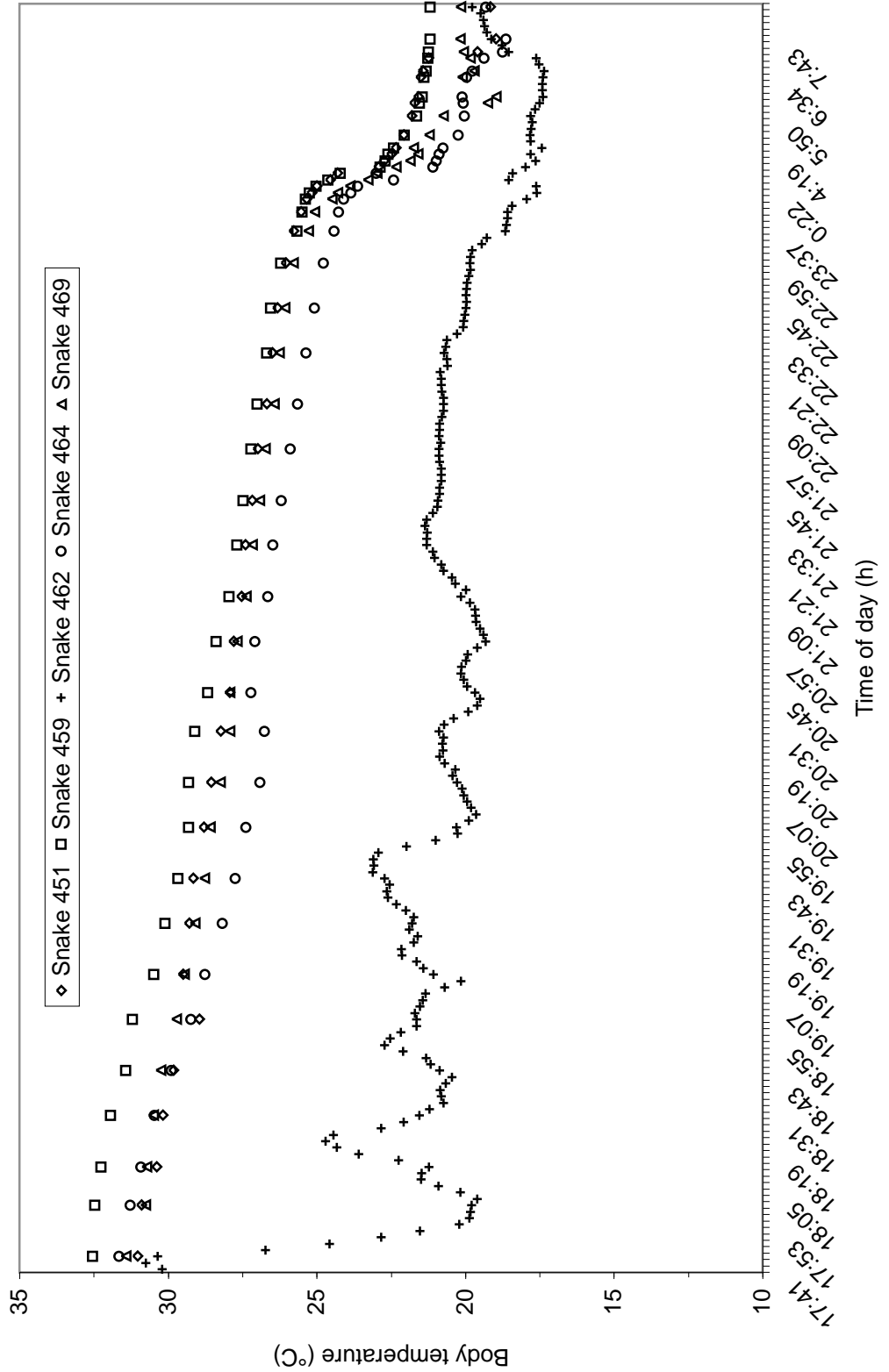


Figure 35. Body temperature profiles of five northern water snakes, one of which foraged late and remained in Lake Michigan all night, on 19–20 June 2002.

during 24 foraging excursions in 2002 averaged $16.41 \pm 1.52^{\circ}\text{C}$ (Figure 36). The variance component associated with subject (i.e. snake) did not differ from zero ($\chi^2 = 1.0$, $df = 1$, $P > 0.1$), nor did the variance component associated with occasion ($\chi^2 = 1.0$, $df = 1$, $P > 0.1$). The lowest recorded lake temperatures available to the snakes during these excursions averaged $14.35 \pm 1.77^{\circ}\text{C}$.

Thermal Compensation

The mean temperature experienced by transmitter-implanted snakes while not in Lake Michigan and when $T_e > 30^{\circ}\text{C}$ was $31.35 \pm 1.48^{\circ}\text{C}$ in 2001 and $30.54 \pm 0.32^{\circ}\text{C}$ in 2002. Snakes did not elevate T_b to above-normal levels during the hours prior to ($T_b = 30.52 \pm 0.87^{\circ}\text{C}$; $t = 0.053$, $P = 0.960$, $n = 5$) or after ($T_b = 29.54 \pm 1.45^{\circ}\text{C}$; $t = 1.34$, $P = 0.253$, $n = 5$) foraging in the lake in 2002. Similarly, they did not exhibit abnormally high T_b s the day before ($T_b = 30.89 \pm 0.36^{\circ}\text{C}$; $t = -1.96$, $P = 0.121$, $n = 5$) or after ($T_b = 30.51 \pm 0.84^{\circ}\text{C}$; $t = 0.091$, $P = 0.932$, $n = 5$) those days during which they foraged in 2002. Dunn-Sidak adjustment of α for the four comparisons involving the seasonal mean T_b of snakes was made for each analysis ($\alpha' = 0.0127$). Too few data were available from 2001 to make such comparisons.

Excursion Duration versus T_b in the Laboratory

Table 3 summarizes the activity of the nine northern water snakes used in the laboratory study. Total time spent in the water by snakes differed significantly among the three temperature treatments ($F_{2,4} = 30.36$, $P = 0.004$). Snakes in the cold water treatment spent significantly less time in the water than did snakes in the two warmer treatments ($F_{1,2} = 49.04$, $P = 0.020$), but there was no difference in time spent in the

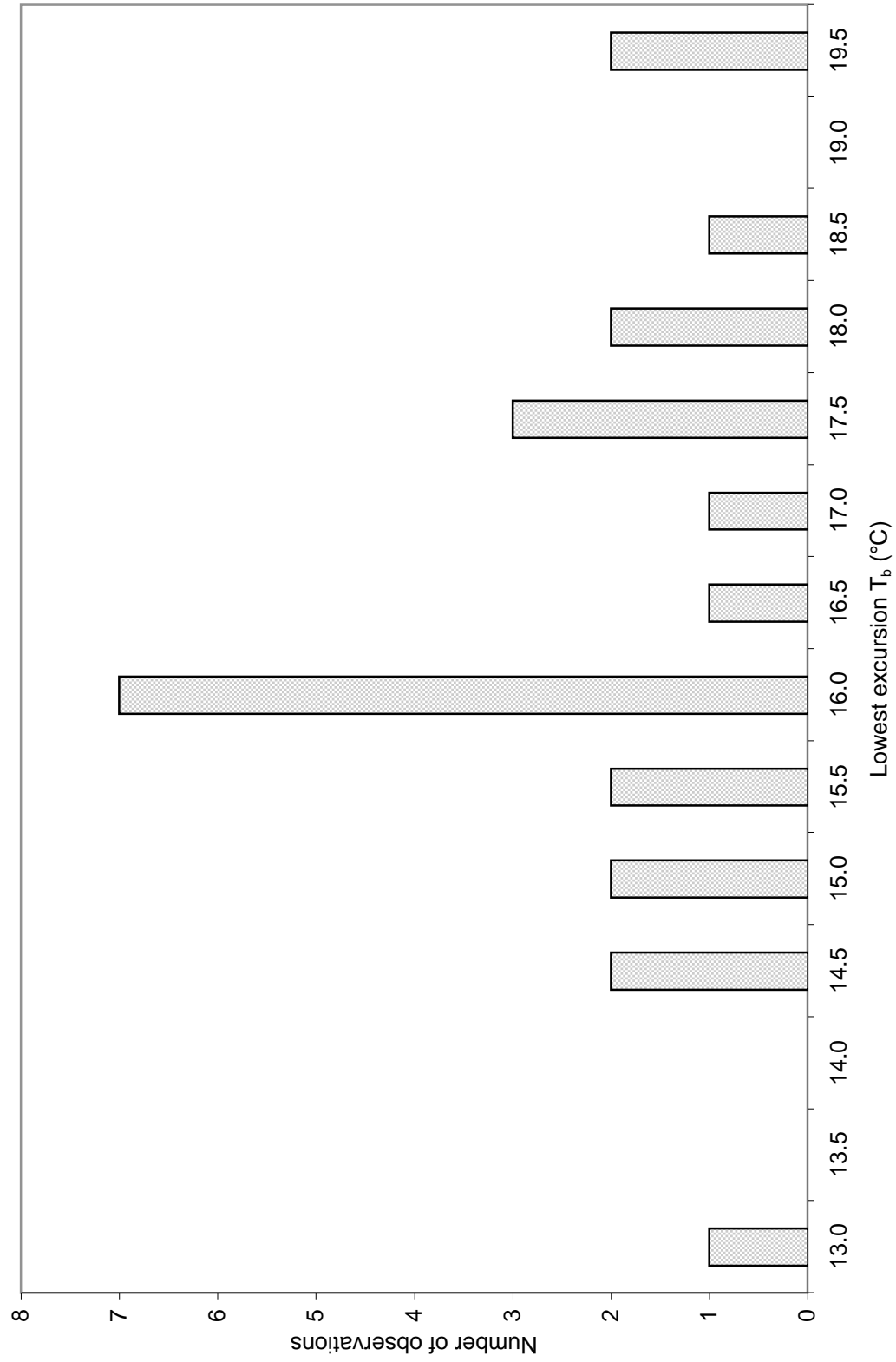


Figure 36. Frequency histogram of the lowest body temperatures experienced by telemetered snakes in 2002.

Table 3. Mean frequency and duration (in minutes) of excursions made by northern water snakes into pools of water of different temperature during 48-hour trial periods.

	Temperature Treatment		
	Low (16–17°C)	Medium (20–21°C)	High (26–27°C)
Mean Number of Excursions	8.7	19.7	7.0
Mean Excursion Duration	21.9	68.5	389.4
Mean Total Time in Water	189.5	1346.9	2726.0

water between the two warmer treatments ($F_{1,2} = 15.89, P = 0.058$). Similarly, \log_{10} [mean duration of excursions] differed among treatments ($F_{2,4} = 11.33, P = 0.022$); this measure differed between the cold water treatment and the two warmer treatments ($F_{1,2} = 24.83, P = 0.038$) but not between the two warmer treatments ($F_{1,2} = 5.64, P = 0.141$). There was no difference among treatments in \log_{10} [number of excursions] ($F_{1,001,2} = 4.25, P = 0.175$). Greenhouse-Geisser adjustment of degrees of freedom was used for the analysis involving \log_{10} [number of excursions] because the assumption of sphericity was not met.

CHAPTER IV

DISCUSSION

The northern water snakes at GHNA appear to apply more than one strategy that allows them to forage in cold Lake Michigan. Like the garter snakes studied by Manjarrez and Drummond (1996) in Mexico, the snakes I observed did not forage in their available cold water body until its temperature had reached a certain threshold. In the case of the Beaver Island *Nerodia*, however, this occurred at a seasonal scale rather than a daily one. Water snakes did not enter Lake Michigan until the end of May, when T_w averaged approximately 14.5°C. Such delayed inception of foraging in the lake may have associated with it various benefits and costs. Entry into open water still cold enough to severely hamper locomotion could clearly be costly by effecting both an increase in susceptibility to predation and a decrease in foraging efficiency (Greenwald, 1974; Stevenson et al., 1985). In addition, the latter might elevate costs beyond a reduction in prey capture rate by bringing with it the need to remain in the lake longer. This would further increase time spent at sub-optimal temperature and affect physiological processes other than those involved only in motor function.

Among the potential benefits of seasonally delaying entry into Lake Michigan might be an increased probability of successfully reproducing. Throughout the season, and especially through late May, most of the water snakes observed at GHNA spent the majority of their time in the terrestrial activity area. In fact, no snakes were found on the Lake Michigan side of the study site, the portion East of Gull Harbor Drive, prior to 28 May. By remaining there early in the year, snakes likely have more opportunities to

exchange gametes soon enough that sufficient time remains for gestation and parturition to occur before environmental temperatures drop in the fall. Additionally, the potential cost of not foraging in Lake Michigan early, particularly in terms of reproductive energetics, may be offset by a limited availability of anurans in the terrestrial activity area. At least two of the telemetered snakes fed upon what were almost certainly American toads (*Bufo americanus*) on three occasions there during May. Although the terrestrial activity area had a great deal of cold standing water through which the snakes had to swim or crawl while searching for mates and toads, the grasses and sedges that predominated the area provided cover. Thus the snakes' vulnerability to predation because of reduced locomotory ability was mitigated there by an ability to remain somewhat invisible.

The primary cue used by snakes in their decision to begin foraging in Lake Michigan for the season is unknown, but it is quite possibly not a thermal one. By the time of initial entry into the lake, operative temperature at the study site regularly exceeded the published MST of northern water snakes as well as the mean T_b of the snakes on land throughout both seasons here when T_e exceeded 30°C. Thus snakes could, and did, achieve T_b s within their preferred range well before they began foraging in the lake. Remote detection of lake temperature is unlikely, though it is conceivable that correlated information could be carried in the form of the temperature of air blown inland from the shore.

The arrival of carp, and possibly sculpin, at the site was almost certainly detected by the snakes, and Drummond's (1979) experiments indicate *N. s. sipedon* will orient to water that emits airborne fish odors. However, it is unknown which taxon, if either,

might have been responsible for attracting snakes to the lake. *Cottus bairdi* is the primary prey of water snakes that forage in Lake Michigan in the Beaver Archipelago (Meyer, 1992; Bowen, 2002). Limited data suggest that these fish do not seek deeper waters (Deason, 1939), presumably even in winter, but Carbone (1993) found that sculpin left his study site in August. Thus my observation of the arrival of *Cottus* to GHNA in May might not be simply an artifact of moderate shifts in patch use by the fish. This does not mean that the snakes were definitely responding to odors from the sculpin, however. Gove and Burghardt (1975) demonstrated that northern water snakes are capable of discriminating odors of different genera of fish, but they also showed that laboratory-reared snakes would respond to chemical stimuli from fish that were not natural prey in the wild. If carp and sculpin have regularly arrived at GHNA simultaneously for at least a few years, or if the sculpin are normally there prior to carp arrival, response by the water snakes to the carp odor would often be reinforced by successful fish captures. Given all of these considerations, it may be a chemical cue rather than a thermal one that is directly responsible for the timing of initial entrance of snakes into the lake. Regardless of the mode of the responsible stimulus, lake temperature may still be an accurate predictor of snake entry, especially if it influences the seasonal timing of fish arrival.

Once snakes began foraging in Lake Michigan, they did so during the day throughout their activity season. The cue primarily responsible for motivating snakes to enter the lake on a day-to-day basis was likely hunger, but temperature also appears to have been involved in determining when, both daily and hourly, snakes foraged. In the spring especially, as seen in 2002, snakes typically went into the lake only if T_e exceeded

30°C (Figures 11 & 15). Unlike the water snakes of warmer regions (Ernst & Barbour, 1989), *N. s. sipedon* here exhibited no apparent shift toward nocturnal activity. This was likely caused by several factors. At night, operative temperature at GNHA dipped below 15°C in the spring and 20°C in the summer, and lake temperature was not appreciably higher than operative temperature during these times, even during the latter half of the activity season. Snakes often spent the night in three small inland ponds (see Figure 4) where they could maintain higher T_b s during those hours than they would have had they remained on dry land, a behavior common among water snakes (Osgood, 1970; Meyer, 1992). Thus they could remain warmer throughout the night if they did not stay in the lake after sunset.

Another possible reason that snakes remained diurnal relates to their homing ability. Most individuals typically returned to the center of the terrestrial activity area after foraging, presumably because it was the most suitable place for them to rest and thermoregulate. However, location of this central area may have been more difficult to achieve at night than during the day, especially if visual landmarks such as large rocks were important in addition to the celestial cues used for general orientation (Newcomer et al., 1974). It is probable, though, that the most important factor determining the timing of foraging by the water snakes here is the activity period of the sculpin upon which they feed. These fish are inactive during the day (Emery, 1973), and this makes them relatively easy targets while they rest beneath the cobble explored by the snakes.

While foraging in Lake Michigan, northern water snakes exhibited numerous T_b fluctuations, particularly during the colder part of their activity season. The reasons for these changes in body temperature were not always evident, but the greatest T_b increases

were typically associated with visits to the shoreline. Occasionally, shoreline visits were obviously made in order to facilitate fish ingestion, but this was not the norm, and prey were typically swallowed underwater at the site of capture. It is possible that snakes would return to shallower waters to rest, but the effort likely required to swim ashore and then back out against the waves seems more costly than remaining stationary while anchored farther out. Although the *N. sipedon* that Carbone (1993) observed never foraged more than 10 m away from shore, GHNA water snakes often visited shoals as far as 50–70 m distant. I very rarely observed individuals in water deeper than their own length, however. Instead, snakes foraged in places where they could pause with their back to the waves and their caudal region anchored in the cobble. It seems, therefore, that the water snakes may have been coming ashore for thermoregulatory purposes.

If this were true, then the snakes employed a second strategy to cope with the low water temperatures. One of my initial hypotheses was that snakes might exit the water once their T_b was lowered to a certain threshold. However, I failed to consider that the temperature of water at the shoreline would be much higher than that where the snakes foraged. This was the case, of course, a fact that resolved the greatest problem associated with my hypothesis. Once the seasonal temperature threshold had been surpassed, the amount of time snakes could spend foraging on a particular day was not limited by water temperature because they could simply make brief visits to warmer water along the shore if their T_b became uncomfortably or dangerously low. As a result of this shuttling behavior, snakes appear to have been free to forage as long as necessary to capture sufficient prey, the only constraint being that they leave the water before sunset during most of the year.

The variance components analysis revealed no systematic difference between snakes of the lowest body temperatures experienced by individuals while in Lake Michigan. Given this, the excursion T_b threshold apparently shared by the study subjects was approximately 16°C. This might serve as a general estimate applicable to most snakes on most occasions. A stricter estimate of this threshold, and one that agrees well with the seasonal water temperature threshold discussed above, is 14.5°C. Only once did a snake exhibit a T_b below this, and it appeared to have great difficulty swimming at the time. Thus the voluntary minimum T_b of *Nerodia sipedon* might more accurately be considered to be 14.5°C rather than 16°C as previously published (Brattstrom, 1965).

Hailey and Davies (1987) described *Natrix maura* as being a K thermoregulator, continuing to thermoregulate after its body had reached a certain temperature plateau. This would seem also to apply to many other snake species, including the garter snakes studied by Peterson (1987). Many lizards, on the other hand, can be classified as r thermoregulators, defined by Hailey and Davies (1987) as those that thermoregulate only until the target T_b is reached and then carry out the activities for which that temperature is required. The *Nerodia sipedon* that forage in Lake Michigan on Beaver Island might be described as both r and K thermoregulators. During the course of most days, the snakes on land could be seen basking regularly, and they maintained a relatively high temperature (~30°C) throughout. While foraging, however, their T_b would fall far below that at which they would normally plateau. This was followed by an increase in T_b that brought it back to within the range at which the snakes are most often observed (21–35°C; Kitchell, 1969), presumably so that they could continue to forage.

In the laboratory, snakes spent less time in water that was cold than in water that was warm. This was expected and seems in agreement with the lack of overnight stays in Lake Michigan. On the other hand, the absence of a correlation between T_b and excursion duration in the field was surprising. Shuttling between deep and shallow waters moderated body temperature and enabled snakes to extend their foraging periods. Duration of foraging excursions also increased with the time elapsed since a snake's most recent excursion. These factors, and their possible contribution to the existence of two outliers (see Figure 23), may explain why no relationship was found between T_b of free ranging snakes and the duration of their foraging excursions. The laboratory experiment involved well fasted snakes, presumably making all equally likely to forage as long as possible, and provided no option for individuals to shuttle between warm and cold water. Thus the arenas seem to have presented conditions similar to those found at GHNA at the beginning of the activity season rather than conditions faced by snakes on a daily basis. This apparently made the study subjects in the coldest treatment reluctant to go into the water, which, like the more general estimate of the excursion T_b threshold, was approximately 16°C.

During foraging, mean T_b was approximately 25°C in 2001 and 20°C in 2002, and excursions often took the better part of a day. Thus it is somewhat surprising, particularly for 2002, that I found no evidence of thermal compensation before or after trips to the lake. Given the duration and frequency of foraging excursions, these snakes may spend as much as 20% less of their time near optimal T_b than do *N. sipedon* that do not forage in cold water. Because this could negatively affect fitness, further investigation is warranted. Specifically, direct comparison needs to be made between this or a similar

population and one whose members forage in warmer waters (such as in a marsh) but at the same latitude and altitude (i.e. in a similar climate). Among the characteristics that should be compared are: dates of egress, courtship and copulation, parturition, and ingress; MST; mean T_b held in the field; and thermal-exploitation indices (see Brown & Weatherhead, 2000). Such a study might reveal, among other things, whether or not snakes from a population such as this one require more time for gestation, maintain higher T_b s overall, or thermoregulate more precisely than snakes that come from a population that does not exhibit the cold-water foraging behavior discussed here.

LITERATURE CITED

- Bennett, A. F. 1982. The energetics of reptilian activity. In: *Biology of the Reptilia Vol. 13*, C. Gans and F. H. Pough, eds. Academic Press, New York, pp. 155–199.
- Birchard, G. F., Black, C. P., Schuett, G. W., and V. Black. 1984. Influence of pregnancy on oxygen consumption, heart rate and hematology in the garter snake: Implications for the "cost of reproduction" in live bearing reptiles. *Comparative Biochemistry and Physiology A* 77:519–523.
- Bowen, K. D. 2002. Morphology and diet of the northern water snake, *Nerodia sipedon sipedon*, in the Beaver Archipelago of Lake Michigan. Unpublished M.S. thesis, Central Michigan University, Mt. Pleasant.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. *The American Midland Naturalist* 73:376–422.
- Brown, E. E. 1940. Life history and habits of the northern water snake, *Natrix sipedon sipedon* Linne. Unpublished Ph.D. dissertation, Cornell University, Ithaca, New York.
- Brown, E. E. 1958. Feeding habits of the northern water snake, *Natrix sipedon sipedon* Linnaeus. *Zoologica* 43:55–71.
- Brown, G. P., and P. J. Weatherhead. 2000. Thermal ecology and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Ecological Monographs* 70:311–330.
- Brown, W. S., and W. S. Parker. 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). *Journal of Herpetology* 10:247–249.

- Carbone, H. M. 1993. Efficient habitat and prey selection by the northern water snake, *Nerodia sipedon*. Unpublished M.S. thesis, Central Michigan University, Mt. Pleasant.
- Charland, M. B. 1995. Thermal consequences of reptilian viviparity: Thermoregulation in gravid and nongravid garter snakes (*Thamnophis*). *Journal of Herpetology* 29:383–390.
- Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* 83:265–296.
- Deason, H. J. 1939. The distribution of cottid fishes in Lake Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* 24:105–115.
- Drummond, H. M. 1979. Stimulus control of amphibious predation in the northern water snake (*Nerodia s. sipedon*). *Zeitschrift für Tierpsychologie* 50:18–44.
- Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *Journal of the Fisheries Research Board of Canada* 30:761–774.
- Ernst, C. H., and R. W. Barbour. 1989. *Snakes of Eastern North America*. George Mason University Press, Fairfax, VA.
- Feaver, P. E. 1977. The demography of a Michigan population of *Natrix sipedon* with discussions of ophidian growth and reproduction. Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor.
- Finkler, M. S., and D. L. Claussen. 1999. Influence of temperature, body size, and inter-individual variation on forced and voluntary swimming and crawling speeds in *Nerodia sipedon* and *Regina septemvittata*. *Journal of Herpetology* 33:62–71.

- Gove, D., and G. M. Burghardt. 1975. Responses of ecologically dissimilar populations of the water snake *Natrix s. sipedon* to chemical cues from prey. *Journal of Chemical Ecology* 1:25–40.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141–148.
- Greenwald, O. E., and M. E. Kanter. 1979. The effects of temperature and behavioral thermoregulation on digestive efficiency and rate in the corn snake (*Elaphe guttata guttata*). *Physiological Zoology* 52:398–408.
- Gregory, P. T. 1982. Reptilian hibernation. In: *Biology of the Reptilia Vol. 13*, C. Gans and F. H. Pough, eds. Academic Press, New York, pp. 53–154.
- Hailey, A., and P. M. C. Davies. 1986. Effects of size, temperature and condition on activity metabolism and defence behaviour of the viperine snake, *Natrix maura*. *Journal of Zoology, London (A)* 208:541–558.
- Hailey, A., and P. M. C. Davies. 1987. Activity and thermoregulation of the snake *Natrix maura*. I. r and K thermoregulation. *Journal of Zoology, London* 213:71–80.
- Hardy, D. L., Sr., and H. W. Greene. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:25–27.
- Heckrotte, C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis s. sirtalis*. *Copeia* 1967:759–763.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. In: *Biology of the Reptilia Vol. 12*, C. Gans and F. H. Pough, eds. Academic Press, New York, pp. 25–91.

- King, R. B. 1986. Population ecology of the Lake Erie water snake, *Nerodia sipedon insularum*. *Copeia* 1986:757–772.
- Kitchell, J. F. 1969. Thermophilic and thermophobic responses of snakes in a thermal gradient. *Copeia* 1969:189–191.
- Lillywhite, H. B. 1987. Temperature, energetics, and physiological ecology. In: *Snakes: Ecology and Evolutionary Biology*, R. A. Seigel, J. T. Collins, and S. S. Novak, eds. MacMillan, New York, pp. 422–476.
- Lutterschmidt, W. I., and H. K. Reinert. 1990. The effect of ingested transmitters upon the temperature preference of the northern water snake, *Nerodia s. sipedon*. *Herpetologica* 46:39–42.
- Manjarrez, J., and H. Drummond. 1996. Temperature-limited activity in the garter snake *Thamnophis melanogaster* (Colubridae). *Ethology* 102:146–156.
- Meyer, C. S. 1992. Foraging, thermal and spatial ecology of the northern water snake (*Nerodia sipedon*). Unpublished M.S. thesis, Central Michigan University, Mt. Pleasant.
- Nelson, K. J., and P. T. Gregory. 2000. Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. *Journal of Herpetology* 34:32–40.
- Newcomer, R. T., Taylor, D. H., and S. I. Guttman. 1974. Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). *Herpetologica* 30:194–200.
- Osgood, D. W. 1970. Thermoregulation in water snakes studied by telemetry. *Copeia* 1970:568–571.

- Passek, K. M., and J. C. Gillingham. 1997. Thermal influence on defensive behaviours of the eastern garter snake, *Thamnophis sirtalis*. *Animal Behaviour* 54:629–633.
- Peterson, C. R. 1987. Daily variation in the body temperatures of free-ranging garter snakes. *Ecology* 68:160–169.
- Pough, F. H., and C. Gans. 1982. The vocabulary of reptilian thermoregulation. In: *Biology of the Reptilia Vol. 12*, C. Gans and F. H. Pough, eds. Academic Press, New York, pp. 17–23.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Quinn, H., and J. P. Jones. 1974. Squeeze box technique for measuring snakes. *Herpetological Review* 5:35.
- Reinert, H. K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- Robertson, I. C., and P. J. Weatherhead. 1992. The role of temperature in microhabitat selection by northern water snakes (*Nerodia sipedon*). *Canadian Journal of Zoology* 70:417–422.
- Scribner, S. J., and P. J. Weatherhead. 1995. Locomotion and antipredator behaviour in three species of semi-aquatic snakes. *Canadian Journal of Zoology* 73:321–329.
- Stevenson, R. D., Peterson, C. R., and J. S. Tsuji. 1985. The thermal dependence of locomotion, tongue-flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiological Zoology* 58:46–57.
- Tu, M. C., and V. H. Hutchison. 1994. Influence of pregnancy on thermoregulation of water snakes (*Nerodia rhombifera*). *Journal of Thermal Biology* 19:255–259.

- Weatherhead, P. J., and I. C. Robertson. 1992. Thermal constraints on swimming performance and escape response of northern water snakes (*Nerodia sipedon*). *Canadian Journal of Zoology* 70:94–98.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th ed. Prentice-Hall, Inc., Upper Saddle River, NJ.
- Zug, G. R., Vitt, L. J., and J. P. Caldwell. 2001. *Herpetology: An Introductory Biology of Amphibians and Reptiles*, 2nd ed. Academic Press, San Diego.