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Sexual size dimorphism and demography,
thermoregulation and mating activity of
northern water snakes (*Nerodia sipedon*).

by

Gregory Paul Brown

A thesis submitted to
The Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy

Department of Biology

Carleton University

Ottawa, Ontario

August 1997

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Sexual size dimorphism and demography,
thermoregulation and mating activity of
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submitted by Gregory Paul Brown

In partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

Abstract

A number of selective forces interact to determine the body size of animals. Differences in the net selective pressures acting on body size result in sexual size dimorphism (SSD). Understanding the factors that maintain SSD requires determining both why one sex is large and why the other sex is small. Here I attempt to identify factors affecting body size in northern water snakes (*Nerodia sipedon*) to explain their apparently paradoxical female-biased SSD. Despite large males having an advantage in competition for mates, males are smaller than females.

A nine year mark-recapture study indicated that females delayed maturity and invested in growth for one year more than males. By maturing later, females can increase lifetime reproductive success through a fecundity advantage associated with large size. Survivorship of subadult females also increased with body size. By investing in rapid growth, juvenile females can simultaneously increase their survivorship and future fecundity. I rejected the hypothesis that survival selection favours small male size. Mean survivorship did not differ between the sexes and male survivorship was independent of body size. However, it remains possible that males pursue a seasonal-survival strategy wherein small males have a survival advantage following the mating season.

Thermoregulatory indices suggest that *N. sipedon* are

moderate thermoregulators, though there are few data from other snakes species for comparison. Body temperature data supported the 'seasonal-survival' strategy hypothesis. Males decreased thermoregulatory behaviour following the mating season, possibly to compensate for high mortality associated with mating activity. Gravid females increased thermoregulation during gestation which may relate to a survival cost associated with reproduction.

I also tested the hypothesis that selection favours small male size through increased mate-searching ability. Although estimated mating success increased with home range size during the breeding period, home range size was not related to male size. Consistent with the seasonal-survival strategy, movement and activity of males tended to decrease following the mating season but the difference was not significant. Although I found no advantage associated with small male size, subtle forms of mating advantage (e.g., sperm competition or female choice), could favour smaller males.

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General Introduction

The difference in body size between adult male and female animals varies substantially among species (Lande 1980, Hedrick and Temeles 1989, Shine 1989). For each species, the direction and degree of sexual size dimorphism (SSD) is thought to reflect the evolutionary consequences of differences between males and females in the costs and benefits of a particular body size. Darwin (1871) proposed three adaptive explanations to account for the occurrence of SSD: sexual selection, fecundity selection and ecological divergence.

Sexual selection is most commonly invoked to explain SSD in instances where males are the larger sex. If males physically compete with one another for access to mates and if larger males win these competitions more often, then selection will favour increased male body size. Similarly, large male body size will be favoured if larger males can better inseminate females forcibly or obtain more mates because they are preferred by females. These same mechanisms can be used to explain female-biased SSD in species in which the sex roles are reversed (e.g., Gwynne 1984).

The evolution of female-biased SSD is usually ascribed to a 'fecundity advantage' for large females (Semlitsch and Gibbons 1982, Shine 1988, Wiklund and Karlsson 1988). In many species, litter size increases with female body size, probably because large females simply have more room in

which to carry offspring (Shine 1988). However, the mere existence of a positive correlation between female size and fecundity is not adequate evidence to conclude that fecundity advantage is the basis for the evolution of female-biased SSD (Shine 1988).

SSD could also arise through natural selection if the sexes are adapted to fill different ecological niches. Slatkin (1984) identified three scenarios under which ecological divergence might result in different body sizes of males and females. First, body sizes may diverge to decrease competition for food between the sexes. If males and females specialize on different sizes or types of food, disruptive selection could result in sexual dimorphism either in size or in some feeding structure (Shine 1991). Second, two or more equally successful optimal body sizes may exist for a species and males and females may converge on different optima. Third, the different social or reproductive roles of males and females may result in different energetic, behavioral or habitat requirements. Different selection pressures may be acting on males and females to fit them to their particular niches and could result in sexual dimorphism (Lande 1980, Shine 1989). Ecological divergence hypotheses are rarely invoked to explain SSD because their predictions are less precise and more difficult to test than those of competing hypotheses (e.g., sexual selection) (Shine 1989).

Nonadaptive factors could also affect the direction and degree of SSD exhibited by a species. SSD could have evolved far back in a species' phylogenetic history and one sex may be larger than the other simply because that pattern of SSD was present in an ancestral species (Fairburn 1990). The original selective pressures that led to the evolution of SSD may no longer be operating among the descendants. The degree of SSD exhibited by a species may also be influenced by allometric effects. Male size, relative to female size, tends to be larger in large species. Thus, in species with male-biased SSD, the degree of SSD increases with the size of the species and in species with female-biased SSD, the degree decreases with species size (Fairburn 1990, Fairburn and Preziosi 1994). Cheverud et al. (1985) found that phylogenetic and allometric factors accounted for over 80% of the variation in SSD observed in a sample of primate species. Barry (1991) performed a similar analysis of the explanatory power of phylogeny and allometry on SSD among snake species. She found that although both factors were statistically significant, over 70% of the variation in snake SSD remained unexplained. Although no male-biased SSD occurs amongst natricine snakes, the degree of female-biased dimorphism varies considerably, suggesting that the factors affecting SSD may be operating within phylogenetic constraints.

Explaining the evolution or maintenance of SSD is

complicated by the possibility that all of the factors noted above could interact to impose different advantages and constraints on body size in each sex. Ultimately, the existence and degree of SSD is determined by differences in net selective pressures acting on body size in each sex (within the constraints imposed by phylogeny and allometry) (Arak 1988, Hedrick and Temeles 1989, Preziosi and Fairburn 1996). Thus, in investigating SSD it is useful to identify as many of the possible costs and benefits associated with different body sizes in both sexes.

Ideally the goal of such studies should be to determine not only why one sex gets big, but also why the other sex stays small (Montgomerie and Lundberg 1989, Weatherhead et al. 1995, Preziosi and Fairburn 1996). For instance, in a species with male-biased SSD and male-male combat, intrasexual selection may explain why it is advantageous for a male to be larger than other males, but it is not a complete explanation for why males are larger than females (Greenwood and Adams 1987). Furthermore, if body size characteristics are under polygenic control and given a high degree of genetic correlation between the sexes, then an increase in body size of one sex should also increase body size in the other sex unless there is counteracting selection favouring smaller size (Lande 1980).

In this study, I attempt to identify various factors affecting adult body size of male and female northern water

snakes, *Nerodia sipedon*. Water snakes present an apparent paradox in their pattern of SSD. Although males compete physically with one another for access to females and larger males appear to have an advantage in these competitions, adult males reach only half the size of females. There are numerous other cases in which the observed pattern of SSD is opposite to that predicted by contemporary patterns of sexual selection. Male toads (*Bufo bufo*) physically compete to dislodge one another from mating positions on females. Although large males are better able to dislodge small males, the observed SSD is female-biased (Davies and Halliday 1977). In male water striders (*Aquarius remigis*), sexual selection acting on male genital-length favours increased male body size, yet males are smaller than females (Preziosi and Fairburn 1996). In European grass snakes (*Natrix natrix*), larger males can better displace the tails of smaller rivals to gain access to females in mating aggregations and yet females are significantly larger than males (Madsen and Shine 1993a). Similarly, larger male European adders (*Vipera berus*) are more often victorious in combat with rival males for access to females, yet SSD is female-biased (Madsen et al. 1993). In all these cases, factors other than the apparent intrasexual selection on males must affect the pattern of SSD.

My goal in this thesis is to identify potential selective forces maintaining the apparently paradoxical

female-biased SSD. To do so, I determined how the sexes differed in the relationships between body size and various demographic and behavioural factors. Data were obtained through mark-recapture, radio-telemetry and observational field studies on *N. sipedon* populations in the Rideau Lakes region of eastern Ontario.

The focus of the first chapter is the demography of northern water snakes. Demographic information is necessary to substantiate the existence of SSD and can also provide insight into selective factors affecting sexes or sizes differently. Specifically, I investigate the relationships between body size and growth, survival and female fecundity to determine whether these factors can aid in explaining the observed female-biased SSD. I test the hypotheses that i) SSD in water snakes is a result of different growth rates (rather than different survivorship) between the sexes, ii) small male size is favoured by selection for increased survivorship and iii) large female size is favoured through selection for increased fecundity.

Chapters two and three describe the thermal relations and thermoregulation of *N. sipedon*. I investigate how the environment affects the snakes' ability to maintain optimum body temperatures and whether the amount of time spent at the preferred body temperature differs between sexes or among size or reproductive classes. Determining the amount of time spent thermoregulating by different classes of

individuals may provide insight into patterns of survivorship identified in Chapter one that are relevant to SSD. Specifically, I test the hypothesis that temporal differences in thermoregulation of males will reflect a seasonal-survival strategy.

Chapter four addresses how rates of movement and activity differ among sexes and body sizes of water snakes and how these factors relate to reproductive behaviour. I specifically address the hypothesis that small males have an energetic or mobility advantage that allows them to locate more reproductive females.

Study Species

Nerodia sipedon is a medium sized (up to 135 cm snout to vent length, SVL), stout-bodied natricine (Cook 1984). Adult females are up to twice the length of males. They occur throughout much of eastern North America, from Colorado to the Atlantic coast and from Ontario (south of Sudbury) to Georgia. Four subspecies are recognized; my study concerns the most northerly occurring subspecies, *N.s. sipedon*. These snakes are largely aquatic and inhabit most fresh-water habitats throughout their range. Their diet consists almost entirely of minnows, fish and amphibians.

In the spring, soon after emergence from hibernation, females become sexually attractive and are often simultaneously courted by several males. The resulting

mating aggregations may consist of up to a dozen males and a single female. Females are viviparous; follicles develop during May and early June and are ovulated and fertilized in mid to late June. Gestation occurs throughout July and August and parturition takes place in late August or early September. More comprehensive treatments of various aspects of the natural history of *N. sipedon* can be found elsewhere (Bauman and Metter 1977, Feaver 1977, King 1986, Barry et al. 1992, Robertson and Weatherhead 1992, Weatherhead et al. 1995, Brown and Weatherhead 1997).

CHAPTER ONE

Demography of northern water snakes: effects of growth and survivorship on sexual size dimorphism.

Introduction

Studying the demography of a population involves determining the distribution of ages and sizes of individuals, rates of birth, death and migration and estimation of population size and density (Williams 1966, Krebs 1989). Such studies are often done to facilitate management of game animals, conservation of endangered species or, for their own sake, to document population parameters. Increasingly, however, demographic studies are being used as tools to test predictions from evolutionary theory involving life history and sexual size dimorphism (SSD) (Dunham et al. 1988, Madsen and Shine 1992, 1993b, 1994). In this chapter, I use data from a nine year mark-recapture study to investigate the demography of a population of northern water snakes (*Nerodia sipedon*) to identify factors involved in the evolution or maintenance of their female-biased SSD.

SSD is widespread among reptiles (Shine 1978, 1994, Berry and Shine 1980, Fitch 1981). Among snakes, approximately two thirds of species exhibit female-biased SSD (Shine 1994). Paradoxically, however, there is evidence that intrasexual selection favours large males in some of

these species (including *N. sipedon*) (Madsen and Shine 1993a, Madsen et al. 1993, Shine 1994, Weatherhead et al. 1995). This incongruity leads to the expectation that unless some selective pressure is counteracting the intrasexual selection for large males, genetic correlations between the sexes should result in males becoming as large as females (Weatherhead et al. 1995).

When investigating sex differences in body size, an essential insight provided by demographic data is whether or not sexual size dimorphism (SSD) actually exists in a population. Typically, the existence of SSD in a population is determined through a significant difference in mean body size among a sample of adult males and females. Thus, the determination and measurement of SSD is sensitive to any methodological or ecological factors that could result in sexual differences in the age or size of individuals sampled (Dunham and Gibbons 1990). Sampling bias could arise, for instance, if the presence of large aggressive males affects the spatial distribution or behaviour of smaller males and results in their under-representation in capture samples (e.g., Andrews and Stamps 1994, Watkins 1996). This would lead to overestimation of mean male-size and erroneous conclusions regarding SSD.

Differences in survival between the sexes could also result in misrepresentation of SSD. If one sex experiences higher survivorship, most of the old individuals in a sample

will be members of that sex. In species with indeterminate growth, older individuals will also be larger. Several instances of apparent SSD result from sex differences in survival and age distribution (e.g., Howard 1981, Andrews and Stamps 1994, Stamps 1993). Weatherhead et al. (1995) found that females were significantly larger than males in my study population of *N. sipedon*. Based on preliminary estimates of age, they also concluded male and female age distributions did not differ. My first goal in this study was to verify these results using a larger data set and more refined estimates of age.

Comparison of growth curves of males and females with similar age distributions is a preferred means of determining the existence of SSD (Stamps 1993). Differences in rates of growth and body size can then be quantified and compared statistically (Van Devender 1978, Dunham 1978). Comparisons of complete growth curves not only allows reliable determination of the existence of SSD, but can also provide insight into the proximate cause of the SSD (Shine 1990, Stamps 1993). Different hypotheses regarding the evolution of SSD make different predictions regarding where the growth curves should diverge. For example, if SSD is due to differences in size at maturity (and not age at maturity), juvenile growth rates would be expected to differ. If SSD is a result of sex differences in the proportion of energy allocated to reproduction, then post-

maturation growth trajectories should differ (Shine 1990, Stamps 1993). Based on the difference in body sizes and the similarity of ages between males and females, Weatherhead et al. (1995) concluded that the SSD observed in my study population must result from different growth rates, although they did not actually compare male and female growth. Thus, my second objective in this study was to compare growth trajectories of male and female *N. sipedon* to confirm that a sex difference in growth was the proximate cause of the SSD. By quantifying growth rates, I also wished to determine when the growth curves of males and females diverged to identify which potential selective forces might be affecting SSD.

If SSD is a result of different growth strategies rather than different age distributions, the interesting problem then becomes identifying factors involved in the evolution or maintenance of SSD. The body size of each sex is the product of numerous selective pressures (Hedrick and Temeles 1989, Fairburn 1990, Arak 1988). Two important factors affecting the costs and benefits of growth in each sex are the relationships among body size and fecundity and survivorship (Ydenberg and Forbes 1991). If one sex achieves a greater increase in offspring production through faster growth than the other sex, then selection may favour larger body size in that sex (Shine 1988). Similarly, differences between the sexes in the survival consequences of large body size could affect the evolution of SSD (Arak 1988, Ydenberg

and Forbes 1991, Weatherhead and Clark 1994). If the effects of fecundity and survival on body size operate in different directions in each sex, stabilizing selection may maintain different body sizes in males and females (Selander 1972). Weatherhead et al. (1995) tested the hypothesis that sexual selection favoured small males in the population of water snakes studied here. They found that in one of two years, larger males appeared to have an advantage in the intense mating competitions among males. Thus, small male size was not maintained by a mating advantage. They concluded that since males appeared to have higher survival than females, small male size might instead be favoured through survival selection.

Although sex differences in survival have been identified among reptiles, few studies have investigated size-specific survivorship or its contribution to the evolution or maintenance of SSD in reptiles (Schoener and Schoener 1982). A difference in survival between the sexes is expected if the different reproductive roles of males and females expose them to different mortality risks (Howard 1981, Arak 1988). Male water snakes are extremely active and relatively unwary during the mating season as they search for females. Their rates of movement are high (Chapter four) and they may not respond to potential threats (e.g., they will readily approach a human observer). This may result in males being both more easily detected and caught by

predators. If so, male survivorship should be lower than that of females, particularly during the mating season when they are most active. Furthermore, among male water snakes, body size may affect survival. There is evidence that large males participate in more mating aggregations than smaller males (Weatherhead et al. 1995). If reproductive activity disproportionately exposes large males to predation risk, a negative relationship is predicted between survivorship and male body size. Such a relationship would indicate that selection for survival could favour small or intermediate male size. Thus, my third goal was to investigate sex differences in survival and the relationship between body size and survival. I wished to verify that male survivorship was higher than that of females, and to determine if this difference was related to body size.

Among females, the relationship between survivorship and body size also has bearing on the fecundity advantage associated with large size. Litter size typically increases with female size among snakes, including *N. sipedon* (Brown and Weatherhead 1997). Although a positive correlation between body size and litter size indicates a benefit to large females, on its own it may not be an adequate explanation for female-biased SSD (Shine 1988). Unless energy is unlimited, post-maturity growth must occur at the expense of investment in reproduction. Thus, at a given age, larger females must have reduced or foregone reproduction

sometime in the past. This suggests that some advantage besides fecundity may be associated with large female size. Possible advantages include access to a wider range of prey or increased survivorship (Shine 1988). Therefore, the relationship between body size and survivorship of females provides additional insight into selective forces determining female size. The existence of a positive relationship between female survivorship and body size would indicate that fecundity selection could favour large female body size. My final goal was to investigate the relationships between female body size, survival and fecundity, through construction of a life table. I wished to determine how the interaction between survivorship and fecundity might affect the evolution of female body size. Because information on fecundity was not available for male snakes, a life table could be constructed for females only.

Methods

Study area

The study was conducted at two marshes approximately 1 km apart, located 10 km from the Queens's University Biological Station (QUBS) (45° 37'N, 76° 13'W). Barbs Marsh and Beaver Marsh are 4 ha and 3 ha in area, respectively, with maximum depths < 2m. Barbs Marsh is spring fed and does not have any permanent inflow or outflow channels. It is located approximately 400m from the nearest permanent waterbody.

Beaver Marsh is also spring fed but is formed by beaver dams along the watercourse. Both ponds contain numerous muskrat and beaver lodges which are used extensively by snakes for basking, mating and shelter.

Study methods

The populations of water snakes at Barbs and Beaver marshes have been studied annually since 1988 and 1990, respectively. Both marshes were usually visited several times per week during spring and summer and transects were walked throughout. Snakes were hand-captured opportunistically, then weighed, measured and individually marked by branding caudal scutes or by inserting passive integrate transponder (PIT) tags (Anitech, Markham, Ont.). During the mating season from late April to early June the marshes were visited at least once each day. Snakes captured during this period also were individually marked with spots of non-toxic acrylic paint. This allowed them to be identified at a distance in the field and for participants in mating aggregations to be identified without disturbing them. Fat content (% body fat) of each snake was estimated from measures of SVL and mass using the method and equation of Weatherhead and Brown (1996). Whole or partial carcasses of water snakes were occasionally found during surveys of the marshes. When this occurred, I attempted to sex the remains and identify the likely cause of death. Information

on the time and cause of mortality were also available for several radio-transmitted snakes (see Chapter two and four for methods). Further details of the study area and methods have been presented elsewhere (Barry et al. 1992, Robertson and Weatherhead 1992, Weatherhead and Robertson 1992, Weatherhead et al. 1995, Brown and Weatherhead 1997).

Growth calculations

An initial step in measuring growth of ectotherms in temperate climates is estimation of the annual growth period. Because snakes in the study populations spend most of the year hibernating at temperatures presumably too low to allow growth (Chapter two), the length of the annual growth period is less than 365 days. Based on body temperature and activity data gathered through radio-telemetry (Chapter two, four), I estimated that, on average, snakes could reach body temperatures sufficient for growth throughout the period between 21 April and 30 Sept each year (i.e., approximately 160 growing days).

To compare growth of males and females, I calculated separate growth curves for each sex. Annual growth increments were calculated for individuals recaptured in successive years as SVL measured in year two minus SVL in year one. (Individuals that were supplementally fed (see Chapter two) were excluded from the growth analysis). This difference in length was then divided by the number of

growing days between captures to give a rate of growth in cm/day. There were few instances where individuals appeared to decrease in length. This negative growth was assumed to have arisen through measurement error and were set to a value of zero. Growth rate was then regressed against initial SVL:

$$\text{Growth Rate} = a + b \cdot \text{SVL} \quad [1]$$

This equation is a linearized form of the von Bertalanffy growth curve (Van Devender 1978). The X-intercept in Eq. 1, where growth rate = 0, estimates asymptotic body size (A) and is calculated as $A = a/b$.

Because Eq. 1 is in differential form (i.e., change in SVL per unit time), when integrated it relates age to SVL (Van Devender 1978):

$$\text{Age} = (1/b) * \ln(a+b \cdot \text{SVL}) + c \quad [2]$$

where a and b are the same as in Eq. 1. c is the constant of integration and can be determined using the size at a known age. I used size at birth (i.e., age = 0) to calculate c (16.6 cm SVL for males, 16.8 cm SVL for females). Eq. 2 was used to estimate the age of each snake at its first capture. Age at subsequent captures was then determined by adding the time elapsed between captures to the initial age estimate. The age estimate was also used to determine the year in which each individual was born.

The von Bertalanffy equation relates size at recapture (SVL2) to previous size (SVL1) and the time spent growing

between captures (Dur):

$$SVL2 = A - (A - SVL1) * e^{-k \cdot Dur} \quad [3]$$

The two parameters, **A** and **k**, represent asymptotic body size and the characteristic growth rate, respectively. **k** describes the rate of approach to asymptotic size and is analogous to the slope (**b**) of Eq. 1. Because the von Bertalanffy growth curve is nonlinear, to compare parameters between groups (e.g., sexes, years, sites) it is necessary to estimate the parameters using nonlinear regression and calculate confidence intervals around them. Support plane confidence intervals (Schoener and Schoener 1978, Dunham 1978) were constructed around asymptotic size (**A**) and characteristic growth rate (**k**) estimates and significant differences between sexes and among years were determined from overlap of these confidence intervals.

Demography

An initial step in the analysis of mark-recapture data is the estimation of the capture probability of individuals in the study populations. To test for differences in catchability, I compared the size, sex and location of two groups of snakes known to be alive over periods of three consecutive years (Tinkle et al. 1993). The first group consisted of snakes captured in each of the three years. The second group consisted of individuals caught only in the first year and third years (i.e., snakes that 'disappeared'

for one year and then reappeared). I performed a logistic regression with SVL, sex and site as predictor variables and status in year two (i.e., captured vs. not captured) as the response variable. Thus, the regression determined whether the size, sex or location of an individual affected the probability of it being captured during a year when it was known to have been in the population.

Before constructing a life table, I wished to estimate the size of the study populations in each year of the study. This would allow me to determine whether the populations were stable, increasing or decreasing. An 'open' method of analysis was used to estimate the number of animals in each marsh because the study comprised more than two recapture periods. I used Jolly-Seber analysis (Krebs 1989) because it provides estimates of survivorship as well as population size. These survivorship estimates could be compared to direct measures of survival determined from individual capture histories. To determine whether sex or body size affected an individual's probability of survival, these factors were used as predictor variables in a logistic regression. The binary response variable ('survived' vs 'not survived') was based on whether or not the individual was recaptured in subsequent years.

I constructed a life table to summarize the manner in which survivorship, fecundity and body size interacted to affect lifetime reproductive success of females. The data

required for the life table included estimates of annual rates of survival for each age class, age at maturity, age-specific fecundity and reproductive frequency. Because male fecundity could not be readily determined, life table analysis was limited to females.

Assessing the survivorship of the zero age class (i.e., neonates) is more problematic than measuring adult survival because of low capture rates of neonates and one-year olds (see Results). The initial step in estimating survival of newborn snakes is to determine the number of neonates produced in each year. To do this, I used the number of adult females captured each year. To calculate the numbers of neonates produced each year, the number of adult females was multiplied by the mean litter size (19.7 offspring) and then by 0.7 to adjust for reproductive frequency (Brown and Weatherhead 1997). I assumed that the sex ratio of neonates was 50:50 (unpublished data).

The second step in estimating neonate survival is to determine the number of individuals alive after one year. Because catchability of one year olds was also very low, survival to one year could not be measured directly with any accuracy. Thus, the number of neonates that survive to one year could only be estimated indirectly. I used two approaches. First, because most snakes are captured for the first time at two years of age, I used the size of the two-year-old cohort in each year and the rate of survival from

one to two years to reconstruct the size of the one-year old cohort. To illustrate, in 1993 five two-year-old females were captured for the first time, indicating that at least five members of the cohort of females born in 1991 survived its first year. Because survivorship of females between ages one and two is 0.41 (see Results), the five two-year-olds must actually be the remnant of a 12 member cohort that survived to one year old (i.e., $5/0.41$). Similar calculations were carried out for two-year-old males and females each year.

The second approach to estimating the number of neonates that survived their first year was based on Jolly-Seber estimates of the number of individuals entering the population in each year. Analysis was performed separately for males and females using datasets consisting of recapture histories of individuals aged one year and older. The estimate of B (number of individuals entering the population) was taken to represent the number of neonates surviving to one year old. Actual calculation of B does not distinguish recruitment through birth from that through immigration of adults. However, since Barbs Marsh is physically isolated from other waterbodies, for this analysis I assumed that adult immigration was rare and that B represented internal recruitment only.

The relationship between female size and fecundity was determined from females that gave birth in captivity. During

August each year adult females were captured and maintained in captivity until parturition (Brown and Weatherhead 1997). Females were held in tanks indoors with air temperatures maintained above 22° C. Most tanks also had an additional heat source available to the snakes (e.g., heating rocks). Females were fed fresh or previously frozen minnows 2-3 times per week. Tanks were lined with artificial grass carpeting or wood shavings and were checked for the presence of neonates several times per day. Stillborn neonates and undeveloped follicles were included in determination of litter size.

These females were included in all analyses of growth and survivorship because they were in captivity for a relatively short period (approximately two weeks). I judged that longterm patterns of growth and survival would not be measurably altered by this brief period of captivity.

All analyses were performed using a micro-computer version of SAS. Significance was accepted at the 0.05 level, though marginally significant ($0.05 < p < 0.1$) results are discussed when deemed appropriate. Residuals for all parametric tests were inspected for violations of assumptions (Sokal and Rohlf 1981).

Results

Body Size and Sex Ratio

In Barbs Marsh, 428 water snakes were captured between 1988 and 1996. Of these individuals, 210 were recaptured at

least once. Overall, females were significantly longer and heavier than males (Table 1.1, Fig. 1.1). This size difference was also significant in all but one year of the study (1992), when the difference bordered on significance ($p = 0.06$) (Appendix 1). Significantly more males than females were captured in 1988 and 1989, but in other years, sex ratios did not differ from 1:1 (Appendix 1).

In Beaver Marsh, 305 individuals were captured between 1990 and 1996. Of these, 92 were recaptured at least once. Females were significantly longer and heavier than males each year (Table 1.1, Appendix 2). From 1990 to 1993 Beaver Marsh was sampled mainly during the mating season and most captures were of adult snakes. As a result, average body sizes were larger than at Barbs Marsh, where more juveniles were captured (Table 1.1). Sex ratios did not differ from 1:1 in any year. At both sites, pronounced SSD was present throughout the study. Females were 20% longer and 80% heavier than males, on average (Table 1.1).

Growth

I calculated 364 annual growth increments for 206 snakes from Barbs Marsh (115 males, 91 females) and 117 annual growth increments were calculated from 91 snakes from Beaver Marsh (43 males, 48 females). Growth rate was significantly negatively correlated with initial body size for both males and females (Fig. 1.2). The slopes and intercepts of these

relationships did not differ between sites for females (slope $F = 3.51$, $p = 0.064$; intercept $F = 0.03$, $p = 0.85$) or for males (slope $F = 1.18$, $p = 0.28$; intercept $F = 2.47$, $p = 0.12$). Therefore, data from both sites were pooled to calculate male and female growth curves.

Von Bertalanffy growth curves were modelled from recapture data for males and females (Fig. 1.3). Asymptotic SVL estimates (A) were 89.2 cm (95% CI = 84.8-93.6 cm) for females and 63.2 cm (95% CI = 60.9-65.5 cm) for males. Because these confidence intervals do not overlap, the difference in A between the sexes is significant. Examining growth curves for each year separately, asymptotic body size of females was significantly greater than that of males in six of eight years (Appendix 3). Thus, females consistently reach larger adult size than males. However, k did not differ between males and females, indicating that they approached their respective asymptotic sizes at the same rate. Estimates of k were 0.0022 (95% CI = 0.0019-0.0025) for females and 0.0025 (95% CI = 0.0021-0.0029) for males. Estimates of k did not differ between the sexes in any year (Appendix 2). Within each sex, estimates of A and k did not differ among years (Appendix 3).

The observation that A is higher for females than for males while values of k do not differ, indicates that absolute growth rate of females is higher. Even after adjusting for differences in initial SVL with ANCOVA,

females grew significantly faster than males from ages one to five (Table 1.2). Adjusted growth rates of neonates and of snakes older than five years of age did not differ between the sexes. A multiple regression analysis revealed that sex ($F = 430.49$, $p = 0.0001$) and initial body size ($F = 353.02$, $p = 0.0001$) had significant effects on growth rate and together they explained 57.4 % of the variation in growth rate. Thus, female growth rates are substantially higher than those of males. This difference is most evident prior to maturity (see below). Neither site nor fat content at the beginning of the growth period, which might potentially affect growth rate, significantly improved the multiple regression (site $F = 1.99$, $p = 0.16$; fat content $F = 0.26$, $p = 0.61$).

Age estimation

Age was estimated by integrating the linear relation between growth rate and body size, using size at birth (16.8 cm for female, 16.6 cm for males (unpublished data)) to calculate the constant of integration (Van Devender 1978). The following age estimation equations were obtained:

$$\text{Females: Age} = (1/-0.0016) * \ln(-0.0016 * \text{SVL} + 0.1481) - 1318.84$$

$$\text{Males: Age} = (1/-0.0021) * \ln(-0.0021 * \text{SVL} + 0.1314) - 1131.53$$

These equations were used to estimate the age (in days) of each individual at the time of its first capture. Age at subsequent captures was then determined by adding the time

elapsed between captures to the initial estimate of age. Thus, after their initial capture and age estimation, individuals were of 'known' age.

To evaluate the age-size models, I compared the 'known' age of individuals after their first capture to the age calculated from the model based on their body size. A paired t-test comparing 'known' and estimated age of individuals after their first capture indicated a significant difference for both sexes (female mean difference = -0.19 yr, $t = -2.91$, $p = 0.004$; male mean difference = -0.17 yr, $t = -2.36$, $p = 0.019$). However, since ages were rounded off to the nearest year, these differences are trivial. Visually, the fit between 'known' and estimated age was very good (Fig. 1.4).

I found that, on average, males were older than females in Barbs Marsh in all years and significantly older in 1990, 1991 and 1992 (Appendix 4). This is opposite to the pattern of age-bias that would lead to an erroneous determination of female-biased SSD. The distributions of ages of snakes in Barbs Marsh were not different in eight of nine years (Kolmogorov-Smirnov (K-S) tests, all $Z < 1.01$, $p > 0.26$) (Fig. 1.5). In one year (1992) there was a preponderance of young males (K-S $Z = 1.60$, $p = 0.012$). (If α is adjusted to compensate for multiple comparisons, the difference in 1992 is nonsignificant). At Beaver Marsh, mean age of males and females did not differ in any year (Appendix 5), nor did the

age distributions (K-S tests, all $Z < 1.18$, $p > 0.12$). These results indicate that female-biased SSD at the study sites is not due to an over-representation of older (and thus larger) females in the samples.

Age and size at maturity

Based on participation of marked individuals in mating aggregations, minimum SVL at maturity was 42.5 cm for males and 55.4 cm for females. For both sexes, these sizes correspond to an age of two years. However, a frequency histogram of the ages of individuals observed in mating aggregations indicates that few two-year-olds are sexually active (Fig. 1.6). A single female was observed mating for the first time at two years of age. This female was extremely large for her age (58.8 cm). At three-years of age, substantially more males than females are reproductively active (Fig. 1.6). Figure 1.6 suggests that most males do not mature until three years old and most females do not mature until four years old.

Similarly, the ages of female snakes that gave birth in captivity suggest that most do not reproduce until they are four years old. None of the four three-year-old females held in captivity during August produced litters, whereas nine of 12 four-year-olds reproduced. Because of limited space, larger, older females were preferentially held in captivity. No two-year-old females were kept in captivity during August

and thus none are known to have given birth. Thus, although some females appear to mature at three years old, most do not reproduce until their fourth year. On average, females tend to delay maturity for one year longer than males.

Female fecundity

Seventy-nine adult females maintained in captivity during August. Of these, 59 gave birth and complete measurements were available for 54. Postpartum measurements of SVL of females that produced litters ranged from 63.3 to 87.4 cm (mean = 74.6 ± 4.86). Mean litter size was 18.5 (± 4.11). However, the size of litters increased with maternal SVL ($p = 0.0001$, $r^2 = 0.59$, Fig. 1.7).

The populations were surveyed most intensively during spring and most females were captured and measured in May. To estimate annual neonate production based on springtime measurements of females, I also regressed litter size against maternal SVL measurements made in May. May SVL measurements of mothers ranged from 60.9 cm to 81.1 cm (mean = 70.9 ± 4.56). Again, litter size increased significantly with SVL ($N = 40$, $p = 0.0001$, $r^2 = 0.55$).

Catchability

The age distribution of captured snakes indicates an under-representation of one-year-old individuals (Fig. 1.5). I marked 136 neonates with PIT tags soon after birth in 1994

and released 49 in Barbs Marsh (23 females, 26 males) and 87 in Beaver Marsh (39 female, 48 males). Only two of these were ever recaptured. A female in Barbs Marsh was captured in 1995 and again in 1996 and a male in Beaver Marsh was captured in 1995. In the later years of the study, when most adults had already been marked, the majority of newly captured individuals were approximately 40 cm SVL. This corresponds to an age of 1.5 - 2 years. Thus, catchability of snakes in their first year is lower than it is at later ages.

There were few instances of marked individuals 'disappearing' from the population for one or more years before being recaptured. Of 499 recaptures, only 35 involved individuals 'returning' after an absence of one year. The logistic regression of catchability indicated no significant effect of body size ($\chi^2 = 0.06$, $p = 0.8$) or sex ($\chi^2 = 0.11$, $p = 0.74$) on the probability of capture. However, this analysis is based on recapture histories in which one-year-old snakes are under-represented (only three individuals were < 47 cm SVL). Catchability was significantly higher at Barbs Marsh than at Beaver Marsh ($\chi^2 = 12.05$, $p = 0.0005$).

Population size and density

Larger, more consistent recapture samples allowed better estimation of demographic parameters at Barbs Marsh than at Beaver Marsh (Appendix 6, 7). This is apparent from the

large standard errors associated with individual and mean parameter estimates at Beaver Marsh (Appendix 7). Separate Jolly-Seber analyses were carried out for each sex at each site. Mean estimated population size at Barbs Marsh was 101.4 (range 85.5 - 117.4). There was a significant increase in estimated number of females in Barbs Marsh over the course of the study ($N = 7$, $r = 0.87$, $p = 0.01$). At Beaver Marsh, mean population size was 83.6 (range 24.5 - 128.4). The estimates of population-size correspond to mean densities of 25.4 snakes/ha at Barbs Marsh and 33.4 snakes/ha at Beaver Marsh.

Survivorship

Survivorship based on individual recapture histories was significantly higher at Barbs Marsh than at Beaver Marsh (0.53 vs 0.39, $\chi^2 = 16.2$, $p = 0.0001$) (Table 1.1). This site difference was evident among both females ($\chi^2 = 4.38$, $p = 0.036$) and males ($\chi^2 = 13.11$, $p = 0.0001$). Similarly, a multiple logistic regression indicated that site had a significant effect on survival ($\chi^2 = 16.2$, $p = 0.001$) but sex did not ($\chi^2 = 0.18$, $p = 0.67$). Because of these differences, analyses of size and age effects on survivorship were determined separately for each site (see below).

In contrast, Jolly-Seber estimates of survivorship indicated similar survival rates at each site. However, the

variance in survivorship was much higher at Beaver Marsh than at Barbs Marsh (Appendix 6, 7, Table 1.1). Jolly-Seber estimates are consistent with observed survivorship values, indicating that male and female survival rates do not differ. Within each marsh, there was no difference between the sexes in estimated survivorship (Table 1.1).

Size-specific survivorship

As an initial step in investigating size-specific survivorship, I calculated observed survival rates for males and females in 10 cm size classes at both sites. A frequency histogram suggested that at both marshes, survival was higher at intermediate sizes for males and females (Fig. 1.8, 1.9). Because the histograms suggested a curvilinear relationship between survivorship and body size, I included first and second order terms for size (i.e., SVL and SVL²) in a logistic regression model for each sex at each site. These regressions revealed significant polynomial relationships between body size and survival for females at Barbs Marsh ($\chi^2 = 8.25$, $p = 0.016$) and Beaver Marsh ($\chi^2 = 9.85$, $p = 0.007$). At both sites, female-survival probability increased to a peak level at SVL of 53 cm and then decreased as SVL increased further (Fig. 1.8, 1.9). Among males, survivorship of intermediate-sized was somewhat higher at both sites, but the relationships between body size and survivorship were not significantly ($\chi^2 < 3.61$, $p > 0.17$, Fig. 1.8, 1.9).

Age-specific survivorship

Inspection of frequency histograms suggested that survivorship was higher at intermediate ages. Therefore, a second order term was again included in the logistic regressions of survival on age. This indicated a significant curvilinear relationship only among females at both Barbs Marsh ($\chi^2 = 8.61$, $p = 0.014$) and Beaver Marsh ($\chi^2 = 8.88$, $p = 0.012$). At both sites, probability of survival reached a peak level at three years of age and decreased thereafter. There was no relation between age and survivorship among males at either site ($\chi^2 < 1.94$, $p > 0.38$).

Although there was no sex difference in survivorship within any year class at Barbs Marsh (all $\chi^2 < 1.85$, $p < 0.17$), the net effect of minor differences in age-specific survivorship resulted in significantly greater male longevity. Mean age of males when they were last captured (4.0 yr) was significantly greater than that of females (3.4 yr) ($t_{326} = 3.20$, $p = 0.0015$). This trend was also evident from the significant decrease in the proportion of females in each subsequent age class ($r^2 = 0.15$, $F = 9.92$, $p = 0.003$, Fig. 1.10).

At Beaver Marsh there was no sex difference in the mean age of non-surviving individuals over the study ($t_{181} = 0.68$, $p = 0.50$) and there was no relationship between sex ratio and age ($F = 0.07$, $p = 0.80$).

Effects of growth rate and fat content on survival

I used logistic regression to determine whether faster growing snakes suffered higher mortality. I calculated relative growth rates (residuals from the regression of growth rate on SVL (Fig. 1.2)) for each sex to use as the predictor variable (Forsman 1993). The logistic regressions indicated no relationship between survival and relative growth rate for either sex at either marsh (all $\chi^2 < 0.79$, $p > 0.38$). Thus, individuals exhibiting rapid growth rates (independent of body size) did not suffer higher mortality.

I also wished to determine whether individuals with relatively large energy stores had higher probabilities of survival. I calculated the relative size of energy stores by first estimating fat mass (Weatherhead and Brown 1996) and then calculating estimated fat as a proportion of total mass. Logistic regression with relative fat as the predictor variable indicated no effect on survival probability of either sex at either marsh (all $\chi^2 < 0.54$, $p > 0.46$).

Neonate survival

The two methods used to estimate the probability of neonates surviving to one year gave overall mean values of approximately 0.20 for each sex (Table 1.3). However, annual survivorship appears to be highly variable. Neonate survivorship based on reconstruction of the year-one age class ranged from 0.06 to 0.34. Neonate survivorship based

on Jolly-Seber estimates of the number of one year-old individuals entering the population ranged from 0.04 to 0.42.

Observed Mortality

Between 1993 and 1996, I located the carcasses (or radio-transmitters) of 37 snakes (15 females, 22 males) that had been killed by predators or had died while hibernating. Significantly more mortality occurred during May, concurrent with the mating season, than at other times of the year ($\chi^2 = 13.5$ df = 4 p = 0.009, Fig. 1.11). There was no difference between the sexes in the timing of the observed mortality ($\chi^2 = 4.4$, df = 4, p = 0.36).

Mammals (*Procyon lotor*, *Mustela* sp.) appeared to be responsible for the majority of the observed predation. These carcasses were found mutilated and partly consumed along shorelines or on beaver dams. Other predators of water snakes, determined through recovery of radio-transmitters and observation, include snapping turtles (*Chelydra serpentina*), bullfrogs (*Rana catesbaena*) and red-shouldered hawks (*Buteo lineatus*).

Life Table

I constructed a life table for females only at Barbs Marsh because larger samples sizes and numbers of recaptures at Barbs Marsh made estimates of age- and size-specific survivorship more accurate than those for Beaver Marsh. I used information on size-specific growth survival and fecundity presented above, an age at maturity of four years and reproductive frequency of 0.7. A cautionary note should be made concerning the accuracy of the life table. The calculations are dependant upon the accuracy with which the components of the life table estimated. In this case, survivorship of the zero and one-year-old age classes were roughly estimated and this may affect the accuracy of subsequent calculations and values.

The completed life table indicated that R_0 was 0.79 even when the maximum value of neonate survivorship was used in the calculations (Table 1.4). The disagreement between the calculated R_0 and the observed increase in the number of females could be due to excluding the contribution of three year olds from net reproduction. If even one third of three-year olds reproduce, R_0 increases to 1.0. However, R_0 may not reflect actual changes in population size unless certain unrealistic assumptions are met (e.g., stable age distribution, environmental stability, constant survivorship and birth rates (Krebs (1989))).

To assess the effects of varying age at maturity on

lifetime reproductive success, I constructed life tables for hypothetical populations in which age at maturity ranged from two to five years (Table 1.5). Survivorship from ages zero to two were taken from the life table for females from Barbs Marsh. Survivorship between three years and the age at first reproduction was set at 0.61. Survival after maturity was kept constant at 0.48. To determine body size at maturity and subsequent to maturity for each hypothetical strategy, I calculated separate linear regressions of growth rate on SVL for immature females (SVL < 56 cm) and mature females (SVL > 56 cm).

Comparison of R_0 values produced by these hypothetical strategies shows that the highest R_0 occurs in the population maturing at three years old, followed by the population maturing at two and the population maturing at four years old (Table 1.5). Thus, based on the observed growth rate and the relationships between female body size, fecundity and survivorship, female reproductive success is maximized by maturing at three years of age (which corresponds to a body size of approximately 60 cm).

Table 1.1. Summary statistics of age, size, survivorship and population size of *N. sipedon*. Values are means with standard errors in parentheses beneath.

	Barbs Marsh		Beaver Marsh	
	Female	Male	Female	Male
N	369	438	224	201
SVL (cm)	57.5	48.8	62.6	49.9
	(0.77)	(0.41)	(1.03)	(0.62)
Mass (g)	158.9	88.8	206.7	90.5
	(5.72)	(1.97)	(8.45)	(2.73)
Age (yr)	3.3	3.9	4.1	4.4
	(0.09)	(0.10)	(0.14)	(0.16)
Observed				
Survivorship	0.53	0.53	0.42	0.36
Jolly-Seber	0.53	0.58	0.54	0.55
Survivorship	(0.03)	(0.04)	(0.10)	(0.12)
Jolly-Seber	47.6	53.8	35.9	47.7
Pop. Size	(3.33)	(2.68)	(11.9)	(13.4)

Figure 1.1. Size distribution of male and female *N. sipedon* captured in Barbs Marsh in each year of the study.

Figure 1.2. Relation between initial SVL (cm) and growth rate (cm/day) for male (squares) and female (circles) *N. sipedon* from Barbs (open symbols) and Beaver (closed symbols) Marshes.

Figure 1.3. Von Bertalanffy growth curves relating SVL (cm) and age (years) of male and female *N. sipedon*. Symbols represent mean size of known-aged individuals. Vertical bars indicate one standard deviation on each side of the mean.

Table 1.2. Comparison of male and female growth rates in each age-class. Growth rate values are least square means, correcting growth for initial body size.

Age	Sex	N	Growth Rate	F	p
0 ^A	M	8	0.046 (0.01)	4.37	0.057
	F	8	0.076 (0.01)		
1	M	17	0.07 (0.007)	4.64	0.038
	F	20	0.09 (0.007)		
2	M	40	0.046 (0.005)	21.89	0.0001
	F	56	0.078 (0.004)		
3	M	74	0.018 (0.003)	142.38	0.0001
	F	58	0.083 (0.003)		
4	M	52	0.0083 (0.006)	8.41	0.0046
	F	44	0.0427 (0.007)		
5	M	28	-0.0026 (0.008)	10.91	0.0017
	F	31	0.044 (0.007)		
6	M	19	0.006 (0.008)	2.62	0.118
	F	9	0.044 (0.016)		
7+	M	26	0.009 (0.004)	0.71	0.405
	F	5	0.023 (0.014)		

A. Growth rates based on a sample of neonates maintained in captivity.

Figure 1.4. Von Bertalanffy growth curves for male and female *N. sipedon* (dashed lines). Narrow solid lines represent growth trajectories of individual snakes captured in two or more consecutive years.

Figure 1.5. Age (years) distribution of male and female *N. sipedon* captured in Barbs Marsh in each year of the study.

Figure 1.6. Proportion of male and female *N. sipedon* observed in mating aggregations in each age class.

Figure 1.7. Relationship between litter size and maternal postpartum SVL (cm) for *N. sipedon*.

Figure 1.8. Size-specific survivorship of *N. sipedon* at Barbs Marsh. The solid line indicates the significant polynomial relation between survival and body size among females.

Figure 1.9. Size-specific survivorship of *N. sipedon* at Beaver Marsh. The solid line indicates the significant polynomial relation between survival and body size among females.

Figure 1.10. Relationship between sex ratio and age (years)
for *N. sipedon* in Barbs Marsh.

Table 1.3. Estimated survivorship of neonate *N. sipedon* at Barbs Marsh over the study period. See text for explanation of methods of estimating survivorship.

Year	Mature Females	Neonates Produced	Method A		Method B	
			Female Surv.	Male Surv.	Female Surv.	Male Surv.
1989	30	414	0.10	0.12	0.08	0.07
1990	24	332	0.08	0.06	0.19	0.04
1991	17	236	0.23	0.18	0.32	0.08
1992	14	194	0.33	0.34	0.42	0.33
1993	15	208	0.25	0.23	0.16	0.12
1994	11	152	0.28	0.19	0.32	0.16
Mean			0.21	0.19	0.25	0.13

Figure 1.11. Frequency histogram indicating the timing of known incidents of mortality of male and female *N. sipedon*.

Table 1.4. Life table for female *N. sipedon* in Barbs Marsh.
See text for details of calculations.

SVL	AGE	px	lx	mx	lxmx	%R
16.8	0	0.4	1	0	0	0
32.7	1	0.41	0.4	0	0	0
46.4	2	0.61	0.16	0	0	0
57.6	3	0.64	0.1	0	0	0
66.9	4	0.48	0.06	5.54	0.36	0.45
72.1	5	0.48	0.031	6.76	0.218	0.264
76.6	6	0.48	0.0148	7.81	0.115	0.147
81.2	7	0.48	0.0071	8.89	0.063	0.08
82.1	8	0.48	0.0034	9.1	0.031	0.039
82.7	9	0.48	0.0016	9.24	0.015	0.019
						$R_0 = 0.786$

px = age specific survivorship

lx = probability of surviving from birth to age x

mx = age specific fecundity

Table 1.5. Comparison of R_0 values of hypothetical populations of *N. sipedon* in which females mature at different ages. See text for explanation.

AGE	Age at Maturity			
	2 yr	3 yr	4 yr	5 yr
	SIZE lxx	SIZE lxx	SIZE lxx	SIZE lxx
0	16.8 0	16.8 0	16.8 0	16.8 0
1	33.4 0	33.4 0	33.4 0	33.4 0
2	47.5 0.2	47.5 0	47.5 0	47.5 0
3	58.7 0.36	59.5 0.48	59.5 0	59.5 0
4	66.7 0.26	67.3 0.34	69.6 0.47	69.6 0
5	72.4 0.15	72.9 0.2	74.5 0.27	78.3 0.38
6	76.5 0.08	76.9 0.11	78.0 0.14	80.7 0.2
7	79.4 0.04	81.7 0.06	80.5 0.07	82.4 0.1
8	81.5 0.02	83.2 0.03	82.3 0.04	83.7 0.05
9	. .	84.2 0.01	83.6 0.02	84.6 0.02
10	. .	. .	. .	. .
$R_0 =$	1.12	1.23	1.01	0.75

DISCUSSION

Demography

The long duration of mark-recapture of the water snakes in Beaver and Barbs Marsh combined with the high catchability and rate of recapture allowed a rare opportunity to estimate demographic parameters for a snake population. Some authors have decried the difficulty in gathering robust demographic data on snake populations and have suggested that such studies are not worth the effort (Hailey and Davies 1987). A major reason for the success of my study was the high density of snakes in a small localized area. In both marshes density estimates were above 25 snakes/ha. Terrestrial species rarely occur at such high densities, except during periodic, local aggregations (e.g., communal rookeries or hibernacula) (Parker and Plummer 1987). The conspicuous and prolonged mating activity of *N. sipedon* and their frequent basking (Weatherhead and Robertson 1992) also make them suitable subjects for study using mark-recapture techniques.

The R_0 value calculated from the life table for females from Barbs Marsh indicates that the population is declining. Estimates of population size however, indicate that the population has been fairly stable over the study period. The lack of accurate estimates for two important components of the life tables may explain this inconsistency. First, because it takes three to four years for females to mature, R_0 is sensitive to minor changes in the survivorship of young

age classes. Thus, a more reliable measure of neonate survival would certainly improve the accuracy of R_0 . Second, although most females delay maturity until four years old, some females reproduce a year earlier. Because of the age distribution in the population (i.e., many more three-year olds than four-year olds) even if a small proportion of three year olds reproduce, the effect on R_0 would be substantial. Thus, the accuracy of the life table calculations would also be improved by an estimate of the reproductive frequency of three-year olds.

Growth

At both sites, females were consistently larger than males. Comparison of age distributions and rates of survival indicate that the size difference is not a reflection of females tending to live longer than males and thus reaching greater size. Furthermore, there is no evidence that the capture techniques are biased either toward small males or large females. Thus, the female-biased SSD appears to be largely a result of females growing faster than males. The asymptotic body size of females is 40% larger than that of males. At birth, females are slightly but significantly larger than males (0.2 cm longer and 0.1 g heavier (Weatherhead et al. submitted ms)). Females subsequently grow faster than males in absolute terms and also relative to initial size. However, because males and females approach

their asymptotic sizes at the same rate (i.e., k does not differ), relative growth rate (growth in relation to final body size) does not differ between the sexes.

Increased mortality is expected to be a cost associated with growth (Forsman 1993). Growth requires energy and the search for and capture of food should expose an organism to predation. However, I found no relationship between growth rate and survivorship. Even when the sex difference in growth rate is most extreme, females do not appear to suffer higher mortality than males. In the 50-60 cm SVL size class, females grow more than four times faster than males (0.068 cm/day vs 0.016 cm/day), yet female survival is higher than that of males (61.9% vs 50%). A possible explanation is that, at a given size, female water snakes can exploit larger prey than males and thus can sustain higher growth rates through fewer foraging bouts. Indeed, the relative head length of female *N. sipedon* is slightly larger than that of males, which should allow females to subdue and swallow somewhat larger prey (Shine 1991). However, at a body size of 50 cm, the difference in head length is only 1.1 mm and it seems unlikely that this small difference alone could account for females growing faster than males without any survival cost. A more likely explanation may be that the mortality risk associated with reproduction is masking a relationship between growth rate and survivorship. Although slow growing individuals are expected to show higher survivorship, they

may be growing slowly because they are investing more into reproduction (Brown and Weatherhead 1997). If reproduction is associated with increased mortality (see below), then slow-growing, reproductive snakes may exhibit survivorship similar to that of fast-growing, non-reproducing individuals.

The estimated fat content of an individual did not affect its subsequent growth. This result suggests that fat stores often may be used for purposes other than growth. In most cases, fat content was estimated early in the spring. Mature individuals of both sexes may mobilize their stored energy during this period for reproductive purposes rather than for growth. Females would use fat to enlarge their follicles and males would use fat to fuel mate searching activity. It is also possible that individuals with low fat stores fuelled subsequent growth with energy provided by higher levels of foraging (Plummer 1983).

Age at maturity

Age estimates of individuals observed in mating aggregations suggest that a small number of individuals of each sex are reproductively active at two years of age. Most males, however, did not participate in mating activity until they were three years old. Although females may be sexually attractive to males at three or even two years of age, most do not produce a litter until their fourth year. Thus, females may delay maturity by up to two years more than

males. Previously, Weatherhead et al. (1995) concluded that age at maturity in this population was four years and did not differ between the sexes. Minimum sizes at maturity have not changed since that study, but the sample size and the accuracy of age estimates have improved. The difference in these conclusions has important implications regarding SSD, because size at maturity is a major proximate determinant of SSD (Shine 1990).

Why do female *N. sipedon* mature at a larger size than males? The benefit of delayed maturity is probably related to the increased fecundity resulting from investment in growth for an additional year. If a female reproduced in her second year at a SVL of 46.4 cm, she would only be able to produce two offspring. By investing in growth during her second year, she would be 57.6 cm SVL in her third year and could produce 10 offspring. By delaying maturity for a further year, the size of the first litter would increase to 16. Comparison of R_0 values for hypothetical *N. sipedon* populations with different ages at maturity suggest that the best strategy for a female is to reproduce at three years old if she is large enough. If a female is small as a three-year old, delaying maturity an additional year becomes the second best strategy. In either case, selection will favour rapid growth in females prior to maturity. However, growth rate of water snakes is not strictly under genetic control. Environmental conditions can have a significant effect on an individual's size at a

particular age (see Chapter three). Based on relations determined in Chapter three, during the warmest summer of the study, an average-sized, two year-old female (45 cm) would have grown to 65.7 cm. During the coolest summer she would only have grown to 57.7 cm. The data on age at maturity of the study population suggests that some females can follow the optimum strategy of reproducing at three years. Many females, however, delay maturity for a further year. It should be noted, too, that the life table illustrates the mean strategy of many individuals over multiple years. The optimum strategy of an individual female will depend on her particular circumstances.

Survival

The success of the delayed maturity strategy depends on the probability of surviving. Allocating energy to growth to enhance future fecundity is futile unless the individual survives to the next breeding opportunity. In this population of *N. sipedon*, it appears that allocating energy to growth not only enhances future fecundity but also enhances survival of females. This can be illustrated by the hypothetical life tables. R_0 is maximized in the population maturing at three years of age. This is largely due to the high survivorship (0.61) of large immature females. If this survivorship is decreased to the level of reproductive females (0.48), R_0 is maximized by the population maturing at two years of age and

the R_0 's associated with delaying maturity past two years decrease drastically. Thus, female size appears to be a consequence of selection favouring rapid growth, with maturity delayed until a larger size is achieved. The success of this strategy is attributable to both a survival and a fecundity advantage associated with large female size.

Why do intermediate-sized females have higher survivorship than large or small ones? Size-dependant survivorship could be due to predation or food scarcity (Ferguson and Fox 1984, Forsman 1993). The latter factor is unlikely to play a role in the survival of female *N. sipedon*. Amphibian and fish prey were both abundant throughout the study site (Robertson and Weatherhead 1992, pers. obs.). The initial increase in the survivorship curve may indicate that as size increases, females become too large for some predators to capture or that they become better able to escape predators. The increase in female size may also allow them access to more abundant, larger prey (i.e., frogs) which may result in fewer risky foraging bouts. The subsequent decline in survivorship as body size increases further, seems to correspond to females reaching sexual maturity. Peak survival of females occurs at approximately 53 cm SVL at both sites. This is approximately the size at which females begin to participate in mating aggregations. Thus, the decrease in survival as size increases above 53 cm may represent a survival cost associated with reproduction.

There are several ways in which reproduction could impose a survival cost on female water snakes. Gravid snakes often exhibit higher or more precise thermal requirements (Peterson et al. 1993, Charland 1995, Chapter three). More careful thermoregulation by the female may enhance or accelerate the formation of follicles or the development of embryos, but it also may be costly. The principle means of thermoregulation in water snakes is aerial basking, typically on exposed branches or vegetation. Besides exposing snakes to solar radiation, basking may also make them more easily detected or captured by predators (Shine 1980). Thermoregulation may also impose time costs on gravid females. Increased time spent basking decreases the time available for other activities such as foraging. Pregnancy could also impose a survival cost on females if the presence of the litter in the abdomen interferes with locomotion and decreases foraging ability or escape from predators, although that appears not to be the case for *N. sipedon* (Brown and Weatherhead 1997).

A major reproductive cost for temperate reptiles may be decreased overwinter survival. Reproductive females are often in poor condition upon entry into hibernation, which may be due to decreased foraging time or efficiency. Whatever the cause, a result of their poor condition may be reduced overwinter survival (Madsen and Shine 1994). There is evidence from the study population that among sexually mature individuals, reproductive females survive winter less well

than non-reproductive females (Brown and Weatherhead 1997).

Among males, survivorship does not depend on body size. Although the frequency histogram relating survival to body size suggests an advantage associated with intermediate size, neither the polynomial nor linear relation was significant. The increase in survival observed in females around 53 cm SVL is not apparent among males of the same size. The major difference between the sexes at this size is that males are sexually mature and females are not. This may indicate a survival cost associated with male reproduction.

Among females, low postpartum energy stores may impose a survival cost on reproductive individuals. Among males, this is unlikely to be a factor. Although male feeding levels may be low during the mating season (Feaver 1977, King 1986), it is unlikely that males would fast to the point of starvation in the midst of abundant food. Males maintained in captivity during the mating season with access to females will readily accept food (pers. obs.). After the mating season, males have ample time to build up energy stores for hibernation. Predation is a more likely cause of any survival cost associated with male reproduction. The majority of observed mortality of males occurred during the mating season. The tenacious searching behaviour of males during the mating season may make them readily detected and easily captured by predators (Feaver 1977).

The similarity between male and female survivorship

suggests that the lower growth rates of males is not a result of their pursuing a strategy that favours survival over growth. Testing this hypothesis properly would require partitioning male mortality risk into reproductive and foraging components. Feaver (1977) found that the majority of mortality of male *N. sipedon* occurred during the mating season, whereas among females and juveniles, most mortality occurred during the summer. It is still conceivable then, that the male strategy is to reduce mortality costs associated with foraging in order to counterbalance the high risk associated with mating. The result could be similar overall rates of survivorship between males and females, though mortality associated with foraging is expected to be much lower in males. Although both mean survival rates and size-specific survival rates are similar between males and females, the accumulation of minor differences over the lives of the snakes results in a gradual but significant decrease in the proportion of females with age. Thus, on average, males tend to live longer than females. Increased longevity may have important consequences on a male's lifetime reproduction. How longevity relates to body size and previous reproductive activity may be a fruitful area of future research into male growth strategies.

Implications for SSD

Although this study provides insight into why female water snakes become large (through selection for rapid juvenile growth and large size at maturity) it provides little explanation for the maintenance of small male size. Contrary to my prediction, survivorship of males is not higher than that of females and smaller males do not have higher survivorship than larger males. Although males may mature younger and at a smaller size than females, in light of evidence that larger males sometimes have a mating advantage (Weatherhead et al. 1995), this is not an adequate explanation of why they remain small. It remains possible that males employ a 'seasonal-survival strategy', wherein small males have higher survival after the mating season. The nonsignificant increase in survival of intermediate-sized males may indicate that some level of survival selection could be favouring smaller males. Other possible advantages of small male size may relate to a mating advantage. Small males may be more mobile and thus better able to locate mates (Chapter four). Small males might also have a more subtle mating advantage through sperm competition or female choice. Testing this latter hypothesis would require assessment of paternity using molecular methods.

CHAPTER TWO

Thermal ecology of northern water snakes (*Nerodia sipedon*) in eastern Ontario

Introduction

One means of gaining insight into patterns of growth and survival of ectotherms is to study their thermoregulation. The amount of time or the precision with which an individual thermoregulates is determined by associated costs and benefits (Huey and Slatkin 1976). One of the benefits derived from thermoregulation is enhanced growth and energy assimilation (Huey 1982). One of the associated costs is increased risk of mortality (Shine 1980). Thus, differences among individuals in temperature selection may reflect differences in growth or survival strategies. However, before specific differences among groups of individuals are identified and interpreted, it is useful to establish a broad, general knowledge of a populations' thermoregulatory patterns. In this chapter, I describe the general thermal ecology of the study population of *Nerodia sipedon*, as an initial step in investigating sex and seasonal differences in their thermoregulation.

Thermoregulation and thermal ecology have been the central focus of a large body of literature on reptile biology (see reviews by Avery 1982, Huey 1982, Lillywhite 1987, Peterson et al. 1993). This reflects the fundamental importance of temperature in all aspects of ectotherm physiology (Huey

1982). The curvilinear nature of the relation between body temperature of ectotherms and their physiological processes results in a range of temperature wherein performance of a particular process occurs at a peak level (Dawson 1975, Stevenson et al. 1985). Within an individual, the ranges in temperature corresponding to peak performances of several processes may overlap. By maintaining its body temperature (T_b) within this range, an individual can simultaneously maximize several ecologically important functions (e.g., digestion, locomotion, formation of gametes or embryos (Dawson 1975, Huey 1982, Stevenson et al. 1985, Peterson et al. 1993)). This leads to the concept of an optimal or preferred body temperature (PBT) that is expected to be the target of thermoregulatory behaviour (Dawson 1975, Hertz et al. 1993). In this chapter I identify the PBT of a population of northern water snakes in eastern Ontario and determine how well they can maintain this T_b in the wild.

A recent focus of studies of snake thermal ecology has been the extent to which local climatic conditions constrain the amount of time an individual is able to maintain PBT. Because most reptiles generate little metabolic heat, their ability to reach and maintain a particular T_b is almost entirely dependant on ambient biophysical factors (e.g., solar radiation, wind speed, heat retention of substrate) (Peterson et al. 1993). Thus, climatic conditions and particulars of the habitat determine the thermal environment

of a population. Consequently, the quality of the thermal environment may vary temporally and spatially, and thus it must be quantified before the T_b of resident ectotherms can be interpreted (Hertz et al. 1993, Peterson et al. 1993). Knowledge of the range of temperatures potentially available in an individual's habitat provides essential perspective into the T_b actually experienced. For instance, it is useful to know whether an individual is experiencing a particular T_b because it is actually selecting that temperature from a wide range of those possible, whether that temperature is the only one available, or whether that temperature is the closest available temperature to PBT. Because my study population of *N. sipedon* is located near the northern limit of the species distribution, their opportunities to maintain PBT may be limited and thus thermoregulatory behaviour may be especially important for them. Recently, several indices of thermoregulation have been developed to relate reptile temperature selection to the environmental temperatures available to them. At present, none of these indices has been calculated for a snake species.

There were several objectives for my study of thermal ecology. I wished to i) determine the PBT range of *N. sipedon* in the study population, ii) quantify how often thermal conditions allow snakes to maintain PBT. iii) determine the extent to which the snakes exploited these opportunities to maintain PBT and iv) describe annual and daily patterns of T_b

and environmental temperatures. To achieve these objectives, **Tb** of snakes were continuously monitored throughout the activity season. Climatic conditions were monitored concurrently. This intensive monitoring also allowed me to compare daytime and nighttime thermoregulation.

A further goal was to determine whether the nutritional status of northern water snakes affected their thermoregulation. Because snakes can enhance the rate and, to a lesser extent, the efficiency of digestion by elevating **Tb**, they could benefit from maintaining higher, less variable **Tbs** after feeding (Skoczylas 1970, Greenwald and Kanter 1979, Nalleau 1983, Stevenson et al. 1985). Several studies have reported postprandial thermophily among recently fed snakes under controlled conditions (Lysenko and Gillis 1980, Slip and Shine 1988, Gibson et al. 1989, Touzeau and Sievert 1993), while other studies have failed to find this behaviour (Kitchell 1969, Lysenko and Gillis 1980, Tu and Hutchinson 1995). Hammerson (1987, 1989) investigated temperature selection of two species of snakes under semi-natural conditions and found that neither species increased **Tb** after feeding. Although experiments conducted in the wild lack the stringent control of lab studies, they may allow subjects more natural behavioral opportunities (Brown and Brooks 1991). Free-ranging rattlesnakes (*Crotalus* spp.) seek refuge immediately after feeding, but experience higher **Tb** than unfed control snakes when environmental conditions allow

(Beck 1996). Here I test the prediction that free-living water snakes increase Tb after feeding.

Methods

Transmitters and implantation

A recent expansion in the study of reptile thermoregulation is attributable to technological advancements allowing the use of increasingly small, temperature-sensitive radio transmitters. This equipment allows substantial data on body temperature to be gathered from undisturbed, free-ranging individuals over prolonged periods. I used three sizes of radio transmitter (Holohil Systems Ltd, Ottawa Ontario) in this study. The largest (Model SI-2T) weighed 8.6 g and had a battery life of 18 months at 20° C. Intermediate sized transmitters (Model SI-2T) weighed 7.9 g and had a battery life of 12 months at 20° C. The smallest (Model BD-2GT) weighed 1.9 g and had a battery life of 3 months at 20° C. Temperature calibration curves for each transmitter were supplied by the manufacturer and most calibrations were verified before use by placing the transmitters in water baths of different temperatures and recording the pulse rate. In all cases, my own calibrations were within 0.5° C of the manufacturer's. Calibrations were tested for drift opportunistically when transmitters were retrieved before batteries died (i.e., due to snake mortality). There was no evidence that calibration curves drifted over the life of the

transmitter.

Snakes were hand-captured throughout the active season as part of an ongoing mark-recapture study and were selected for transmitter implantation based on the availability of transmitters and on body size (maximum ratio of transmitter mass:body mass 0.075:1). An attempt was made to maintain an approximately equal sex ratio among snakes with transmitters at all times.

Transmitters were surgically implanted into the snakes' abdomen. Subjects were anaesthetized with halothane at a concentration of approximately 4% using an 'open drop' method (Bennett 1991). An incision was made through the skin and coelom just above the ventral scales approximately two thirds of the way from the snout to the vent. The transmitter was inserted posteriorly through the incision and fastened to a rib with a single suture. The coelom was then sutured shut and the antenna was inserted anterior to the incision under the skin (Charland 1991). The skin was then sutured and covered with a spray bandage. Sterile procedures were followed throughout surgery. Post-operative snakes were treated with antibiotic and were given fluids intracoelomically. The snakes were maintained in captivity for three to four days following surgery and then released at their point of capture.

Temperature data were collected at Barbs and Beaver Marshes from mid-May to late August using an automated

telemetry receiver/data logger (SRX400, Lotek Engineering Inc., Newmarket, Ontario). Data relating transmitter pulse rates to temperature for each transmitter were programmed into the receivers, allowing pulse rates to be directly translated and stored as temperature data. At each marsh, a receiver was placed on a hilltop along the shoreline and connected to a four-element antenna mounted on a 4m pole. Receivers were returned to the lab every five to six days to be downloaded and were returned to the field the next day. From the hilltop locations the receivers could usually pick up transmitter signals from all resident snakes. Occasionally, the signal was too faint to be recorded when a snake was hidden among rocks or deep within a beaver dam. Transmitter frequencies of resident snakes were scanned continuously and **Tbs** recorded at 10 min intervals. Because a series of **Tbs** recorded from a single individual are not independent observations, all analyses were performed on **Tb** data averaged for each individual over the period appropriate for specific analyses (e.g., year, month, hour of the day; see below). For individuals studied in more than one year, however, mean **Tbs** in different years were considered independent. A weighted values of overall means and standard deviations (adjusted for the number of observation from each individual) were also calculated to account for the fact that each individual's mean **Tb** also had associated variance.

Between September and April (i.e., the snakes' hibernation

period), the study sites were visited approximately once per month during daylight hours. Transmitter pulse rates from hibernating snakes were timed on a stopwatch and used to estimate temperatures.

Microclimatic data

To interpret Tbs experienced by free-ranging reptiles, it is first necessary to determine what temperatures are available to the animal in their environment. Ideally, this can be accomplished by placing precise thermal models of the organism under study in different areas throughout the habitat and monitoring the temperatures of these models concurrently with the organisms' Tb (Hertz et al. 1993). Alternatively, multiple regression equations can be used to relate climatic conditions to the temperatures of these models and thereby to estimate temperatures available to the organism throughout its habitat at any given time (Christian and Weaver 1996). I used both of these approaches to provide an estimate of the thermal conditions of water snake habitat throughout the study.

Thermal models of water snakes were constructed from 30 cm lengths of copper tubing 2.5 cm in diameter. Each tube was sealed at both ends with corks and painted with grey primer paint to approximate the reflectance of a water snake (Peterson et al. 1993). A thermocouple was inserted through the cork into the model. Three models were placed in the

microhabitats most commonly inhabited by water snakes based on personal observation of snakes, both with and without transmitters (i.e., on sticks fully exposed to sunlight, in shallow water, and beneath sticks on a beaver dam at Beaver Marsh during July and August 1994). Temperatures of the snake models were measured at 10 min intervals using a portable data logger. Solar radiation, wind speed, air temperature and relative humidity were recorded by an automated weather station located at the Queen's University Biological Station, approximately 10 km from Beaver Marsh. The climatic variables were monitored continuously and mean values were recorded at 20 min intervals. Mean hourly values were calculated for the temperature of each model as well as for each climatic variable. Multiple regressions were then conducted to determine the combination of microclimatic variables that best estimated the temperatures experienced by the models. All possible combinations of variables were evaluated using the SAS 'rsquare' process. The combination of predictor variables in which all variables were significant was chosen as the final model. Because temperatures of the snake models were greatly affected by solar radiation, separate regressions were performed for day and night.

A series of experiments was carried out to determine the accuracy with which the snake models mimicked the thermal properties of a real water snake. Temperature-sensitive transmitters were placed inside a copper snake model and into

a dead water snake (a recent roadkill). The model and the carcass were then placed side by side on a wire mesh platform fully exposed to sunlight and wind for six to 12 hours during daylight. This experiment was replicated on five different days under different climatic conditions during September 1996. Temperatures of the transmitters inside the model and the carcass were continuously recorded on an automated telemetry receiver. Mean hourly temperatures were calculated for the model and the dead snake and a regression was performed to determine the relationship between them.

Thermal preference

Robertson and Weatherhead (1992) previously reported temperature preference in this population of water snakes using a thermal gradient chamber. Most of their data were obtained by extrapolating T_b from ambient temperatures within chamber compartments rather than from direct measurement of T_b . To confirm the accuracy of their results I wished to determine temperature preference using telemetry. Also, their study was only conducted using fasted snakes and snakes of unknown reproductive condition. I incorporated absorptive individuals and reproductive and nonreproductive females in my determination of temperature preference to reflect more accurately the constituency of a wild population.

A thermal gradient chamber was constructed using a rectangular fibreglass tank (155 x 58 x 60 cm). A plastic

coil circulated cold water beneath one corner of the tank. A heating pad was placed beneath the opposite corner. Two temperature-sensitive transmitters were taped in place on the inside of the tank, one over the cold corner and the other over the hot corner, to monitor the range of temperature available within the chamber. In late August and early September 1996, three male and ten female snakes with implanted transmitters were placed individually in the thermal gradient for 24 h periods. Tb of snakes in the chamber and the temperatures of the hot and cold corners of the chamber were recorded continuously on an automated receiver/data logger. Because snakes typically explored the chamber initially, body temperatures recorded during the first 12 h of each test were discarded. All individuals were tested more than once but under different nutritional or reproductive conditions (fasted vs. fed; prepartum vs. postpartum). Fasted snakes had not been fed for at least four days prior to being placed in the thermal gradient. Fed snakes were placed in the thermal gradient immediately after being fed a large meal of minnows (i.e., at least 10% of body mass). For each test, the mean and 25% and 75% quartiles of temperatures recorded from the snakes were determined. The 25% and 75% quartiles were used to represent the lower and upper set-point temperatures delimiting the preferred temperature range (Hertz et al. 1993). Individual values were averaged to give the mean preferred temperature and the

preferred temperature range of the study population.

Comparison of the T_b s selected by recently fed and nonfed subjects using paired t-tests allowed me to determine whether water snakes exhibit post-prandial thermophily in captivity.

Thermoregulatory indices

Once an organism's thermal environment has been described and its PBT range identified, it is possible to determine when and how carefully the organism thermoregulates. I calculated the 'effectiveness of thermoregulation' index (E) described by Hertz et al. (1993). This index compares the extent to which T_b s falls within the PBT range relative to what would be expected if an individual moved randomly throughout its environment. Calculating E required determining the extent to which each hourly observation of T_b deviated from the PBT range ($= db$). db is calculated as the absolute value of the difference between an observed T_b and the lower (or upper) set point T_b . Thus, for T_b within the range of 25-30° C (see results), $db = 0$. Similarly, de is a measure of the quality of the thermal habitat at each observation. If T_e exceeded the lower set point T_b , then snakes would have been able to maintain T_b within the preferred range. To determine the mean thermal quality of the habitat each hour, I averaged the de 's of the three snake models representing the temperatures in the most commonly used snake habitat types. This measure of the average thermal

quality of the habitat should reflect the T_b experienced by a snake spending equal time in each of the three microhabitats. The mean hourly values of db and de were used to determine E for each transmitter-equipped snake each year. E was calculated as $1 - (\text{mean } db / \text{mean } de)$ (Hertz et al. 1993). As E approaches 1 it indicates T_b is stable relative to T_e , suggesting precise thermoregulation. If E is close to 0, db fluctuates with de , suggesting that animals select microhabitats without regard to ambient temperature (i.e., non-thermoregulators). E can be less than 0 if db is large relative to de , indicating that individuals are actually avoiding habitats with favourable thermal properties.

I also calculated the 'thermal exploitation' (Ex) index described by Christian and Weavers (1996). Ex measures the extent to which an animal exploits the opportunities the thermal environment provides for maintaining PBT . Ex is less ambiguous than E because by excluding observations when T_e limits attainment of PBT it separates thermoregulatory responses of the animal from the thermal quality of the environment (Christian and Weavers 1996). Ex is calculated as the amount of time an individual's T_b is within PBT range divided by the amount of time that T_e would potentially allow T_b to reach the PBT range. Thus, the analysis is limited to periods when T_e of at least one of the three models exceeded 25°C . I modified this approach somewhat in that I also calculated separately the proportion of the observations that

fell above and below PBT. The E and Ex indices quantify T_b s within the PBT range but do not directly allow interpretation of the direction of deviations outside the PBT range. I classified the T_b observations of each individual during the period when T_e exceeded $25^\circ C$ into three categories: the proportion of observations when T_b was within the range of PBT ($= Ex$) (i.e., $25^\circ C \leq T_b \leq 30^\circ C$), the proportion when T_b was below PBT (i.e., $T_b < 25^\circ C$) and the proportion when T_b was above PBT (i.e., $T_b > 30^\circ C$). An overall mean for each thermoregulatory index was calculated from the mean values for each individual snake.

Feeding experiments

I tested for postprandial thermophily under captive and natural conditions. Because the thermal preference study (see above) included captive individuals that were both fed and fasted, I compared T_b 's selected by individuals in each state. To determine whether free-living snakes exhibit postprandial thermophily, 12 of the transmitter-equipped snakes were fed in the wild over the course of the study (some were fed during more than one year). Their subsequent temperature selection was monitored and compared to T_b 's selected prior to being fed using paired t-tests.

Transmitter-equipped snakes were located and offered a dead fish or minnow of known weight clasped on the end of an extendable pole. Snakes readily learned to accept food

offered in this manner. Some snakes became so accustomed to the procedure that they would rapidly approach as soon as they became aware of my presence. Some individuals would climb into the canoe to be fed more quickly. Each time an individual was fed more than 10% of its body mass in fish, I calculated its mean T_b during the 24 h prior to feeding and the mean T_b over the 24 h after feeding. For each individual, I averaged the mean pre- and post-prandial T_b 's over all its trials. Thus I obtained two grand mean values for each subject; a mean pre-feeding T_b and a mean post-feeding T_b . Some snakes were fed frequently (approximately once per week) while others were only fed once or twice per summer. For snakes that were fed in more than one year ($N = 3$), I calculated separate means for each year.

All analyses were performed using a micro-computer version of SAS. Significance was accepted at the 0.05 level, though marginally significant ($0.05 < p < 0.1$) results are discussed when deemed appropriate. Residuals for all parametric tests were inspected for violations of assumptions (Sokal and Rohlf 1981).

Results

In total, 18 females and 20 males were implanted with transmitters over the course of the study. The mean ($\pm$ S.D.) body size of transmitter-equipped females was 74.6 cm ($\pm$ 7.43) SVL and 318 g ($\pm$ 121.5) mass. The mean body size of

males was 57.5 cm (± 6.5) SVL and 131 g (± 38.1) mass. Thirty one snakes had transmitters during only one year, three for two years and four for three years, giving a total of 49 'snake-years'.

Microclimatic relations

Using climatic variables (air temperature, surface water temperature, solar radiation relative humidity and wind speed), I calculated daytime and nighttime predictive equations for snake models located in the three microhabitats most commonly used by water snakes. All six multiple regression models were highly significant (Table 2.1). The copper-tube snake models accurately duplicated the thermal properties of a water snake body. The temperatures of snake carcasses and snake models were highly correlated ($N = 38$, $p = 0.0001$, $r^2 = 0.89$) and did not differ significantly (mean difference = 0.55°C , $t = 1.16$, $N = 38$, $p = 0.25$, Fig. 2.1). Thus, the models could be used to estimate the equilibrium T_b attained by a snakes in each of the three microhabitats.

Thermal preference

The mean T_b experienced by snakes in the thermal gradient was 27.1°C (± 2.43). The mean 25% and 75% quartile temperatures were 24.7°C (± 3.02) and 29.8°C (± 2.26), respectively. For convenience, the quartile values were rounded off to give low and high T_b set points of 25° and 30°

C, respectively.

Body temperature telemetry

In total, 326,654 **Tb**s were recorded between May and August over three years from the transmitter-equipped snakes (Fig. 2.2). These were condensed to 35,285 mean hourly **Tb**s.

Climatic data were available to estimate model temperatures for 34,087 of these mean hourly observations. **Tb** and mean **Te** had similar distributions, but mean **Tb** was higher than mean **Te** (24.0° C vs 21.7° C, Fig. 2.3). The mean **Te** estimated for a model exposed to the sun was 23.7° C. Mean **Te**'s estimated for the model in the water and the model in the beaver dam were 23.1° C and 18.4° C, respectively (Table 2.2).

Annual variation

The annual variation in water snake **Tb** reflects their annual activity cycle. During the period of snow cover (December to April), snakes hibernate at **Tb**'s of approximately 7° C (Fig. 2.4). Mean **Tb** increases in May when the activity season begins and remains high through August. Mean **Tb** decreases through September and October. During these months, snakes have moved to hibernation sites but may bask on warm days. The actual mean temperatures during September and October may be lower than indicated in Figure 2.4. Because temperatures were recorded only during the daytime after August, the mean values do not incorporate cooler temperatures experienced by

snakes at night. During the period of snow cover, snakes remain underground and thus T_b s are unlikely to have fluctuated over the course of a day.

Daily variation

The typical daily pattern of variation in mean body temperature is consistent with the 'plateau' pattern exhibited by many of the snake species that have been studied (Peterson et al. 1993). Typically, the T_b increased in late morning (i.e., after 1000 h) to a plateau temperature in the preferred range that was maintained throughout the afternoon and decreased again during the night (Fig. 2.5). During the night, T_b was maintained at approximately the same temperature as the water (Fig. 2.5). During July and August, estimated water temperature was close to or above 25° C all day and night which could have allowed snakes to maintain T_b in the preferred range for almost the entire 24 h period (Fig. 2.5).

Snakes did not begin to elevate their T_b as early in the morning as they could. The morning heating phase of T_b lagged behind the heating phase in T_e of the exposed model by two to three hours. This lag in heating became more apparent as the summer progressed. In the afternoon, however, T_b decreased more slowly than T_e of the exposed model and remained higher throughout the night. Snakes often maintained T_b in the preferred range for several hours during late afternoon and

evening, even though estimated T_e in the three representative microhabitats was below 25°C (Fig. 2.5).

Other common patterns of daily T_b variation were also observed among individuals (i.e., 'oscillating' and 'smooth' (Peterson 1987, Peterson et al. 1993)). The oscillating pattern refers to the occurrence of variable T_b s throughout the day. The smooth pattern refers to occasions when T_b remains relatively constant during an entire 24 h period. Although these patterns were often associated with specific climatic conditions (moderate or cool days), even on the same day, different individuals exhibited different patterns of thermoregulation. For example, 2 July 1995 was a sunny, warm day and yet three individuals followed three distinct patterns of T_b fluctuation (Fig. 2.6).

Thermoregulatory indices

The mean deviation of T_b from the preferred range was -2.35°C . The mean deviation of the temperatures of the three models from the preferred range was -4.04°C . Using these values, the effectiveness of thermoregulation (E) was calculated to be 0.48 (Table 2.2). Thus, the snakes in this study might be referred to as moderately precise thermoregulators.

To investigate how E varied over a 24 h period, I calculated mean hourly values based on mean values of individual snakes. This revealed that snakes thermoregulated most precisely during the night and less so during the day

(Fig. 2.7). Between 1800 h and 0600 h E remained relatively stable around 0.6. E decreased to negative values during the morning, rose to approximately 0 through midday and continued to rise throughout late afternoon and early evening. Thus, during the morning, snakes appeared to avoid habitats that would have allowed them to maintain T_b in the preferred range. At other times, they behaved as if they were moving at random among the three representative habitat types, without consideration of their thermal properties.

T_e of at least one of the three models exceeded 25°C on 55% of observations. When the analysis was limited to these occasions, snakes exploited 44.4% of opportunities to maintain T_b in the preferred range. Snake T_b s were below the PBT range on 31.0% of occasions when T_e exceeded 25°C and was above PBT (i.e., $> 30^{\circ}\text{C}$) on 25.1% of occasions when T_e exceeded 25°C (Table 2.2).

Post-feeding temperature selection

The mean T_b selected by seven recently-fed snakes in the thermal gradient was 1.0°C higher than that selected by the same snakes when they had been fasted. This difference in T_b was not significant (Table 2.3). Among 12 free-living snakes fed in the wild, the mean T_b increased by 1.1°C after eating (Table 2.3). This increase in temperature was not significant and is attributable to differences in mean T_e between the pre- and post-feeding periods (Table 2.3). Mean values of E

did not differ between pre- and post-feeding periods (Table 2.3). Limiting the analysis to daytime observations only (i.e., periods when snakes were best able to thermoregulate), also indicated no postprandial increase in T_b or thermoregulatory efficiency (Table 2.3).

Table 2.1. Multivariable regression equations used to predict model snake temperatures in three microhabitats during day and night. Climatic predictor variables include air temperature (AIR °C), surface water temperature (SW °C), solar radiation (RAD kW/m²) relative humidity (HUM kPa), wind speed (WIND m/s). Data relating model temperature to climatic variables were 274 hourly observations during daytime and 123 hourly observations during night.

Model Location	Period	Equation	R ²	p
Exposed to sun	day	-22.4 - 0.41*WIND + 2.0*AIR - 0.03*AIR ²	0.91	0.0001
		+ 0.5*HUM - 0.006*HUM ² + 43.3*RAD		
		- 21.6*RAD ²		
Shallow water	night	-279.8 - 0.35*WIND + 22.3*SW - 0.5*SW ²	0.76	0.0001
		+0.9*AIR + 0.002*HUM ²		
	day	-8.1 + 0.6*AIR + 0.95*SW - 0.01*AIR ²		
		+ 3.4*RAD ²	0.74	0.0001
	night	-386.5 + 34.3*SW + 0.97*AIR + 0.71*SW ²	0.61	0.0001
		+ 0.03*AIR ²		

Table 2.1. (Continued)

Model Location	Period	Equation	R²	p
In Beaver Dam	day	-16.21 + 0.3*AIR + 1.21*SW	0.78	0.0001
	night	-20.58 + 0.4*AIR + 1.4*SW	0.77	0.0001

Figure 2.1. Comparison of temperatures experienced by *N. sipedon* carcasses (solid circles) and a copper snake model (open circles) on five days. Solid vertical lines delineate different days.

Figure 2.2. Frequency histogram indicating the number of body temperature observations recorded per month during the study. Numbers above bars indicate the number of snakes bearing radio-transmitters in each month.

Figure 2.3. Frequency histograms of *N. sipedon* body temperatures (T_b) and mean operative environmental temperatures of the habitat (T_e). Shaded areas represent the preferred body temperature range. Arrows on the x-axis indicate mean values.

Table 2.2. Mean values of *N. sipedon* body temperatures, estimated snake model temperatures and thermoregulatory indices (see text for description) during the activity season (May - August). Weighted means are adjusted for the number of observations from each individual.

	N	Mean (SD)	Weighted Mean (SD)	Range
Body Temperature (C)	49	24.0 (3.10)	24.9 (56.2)	7.9 - 27.9
Model exposed to sunlight (C)	48	23.7 (2.26)	23.9 (43.6)	13.9 - 26.4
Model inside beaver dam (C)	48	18.4 (4.81)	18.8 (94.9)	0.6 - 25.2
Model in water (C)	48	23.1 (3.0)	23.3 (58.8)	11.9 - 27.0
Effectiveness of thermoregulation (E)	48	0.48 (0.28)	0.51 (6.1)	-0.41 -0.98
Thermal exploitation (%)	48	44.4 (10.2)	41.0 (145.6)	25 - 73.5
< PBT (%)	48	31.0 (13.9)	27.7 (191.9)	3.1 - 75
> PBT (%) (13.7) (235.2)	48	25.1	31.3	1.9 - 53.3

Figure 2.4. Annual body temperature profile of *N. sipedon* in eastern Ontario. Error bars indicate one standard error on either side of the monthly mean temperature.

Figure 2.5. Mean daily temperature profiles for *N. sipedon* during four months of the activity season. Shaded areas indicate the preferred body temperature range.

Figure 2.6. Daily temperature profile of three *N. sipedon* recorded on 2 July 1995. Solid lines represent body temperatures of individual snakes. The dashed line indicates T_e of a copper snake model fully exposed to sunlight. The dotted line indicates T_e of a copper snake model in water.

Figure 2.7. Mean hourly values of effectiveness of thermoregulation for *N. sipedon*. Vertical lines indicate one standard error on either side of the mean.

Table 2.3. Paired t-test comparison of pre-feeding and post-feeding temperature selection of *N. sipedon* in a controlled thermal gradient and in the wild.

	Pre-feeding	Post-feeding	t	p
Thermal Gradient (N = 7)				
Body temperature (C)	26.7 (2.26)	27.6 (3.16)	0.66	0.54
Wild (N = 17)				
Body temperature (C)	25.3 (1.81)	26.2 (1.83)	0.15	0.89
Daytime	26.5 (1.72)	27.2 (1.45)	1.67	0.12
Nighttime	23.5 (2.71)	24.3 (2.15)	0.75	0.46
Mean Te (C)	22.3 (3.08)	23.0 (2.95)	0.02	0.99
Daytime	24.3 (3.06)	24.6 (3.17)	1.42	0.18
Nighttime	19.3 (4.47)	20.4 (2.84)	0.25	0.81
Effectiveness of thermoregulation (E)				
Daytime	0.51 (0.33)	0.51 (0.36)	0.34	0.74
Nighttime	0.29 (0.59)	0.12 (0.74)	-0.37	0.72
	0.62 (0.22)	0.66 (0.20)	0.60	0.56

Discussion

The mean preferred body temperature exhibited by *N. sipedon* in this study (27.1°C) is comparable to those reported elsewhere; 28.0°C (Kitchell 1969), 27.4°C (Weil and Aldridge 1981), 27.7°C (Lutterschmidt and Reinert 1990), including the same study population (27.7°C , Robertson and Weatherhead 1992). This supports the view that thermal preference is a relatively stable, species-specific trait and that thermal dependence in general is evolutionarily conservative (Huey 1982). However, these PBTs are notably lower than the PBT of 31.4°C reported by Justy and Mallory (1985). The latter study involved only three individuals and body temperatures were monitored via ingested transmitters. Lutterschmidt and Reinert (1990) found that ingestion of a transmitter evokes a thermophilic response in *N. sipedon*. The higher PBT reported by Justy and Mallory may have reflected a post-feeding T_b increase (but see below).

I estimated the lower limit of the preferred temperature range to be approximately 25°C . Despite the fact that the study population is close to the northern limit of the species' distribution, the environment provides ample opportunity for the snakes to maintain T_b in the preferred range. Between 1 May and 31 August over the three years of the telemetry study, hourly T_e values in at least one of the three sampled microhabitats exceeded 25°C 53% of

the time. During July and August, the estimated T_e in the water was usually above 25°C all day and night. During late afternoon and early evening, snakes were able to maintain T_b higher than any of my three estimates of T_e . During these times, snakes must have been exploiting a microhabitat subtly different than the ones I choose as representative. Shallow, weed-choked water, muddy shoreline flats or beneath dense aquatic vegetation, for instance, may be microhabitats that retain heat for long periods and might be preferentially used by snakes during the evening.

When the analysis was limited to periods when snakes could reach PBT, the distribution of T_b 's of free-living snakes was very similar to that exhibited by snakes in the controlled thermal gradient. The mean T_b when T_e exceeded 25°C was 26.8°C , almost identical to the mean T_b selected in captivity. In the gradient, 25°C and 30°C were the 25% and 75% boundaries of the T_b distribution. For free-living snakes on warm days, 25°C and 30°C represented the 31% and 75% boundaries of the T_b distribution. Thus, the temperatures selected by snakes in the lab closely approximated T_b 's selected by snakes in the wild.

The typical pattern of daily variation in T_b of *N. sipedon* revealed that the heating phase lagged several hours behind that of the exposed model. This result indicates that the snakes were not using their thermal environment to its fullest extent. Basking in the sun earlier in the morning

would have allowed the snakes to maintain T_b in the preferred range for an additional two to three hours per day, particularly early in the season. Although the peak in observations of basking snakes in the study population corresponds to the heating phase of the exposed model (Robertson and Weatherhead 1992), this may not be indicative of the overall thermoregulatory strategy of most individuals in the population. The potential benefits of basking early in the morning (i.e., more time at PBT) may not outweigh the potential risks (predation). It may be better to forgo a rapid, early increase in T_b and to instead remain hidden and wait for T_e to increase in a more protected habitat. However, based on observations of basking frequency, increasing T_b as early as possible is the strategy of some individuals some of the time. This may indicate differences in the costs and benefits of thermoregulation among individuals (see Chapter three).

The daily pattern of variation in E also illustrates the snakes' avoidance of thermally favourable habitats in the morning. The negative values of E throughout much of the daytime suggests snakes may be involved in activities other than thermoregulation. *N. sipedon* are typically diurnal at northern latitudes although southern populations may be nocturnal (Feaver 1977). To forage or search for mates, snakes may have to inhabit thermally less favourable microhabitats during warm parts of the day (Hertz et al.

1993). During the night, however, there may be no conflicting activity demands and snakes may be able to select sites based solely on their thermally favourable characters.

The indices of thermoregulation calculated for transmitter-equipped snakes were intermediate ($E = 0.48$, $Ex = 44.4\%$), suggesting that water snakes are not especially careful thermoregulators. However, to my knowledge, these indices have not been calculated for a snake species before and thus comparisons cannot be made. Values of E calculated for several populations of *Anolis* lizards range from 0.0 to 0.67 (Hertz et al. 1993), indicating that the study population of *Nerodia* thermoregulates almost as precisely as the most precise *Anolis* thermoregulators. The mean value of Ex calculated for tropical populations of *Varanus* lizards during different seasons (when attainment of PBT was possible) is 54.4% (range 0 - 100%) (Christian and Weavers 1996). This is comparable to the mean Ex of water snakes during their active season. Application of these specific indices to more snake species is required before any useful comparisons can be made. However, Peterson (1987) reported 'thermal utilization' (analogous to Ex) on 11 warm days for a population of garter snakes (*Thamnophis elegans*) to be 93%. Compared to this, *N. sipedon* are exploiting their thermal environment much less fully. An obvious explanation for this difference involves the different lifestyles of

garter and water snakes. Terrestrial garter snakes may be able to forage or search for mates without leaving thermally favourable habitats. Water snakes, however, must enter a typically cooler aquatic habitat to forage or to flee from predators (Scribner and Weatherhead 1997).

Feeding did not elicit a thermophilic response among captive water snakes. This is similar to the finding of Kitchell (1969), but in contrast to the significant post-feeding increase in *T_b* reported by Lutterschmidt and Reinert (1990). Several studies have reported an increase in *T_b* among recently-fed snakes under controlled conditions (Lysenko and Gillis 1980, Slip and Shine 1988, Gibson et al. 1989, Touzeau and Sievert 1993). However, postprandial thermophily has not been demonstrated in other studies (Kitchell 1969, Lysenko and Gillis 1980, Tu and Hutchinson 1995). It is unclear why similar studies on the same species should yield different results, but possible confounding factors could include the amount eaten, previous feeding regime or the thermal history of the subjects.

I found that although the mean *T_b* of snakes increased slightly after feeding, the increase was attributable to differences in environmental temperatures rather than to changes in temperature preference. The lack of postprandial thermophily demonstrated by snakes in my study may be related to the relatively high *T_b* selected by normally active subjects. Because the snakes spend substantial

amounts of time at the PBT, a further elevation in T_b following feeding may not offer a substantially increased benefit (Hammerson 1989, Tu and Hutchison 1995).

This study presents an accurate picture of T_b s experienced by water snakes during their active season. Future study could focus in more depth on T_{es} available throughout the entire habitat and information on daily patterns of habitat use by snakes which would allow fine-scaled understanding of the role of thermal characteristics in microhabitat selection. This study also illustrates the value of combining temperature-telemetry and experimental manipulation in the field (e.g., supplemental feeding) in the study of reptile thermoregulation. Although more difficult to control, this approach may offer more realistic and accurate information on the behaviour of free-living subjects (Brown and Brooks 1991). It would be useful in future research to compare rates of movement and activity among fed and unfed subjects. It is conceivable that increased postprandial thermoregulatory precision demonstrated under laboratory conditions may represent postfeeding ataxia (e.g., Brown and Brooks 1991) rather than a change in temperature selection *per se*.

CHAPTER THREE

Seasonal and sex differences in thermoregulation of northern water snakes

Introduction

Many studies of ectotherm thermoregulation have used concepts of cost-benefit analysis to interpret patterns of body temperature variation (Hainsworth and Wolf 1978, Crowder and Magnusson 1983, O'Connor and Tracey 1992, Porter and Tschinkel 1993, Charland 1995, Shine and Madsen 1996). The variation in benefit associated with different T_b s is due to the nature of the thermal physiology of ectotherms (Huey and Slatkin 1976). The performance of ectothermic organisms varies with T_b because the biochemical reactions underlying ecologically important activities typically occur at maximal levels within a narrow range of temperature (Dawson 1975). By maintaining T_b within this range of temperature, an individual could accrue several benefits, including elevated rates of growth, digestion, assimilation, formation of gametes or embryos, and locomotion (Dawson 1975, Huey 1982, Stevenson et al. 1985). When placed in a controlled thermal gradient in which they could select a wide range of T_b , subjects typically spend the majority of their time within a narrow, species-specific range of preferred body temperature (PBT). This PBT range generally coincides well with the T_b range over which ecological performance occurs at elevated levels (Dawson 1975, Huey

1982).

Most major costs associated with a particular T_b relate to the fact that individuals often have to thermoregulate actively to reach and maintain a T_b in the preferred temperature range. This is especially so in habitats with less moderate thermal environments. One cost associated with thermoregulation is the time required that could otherwise be spent at different important activities, such as foraging or mating (Huey and Slatkin 1976). Thermoregulation may also have an associated survival cost. For example, efficient temperature regulation in a particular habitat may require an individual to be exposed to solar radiation. This may necessitate prolonged periods spent basking fully exposed in sunlight, which may make the snake more visible to predators (Shine 1980).

Given identical environmental conditions, differences in T_b among individuals may represent differences in the cost-benefit ratio of their thermoregulation. Identification of thermoregulatory differences then, may provide insight into other aspects of the subjects' biology. Several studies have predicted differences in the benefits associated with thermoregulation, based on reproductive or nutritional condition (Congdon 1989, Brown and Brooks 1991). However, no studies have focused on identifying differences in T_b predicted by the varying costs and benefits related to different growth or survivorship strategies. In this

chapter, I investigate temporal and sexual differences in the thermoregulation of northern water snakes (*Nerodia sipedon*), near the northern limit of their range. The main objective of the study was to identify thermoregulatory patterns that might provide insight into the female-biased sexual size dimorphism observed in *N. sipedon*.

Because thermoregulation could affect both growth rate and survival of snakes, it is relevant to the investigation of SSD. Four issues raised in Chapter one, regarding the effects of demographic factors on SSD, could be elucidated by data on the thermal relations and thermoregulation of the snakes under study. First, I found that even after adjusting for body size, female growth rate exceeded that of males from ages one through five. Since digestion and assimilation of food are enhanced at PBT, it seems likely that females would have to maintain higher body temperatures to maintain their elevated growth. Thus, I predicted that female water snakes would spend more time close to PBT than would males.

The second issue raised in Chapter one was the possibility that the survival strategy of male water snakes' might vary seasonally. Because there may be a high mortality risk associated with their reproductive behaviour during May, males may compensate by attempting to lower mortality risk throughout the rest of the summer. One way to decrease mortality risk would be to avoid basking. Therefore, I predicted that males would select cooler temperatures as the

summer progressed to increase post-mating survival.

The third issue raised in Chapter one concerned female survival after sexual maturity. The size-specific survivorship curve for females indicated an increase in mortality coincident with sexual maturity, suggesting a substantial survival cost associated with reproduction. A previous study indicated that mating activity itself did not decrease survival of females nor did pregnancy reduce their locomotor ability (Brown and Weatherhead 1997). Another survival cost potentially associated with female reproduction relates to increased thermoregulatory demands (Shine 1980). Because females may realize additional benefits by accelerating the development of or enhancing the quality of their offspring (Beuchat 1988, Schwarzkopf and Shine 1991, Shine and Harlow 1993), pregnant snakes may spend more time thermoregulating than nonreproductive females. Thus, I predicted that reproductive females would maintain temperatures within the PBT range to a greater extent than would nonreproductive females.

Finally, in Chapter one I observed that most females in the study population did not mature until four years old. However, based on life table calculations, I estimated that lifetime reproductive success of females should be maximized by maturing at three years of age. The life table calculations were based on the average growth rate over the eight year study. I wished to determine the extent to which

this difference between expected and observed age at maturity could be affected by variation in annual temperatures (Andrews 1982). Because female maturity is more likely to be determined by size at a given age rather than by age *per se*, the age at which a female is able to begin reproducing may depend on her growth rate. The cool temperatures at northern latitudes could constrain growth rate to the extent that female age at maturity was affected. I predicted that the temperatures experienced during the warmest summers would allow females to grow large enough to mature at three years of age and that at temperatures associated with cooler summers, females would require an additional years growth to reach mature size.

Methods

Transmitters and implantation

Temperature-sensitive radio transmitters (Model SI-2T or BD-2GT, Holohil Systems Ltd., Ottawa, Ontario) ranging in size from 1.9 to 8.6 g were surgically implanted into the coeloms of 38 water snakes. Temperature calibration curves for each transmitter were supplied by the manufacturer and most were verified before use by placing the transmitters in water baths of different temperatures and recording the pulse rate. In all cases, my own calibrations were within 0.5° C of the manufacturer's.

Temperature data were collected at each site on an automated telemetry receiver/data logger (SRX400, Lotek,

Newmarket, Ontario). Temperature calibration data for each transmitter were programmed into the receivers, allowing pulse rates to be translated directly and stored as temperature data. Transmitter frequencies of resident snakes were scanned continuously and T_b was recorded each time a signal was picked up (occasionally signals were missed if snakes moved away from the marshes or were beneath large solid objects).

Microclimatic data

I used hollow copper tubes 2.5 cm in diameter and painted grey to approximate the reflectance of a water snake to monitor operative environmental temperatures (T_e) in different habitats (Peterson et al. 1993). These models closely mimic the thermal properties of a water snake carcass (Chapter two). At Beaver Marsh, models were placed in three microhabitat types most commonly used by *N. sipedon*. One model was placed in shallow water, one placed in an area exposed to sunlight all day, and a third placed under sticks inside a beaver dam. The temperatures of these models were recorded over 28 days during July and August 1994. Air temperature, relative humidity, wind speed, solar radiation and surface water temperature of Lake Opinicon were recorded concurrently by a weather station located at QUBS, approximately 10 km from Beaver Marsh. Multiple regression equations were constructed using climatic

variables to predict T_e of each model during the day and night (Chapter two).

Data analysis

Mean hourly T_b s were calculated for each snake from the raw temperature data collected by the automated receivers. For each hourly observation of mean T_b , I used the multiple regression equations to estimate the mean T_e of the snake models in each of the three representative microhabitats, during that hour. The hourly values of T_e of the three models were also averaged to estimate the mean thermal quality of the water snakes' habitat each hour. Because a series of T_b s recorded from a single individual are not independent observations, I averaged the mean hourly T_b s for each individual each month. These individual mean monthly T_b s were the observations used in analyses for differences in thermoregulation.

To determine whether sex or the reproductive status of females affected thermoregulation I grouped individuals into three classes for data analysis (male, nonreproductive female, reproductive female) (Table 3.2). These groups were used as one of the factors in two-way analyses. The other factor in the analyses was month (May, June, July, August), which was included to determine if thermoregulation changed over the activity season. I measured thermoregulation in three ways. First, because T_b depends on the thermal

environment available to the individual and because the environmental conditions corresponding to Tb observations may have varied among individuals, I used mean Te of the three representative microhabitats as a covariate in a two-way ANCOVA. By removing variation attributable to differences in environmental temperatures I could better compare Tb selection among groups and months.

Second, I calculated the thermoregulatory indices described in Chapter two (E, EX, proportion of Tb observations below and above PBT during periods when $T_e \geq 25^\circ\text{C}$) for each individual each month. These indices were compared among reproductive classes and months using two-way ANOVA with the interaction term included. Because several subjects were depredated over the study and their transmitters subsequently placed in different individuals, repeated measures analyses were not appropriate. Data were pooled within each individual and these mean individual values were used in subsequent analyses. This eliminated statistical problems related to lack of independence of multiple observations from the same animal (Leger and Didrichsons 1994, Shine and Madsen 1996). Because time costs associated with thermoregulation (i.e., conflicts with mating or foraging activity) may differ over the course of the day for diurnal animals like *N. sipedon* (Chapter two), I also conducted these analyses separately for daytime (0600 h to 1800 h) and nighttime (1800 h to 0600 h) periods. To

estimate how environmental conditions affected growth rate, I calculated the mean air temperature and mean amount of solar radiation between captures for 98 females (144 observations) and 94 males (118 observations) captured in two consecutive years. Climatic data were available for the period between 1 May and 31 August for all years from 1989 to 1996, with the exception of 1991. The snakes' active period usually extends from late April until mid-September. All analyses were performed using a micro-computer version of SAS. Significance was accepted at the 0.05 level, though marginally significant ($0.05 < p < 0.1$) results are discussed when deemed appropriate. Residuals for all parametric tests were inspected for violations of assumptions (Sokal and Rohlf 1981). Type III sums of squares were used to evaluate significance in ANOVA and ANCOVA because there was no *a priori* preference for the order in which variables were entered in models.

Results

In total, 18 females and 20 males were implanted with transmitters over the course of the study. The mean ($\pm$ S.D.) SVL of transmitter-equipped females was 74.6 cm ($\pm$ 7.43) and mean mass was 318 g ($\pm$ 121.5). The mean body size of males was 57.5 cm ($\pm$ 6.5) SVL and 131 g ($\pm$ 38.1) mass. Thirty one snakes had transmitters during only one year, three for two years and four for three years, giving a total of 49 'snake-

years'. A total of 326,654 T_b s were recorded between May and August over three years from these snakes. These raw temperature data were condensed to 35,285 mean hourly T_b s. Climatic data were available to estimate model temperatures for 34,087 of these mean hourly observations. Temperature data were further condensed to a single mean monthly temperature for each individual each year. Pooling the data in this manner reduced the sample size for further analyses to 150 observations.

Differences in thermoregulation among months and reproductive classes

Values of temperature and thermoregulatory indices for each reproductive class averaged over the activity season suggest differences in temperature selection (Table 3.1). Including month as a factor in statistical analyses, however, indicates a seasonal component to differences in temperature selection. The different analyses comparing thermoregulation among reproductive classes and months gave similar results. Snakes in all three classes selected similar T_b 's during the early part of the activity season, but later on in the summer, females selected higher T_b 's than males and reproductive females select higher T_b 's than nonreproductive females. Mean monthly T_b of individuals was correlated with mean T_e measured concurrently to T_b ($r = 0.49$, $p = 0.0001$). Thus, mean T_e was a significant covariate in the two-way

ANCOVA for the effects of reproductive class and month with **Tb** (Table 3.2). This analysis also indicated a significant interaction between reproductive class and month (Table 3.2). To determine the source of this interaction, I performed separate one-way ANCOVAs for each month. These analyses indicated that after adjusting for **Te** differences, **Tb** differed among reproductive classes only during July ($F_{2,42} = 13.49$, $p = 0.0001$) and August ($F_{2,35} = 8.23$, $p = 0.0013$) (Fig. 3.1). Analysis of differences among least-square mean **Tb** each month indicated that during July, mean **Tb** of all three reproductive classes differed from one another. Reproductive females had the highest adjusted mean **Tb** followed by nonreproductive females and then by males (Fig. 3.1). During August, least-square mean **Tb** of reproductive females was again significantly higher than that of males and nonreproductive females, but the adjusted **Tb** of males and nonreproductive females did not differ. Thus, as predicted, reproductive females maintained higher **Tb** than nonreproductive females and males, but only during July and August. Also as predicted, males selected lower temperatures than females in the later part of the summer.

The difference in **E** among months was not significant but the differences among reproductive classes and the interaction term were close to significant (Table 3.2). Separate ANOVAs for each month indicated that **E** differed significantly among reproductive classes only in July ($F_{2,40} =$

3.76, $p = 0.032$). During July, mean E of reproductive females was significantly higher than that of males. Mean E of nonreproductive females was intermediate, but did not differ significantly from either other class (Fig. 3.2). During August, the patterns were identical to those in July but the differences among reproductive classes were not quite significant ($F_{2,33} = 3.03$, $p = 0.062$). These results are consistent with the prediction that reproductive females should thermoregulate more carefully than nonreproductive females (at least during July and August), and that males should select cooler temperatures than females after the mating season.

Analyses of the proportions of time snakes spent at, below and above PBT during periods when T_e exceeded $25^{\circ}C$ also indicated that the reproductive classes were thermoregulating differently over the course of the active season. Mean Ex did not differ among months or among reproductive classes (Table 3.2, Fig. 3.3). However, ANOVAs of the proportion of observations below and above PBT indicated significant reproductive class*month interactions (Table 3.2). Separate ANOVAs for each month revealed that the proportion of T_b 's below PBT did not differ among reproductive classes during May or June. During July, however, the three reproductive classes varied significantly from one another ($F_{2,40} = 10.16$, $p = 0.0003$). Males had significantly more T_b observations below $25^{\circ}C$,

nonreproductive females were intermediate in value and reproductive females had the fewest observed Tb's below 25° C (Fig. 3.3). During August there was also a significant difference in the proportion of Tb observations below PBT ($F_{2,32} = 8.21$, $p = 0.0013$). Proportions did not differ between males and nonreproductive females but the proportion of Tb's for reproductive females was significantly lower than both of the other classes (Fig. 3.3).

Comparing the proportion of observations above PBT each month revealed no significant differences among reproductive classes during May. During June, reproductive females had significantly more observations above 30° C than either males or nonreproductive females ($F_{2,43} = 6.27$, $p = 0.0041$) (Fig. 3.3). During July, all three classes differed significantly from one another ($F_{2,37} = 26.18$, $p = 0.0001$). Reproductive females had the highest proportion of observations followed by nonreproductive females and then by males (Fig. 3.3). During August, the three classes again differed from one another ($F_{2,29} = 57.4$, $p = 0.0001$) and again the value for reproductive females was highest, nonreproductive females intermediate and males lowest (Fig. 3.3).

Taken together, these results support my three predictions. Males selected lower Tbs than females. This was especially evident during the latter half of the activity season when ambient temperatures were highest. Reproductive

females maintained higher T_b s than nonreproductive females. This difference was also most evident during the latter half of the activity season, corresponding to the gestation period.

Daytime - nighttime differences in thermoregulation

During the night, snakes thermoregulated more efficiently (i.e., higher E) and spent a higher proportion of time with T_b within PBT when ambient conditions allowed (i.e., higher E_x). Although thermoregulatory indices differed between daytime and nighttime periods, the seasonal and sex differences in thermoregulation noted above were still apparent in the separate analyses (Tables 3.3, 3.4). During both day and night, adjusted T_b s differed among reproductive classes only in July and August (Fig. 3.4). During these months, adjusted T_b 's of males were lowest, nonreproductive females intermediate and reproductive females highest (Fig. 3.4). Mean E did not differ among reproductive classes during daytime or nighttime in any month (Table 3.3, 3.4). During the daytime in July and August, mean values of E for males and, to a lesser extent, for nonreproductive females were large and negative (Fig. 3.5a). This indicates that during these months snakes were actually avoiding thermally favourable microhabitats during the day to a large extent (Hertz et al. 1993). At night, mean values of E were positive for all reproductive classes each month and did not

differ significantly among classes in any month (Table 3.4, Fig. 3.5b).

Separate daytime and nighttime analyses of the proportion of observations at, below and above PBT during periods when T_e exceeded 25°C also indicated sex and seasonal differences (Tables 3.3, 3.4). During both day and night, all three indices differed among reproductive classes during July and/or August (Fig. 3.6, 3.7). Males had the most observations of Tb below PBT and the fewest observations of Tb above PBT (Fig. 3.6, 3.7). Reproductive females had the fewest observations of Tb below PBT and the most observations of Tb above PBT (Fig. 3.6, 3.7). Nonreproductive females were always intermediate between the other classes (Fig. 3.6, 3.7).

Effect of climatic conditions on growth rate

Multiple regressions were carried out to determine the effects of air temperature and solar radiation on growth of males and females. Because growth rate of both sexes is strongly correlated with body size, SVL was also used as a predictor variable in the regressions. Together, mean air temperature and SVL explained a significant amount of variation in growth rate for both sexes (both $p < 0.0001$). For males, addition of air temperature to SVL increased the model R^2 from 0.58 to 0.65. For females, addition of air temperature improved R^2 from 0.49 to 0.61. Solar radiation

did not have a significant effect on growth rate of either males or females. Mean activity season air temperature varied significantly among years, ranging from 17.0° C to 21.3° C. I wished to determine the extent to which these ambient temperatures affected the age at which females could reach mature size (approximately 55 cm). Substituting the extreme annual mean air temperatures into the multiple regression equation, I constructed growth curves for females from ages one to four (Fig. 3.8). If growth occurs at a constant air temperature of 21.3° C and a growing period of 160 d, females would reach minimum mature size at 2.4 years and could reproduce for the first time at the beginning of their third year. At a constant temperature of 17° C, females would reach a size of 55 cm at 3.2 years and could first reproduce during the spring of the following year. Thus, natural variation in ambient temperatures could affect female growth to the extent of delaying maturity until four years old.

Table 3.1. Summary of body temperatures (Tb), concurrent snake model temperatures and thermoregulatory indices for different reproductive classes of *N. sipedon*. Overall mean values are based on a single monthly mean value for each individual each month. Means are followed by standard deviations in parentheses.

	Male	Nonreproductive Female	Reproductive Female
Mean Tb	24.1 (2.07)	24.4 (3.10)	25.6 (3.10)
Model exposed to sunlight	23.8 (3.26)	23.6 (2.85)	24.6 (2.94)
Model in water	23.5 (3.32)	23.5 (3.31)	23.1 (3.26)
Model in dam	19.1 (5.34)	19.1 (5.36)	18.3 (5.21)
Mean Te	22.1 (3.65)	22.1 (3.52)	22.0 (3.75)
db	-2.00 (1.66)	-2.07 (2.49)	-1.36 (2.47)
de	-3.75 (3.37)	-3.71 (3.26)	-3.83 (3.48)
E	0.36 (0.59)	0.37 (0.51)	0.66 (0.31)
Ex	46.9 (15.74)	42.3 (15.59)	42.6 (11.02)
Tb < 25 C	39.0 (22.00)	34.0 (18.93)	16.6 (10.72)
Tb > 30 C	19.5 (14.35)	25.4 (15.59)	41.4 (13.05)

Table 3.2. Two-way ANCOVA and ANOVA results for effects of reproductive class and month on temperature selection and thermoregulatory indices. See methods for details of analyses.

Source	df	Mean Square	F Value	p
<hr/>				
ANCOVA: Mean Tb				
Mean Te	1	236.98	93.20	0.0001
CLASS	2	17.57	6.91	0.0014
MONTH	3	4.91	1.93	0.1275
CLASS*MONTH	6	8.03	3.16	0.0062
ANOVA: E				
MONTH	3	0.33	1.27	0.2858
CLASS	2	0.78	3.01	0.0525
CLASS*MONTH	6	0.56	2.18	0.0489
ANOVA: Ex				
MONTH	3	333.30	1.66	0.1787
CLASS	2	264.45	1.32	0.2714
CLASS*MONTH	6	364.81	1.82	0.1003
ANOVA: Percent Tb observations < 25° C				
MONTH	3	1331.52	4.17	0.0073
CLASS	2	4606.02	14.44	0.0001
CLASS*MONTH	6	805.22	2.52	0.0240
ANOVA: Percent Tb observations > 30° C				
MONTH	3	1605.00	11.22	0.0001
CLASS	2	3640.80	25.44	0.0001
CLASS*MONTH	6	894.58	6.25	0.0001
<hr/>				

Figure 3.1. Least-square mean body temperatures (adjusted for mean T_e) of *N. sipedon* over 4 months of the activity season. Letters above bars indicate differences in adjusted T_b among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.2. Effectiveness of thermoregulation (E) for *N. sipedon*. Letters above bars indicate differences in E among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.3. Proportion of *N. sipedon* Tb observations a) below, b) within and c) above the preferred body temperature range (25 -30 C) during periods when Te exceeded 25 C. Letters above bars indicate differences in proportion of observations among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Table 3.3. Two-way ANCOVA and ANOVA results for effects of reproductive class and month on temperature selection and thermoregulatory indices during daytime (0600h - 1800h).

Source	df	Mean Square	F Value	p
<hr/>				
ANCOVA: Mean Tb				
Mean Te	1	236.8	82.7	0.0001
CLASS	2	22.9	8.0	0.0005
MONTH	3	6.1	2.1	0.10
CLASS*MONTH	6	7.0	2.4	0.028
ANOVA: E				
MONTH	3	20.7	2.96	0.035
CLASS	2	17.3	2.46	0.09
CLASS*MONTH	6	4.9	0.7	0.65
ANOVA: Ex				
MONTH	3	54.1	0.22	0.88
CLASS	2	331.4	1.37	0.26
CLASS*MONTH	6	596.2	2.46	0.03
ANOVA: Percent Tb observations < 25° C				
MONTH	3	1125.5	3.2	0.025
CLASS	2	4216.1	11.98	0.0001
CLASS*MONTH	6	402.6	1.14	0.34
ANOVA: Percent Tb observations > 30° C				
MONTH	3	1585.7	9.02	0.0001
CLASS	2	6513.8	37.04	0.0001
CLASS*MONTH	6	1416.6	8.06	0.0001
<hr/>				

Table 3.4. Two-way ANCOVA and ANOVA results for effects of reproductive class and month on temperature selection and thermoregulatory indices during nighttime (1800h - 0600h).

Source	df	Mean Square	F Value	p
<hr/>				
ANCOVA: Mean Tb				
Mean Te	1	261.99	78.2	0.0001
CLASS	2	9.71	2.9	0.059
MONTH	3	4.94	1.47	0.22
CLASS*MONTH	6	11.5	3.43	0.0035
ANOVA: E				
MONTH	3	0.39	3.95	0.010
CLASS	2	0.28	2.77	0.066
CLASS*MONTH	6	0.18	1.81	0.1
ANOVA: Ex				
MONTH	3	2558.6	5.71	0.0012
CLASS	2	2350.8	5.24	0.0068
CLASS*MONTH	6	3915.1	8.73	0.0001
ANOVA: Percent Tb observations < 25° C				
MONTH	3	6188.2	15.42	0.0001
CLASS	2	1208.5	3.01	0.054
CLASS*MONTH	6	4391.9	10.9	0.0001
ANOVA: Percent Tb observations > 30° C				
MONTH	3	883.1	8.5	0.0001
CLASS	2	495.4	4.8	0.01
CLASS*MONTH	6	214.0	2.06	0.065
<hr/>				

Figure 3.4. Least-square mean body temperatures (adjusted for mean T_e) of *N. sipedon* a) during daytime (0600 - 1800 h) and b) during nighttime (1800 - 0600 h). Letters above bars indicate differences in adjusted T_b among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.5. Effectiveness of thermoregulation (E) for *N. sipedon* a) during daytime (0600 - 1800 h) and b) during nighttime (1800 - 0600 h). Letters above bars indicate differences in E among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.6. Proportion of *N. sipedon* Tb observations a) below, b) within and c) above the preferred body temperature range (25 -30 C) during periods when Te exceeded 25 C in the daytime (0600 - 1800 h). Letters above bars indicate differences in proportion of observations among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.7. Proportion of *N. sipedon* Tb observations a) below, b) within and c) above the preferred body temperature range (25 -30 C) during periods when Te exceeded 25 C in the nighttime (1800 - 0600 h). Letters above bars indicate differences in proportion of observations among reproductive classes during that month. In each month, bars with the same letter are not significantly different.

Figure 3.8. Expected growth curves of immature female *N. sipedon* when mean air temperature during the growth period is 17 C and 21.3 C. See text for explanation. Arrows on the x-axis indicate age at which females would reach mature size (55 cm SVL).

Discussion

The temperatures selected by snakes and the extent to which they exploited thermal opportunities, depended on sex, reproductive status and the time of year. All of the indices of thermoregulation (adjusted T_b , E , proportions below, within and above PBT) indicate that males select lower temperatures than females, especially in the latter half of the activity season. These trends were most apparent during daytime, when diurnal snakes may have time and activity demands that conflict with thermoregulatory behaviour, relative to nighttime, when activity conflicts are minimal. These results may help explain the sex difference in growth rate described in Chapter one. Even after adjusting for body-size differences, female growth significantly exceeded that of males from ages one to five. The elevated T_b of females may allow them to assimilate energy more quickly or efficiently than males, and thus to grow faster. I can rule out the possibility that higher T_b in females was a consequence rather than a cause of more rapid growth. Presumably females eat more than males, so they might have had higher T_b than males, on average, if they elevated T_b following meals. However, in Chapter two I showed that there is no evidence of post-prandial thermophily in these snakes.

Males thermoregulate less precisely as the summer progresses and increase the amount of time spent at T_b below PBT , consistent with the prediction that they attempt to

increase survival after the mating season. Males could conceivably increase their survival in at least two ways by maintaining relatively cool *T_b*s. Less time spent basking could directly decrease the risk of mortality if basking snakes are more easily observed or captured by predators. Lower *T_b* could also result in decreased energetic costs, and hence a decrease in foraging demands and mortality costs associated with foraging. Feaver (1977) found that male *N. sipedon* suffered higher mortality in the spring than in the summer. The fact that males were less visible to that researcher later in the summer may have indicated a decrease in their basking frequency.

What does this reveal about the female-biased SSD in *N. sipedon*? Male water snakes may adopt a 'survival strategy' after the mating season to compensate for the high mortality risk associated with their mating behaviour. If so, there could be some advantage associated with small male body size. If a male survives the mating season, his priority may be to recover or assimilate just enough energy to meet maintenance and storage demands to last until the next mating season, and sufficient energy to produce enough sperm to allow him to mate. The benefit of additional energy intake (i.e., for growth) may not outweigh the mortality risk associated with harvesting and processing that energy. An additional advantage of a small body size under this scenario is the lower amount of energy required for

maintenance, thereby making the survival strategy more efficient. Two predictions generated from this seasonal survival strategy hypothesis are that male survivorship should increase after the mating season and that after the mating season, small or intermediate sized males should have higher survival than large males. Feaver's (1977) observation that peak male mortality occurs during spring provides support for the former prediction. However, he did not examine size-specific patterns of post-mating survival among adult males.

Reproductive females tended to maintain higher T_b than males or nonreproductive females during July and August. This period largely coincides with the period of gestation (Baumann and Metter 1977, Aldridge 1982). There was no apparent difference in thermoregulation or T_b of reproductive and nonreproductive females earlier in the summer during the period when follicles were being developed. Elevation of T_b and increased thermoregulatory precision during embryogenesis have been shown to improve offspring quality among viviparous lizards (Beuchat 1988, Shine and Harlow 1993). Selection of higher temperatures by females during gestation may also reduce the length of the gestation period (Schwarzkopf and Shine 1991, Weatherhead et al. submitted ms). Accelerating parturition may be especially important in northern populations, where the time available for neonates to forage prior to hibernating is

severely limited by the short activity season. If increased basking increases mortality, then the higher T_b selected by pregnant *N. sipedon* could represent a survival cost associated with reproduction. Female survivorship decreases after sexual maturity (Chapter one), suggesting that such a cost does exist.

Several of the predictions tested in this study were based on the assumption that thermoregulation imposed a survival costs on individuals. The relationship between thermoregulation and mortality risk for snakes is not well understood. My hypotheses require that basking water snakes are more easily detected by predators, especially avian predators. Hawks were often seen circling over the study area and have been observed capturing basking snakes (pers. obs.). Alternative reasoning suggests that when individuals are at PBT their ability to detect and escape predators is enhanced (Christian and Tracey 1981), or that visual predators ignore stationary snakes (Madsen and Shine 1993b). Thus, mortality should be lower among thermoregulating individuals. Andren (1985) reported that only 6-8% of model snakes placed in basking positions were attacked by predators. Obviously more study is necessary to determine whether a larger survivorship cost is associated with thermoregulation or with the lack of thermoregulation. This information is crucial for testing my hypotheses regarding temperature selection and survival strategies and costs for

males and reproductive females.

Mean air temperature significantly affected growth rate of water snakes. The mean air temperature during the activity season could have a dramatic effect on the body size a female is able to attain by three years of age. This in turn could influence whether a female becomes sexually mature at three years or whether she delays maturity for an additional year. In Chapter one I concluded that selection should favour rapid pre-maturity growth in females. Females that can reach a large size, and thus produce a large litter at three or even two years of age, should realize greater lifetime reproductive success. However, the results of this study indicate that the body size that an individual can attain at a given age is determined, to a substantial extent, by non-genetic factors. Thus a female's lifetime reproductive success depends partially on climatic conditions over her lifespan.

The variation in thermoregulatory strategies documented here may have implications for studies focusing on different aspects of ectotherm biology. If study subjects are captured based on their visibility, capture samples could largely consist of thermoregulating individuals. Thus the sex ratio or reproductive condition of the sample may not be representative of the entire population. Often, studies of thermal ecology employ 'grab and jab' methodology whereby **Tbs** are recorded immediately after an individual is

captured. Again, if samples consists mainly of basking individuals, their T_b s may not be representative of the population as a whole, especially if some individuals are avoiding opportunities to thermoregulate. Radiotelemetry techniques employed on as representative a sample of individuals as possible are necessary to detect differences in thermoregulatory strategies among groups.

This study illustrates the utility of the concept of costs and benefits of thermoregulation to test hypotheses pertaining to sexual size dimorphism and life history. Recent technological advances have made it possible to record large amounts of T_b data from a variety of organisms. My study shows that it is possible to use these data to address questions of broader interest than those pertaining solely to thermal ecology. The thermoregulatory indices used in my study were originally designed to characterize populations and allow broad-scale comparisons of thermoregulation. However, they are also useful in making finer scale comparisons of thermoregulation among groups within a population.

CHAPTER FOUR

Body size and seasonal differences in movement and home range area of male water snakes (*N. sipedon*).

Introduction

In attempting to explain cases of sexual size dimorphism, biologists must consider why one sex remains small, as well as why the other sex becomes large (Weatherhead et al. 1995). In instances where males are smaller than females, one possible advantage involved in maintaining small male size is an enhanced ability to locate mates (Ghiselin 1974). Male animals are often able to increase their reproductive success by mating with many different females and an initial step in this strategy is locating more receptive females (Williams 1966, Ghiselin 1974). If receptive females are mobile or have an unpredictable spatial distribution, males may have to search extensively for mates during the breeding period (Trivers 1972, Bondrup-Nielsen and Ims 1990, Duvall et al. 1993). In mating systems such as this (i.e., 'scramble competition polygyny' or 'prolonged mate-searching polygyny'), males that are better able to search out mates may have a selective advantage (Ghiselin 1974). In this chapter, I investigate the relationships between body size, movement, energetics and mating activity to determine whether small male water snakes are more proficient mate-searchers and

whether this corresponds to increased reproductive success.

Small individuals are often expected to have a competitive advantage over larger ones if search ability depends upon energetics (Berry and Shine 1980, Woolbright 1983, Bondrup-Nielsen and Ims 1990, Blanckenhorn et al. 1995) or agility (Ralls 1976, Andersson 1994). If smaller males have relatively larger energy stores they may be able to fuel more prolonged mate searching activity than larger males. This energetic advantage may be especially important if the mating season is protracted. Small males may also be better able to locate mates in spatially complex habitats if they are more maneuverable than large males (Andersson 1994).

Among snakes, males often appear to increase movement or activity levels during the mating season (Madsen 1984, Gibbons and Semlitsch 1987, Reinert and Zappalorti 1988, Madsen et al. 1993, Aldridge and Brown 1995). Male fat reserves may decrease dramatically over the breeding period, indicating the high energetic expense of mate-searching (Bonnet and Nalleau 1996). Among water snakes, small adult males have relatively larger fat reserves than do larger males (Weatherhead and Brown 1996). Thus, if mate-searching ability is related to energetics, selection could favour smaller males. Although it has been suggested that selection for enhanced mate searching ability could favour small male size among snakes (Shine 1978, 1988, Weatherhead et al.

1995), only one study has directly addressed the question. Madsen et al. (1993) found that mate-searching ability is an important component of male reproductive success in European adders (*Vipera berus*). However, mate-searching ability was not related to male body size.

Given the nature of the mating system of *N. sipedon*, a male's energy balance could have a major effect on his reproductive success. Females breed asynchronously over the mating season which may last up to five weeks (Weatherhead et al. 1995). Females may mate with several males during the breeding period and multiple paternity of litters is common (Barry et al. 1992). Although some reproductive females may be predictably located on beaver lodges or dams (Barry et al. 1992), others are not (pers obs). Thus, males may have to search widely over an extended period to maximize the number of potential mates. There is also evidence that males forego feeding during the mating season, which would amplify the importance of their energy stores. Previous research on water snakes has shown that the amount of stored energy was an important correlate of male mating effort in one of four years (Weatherhead et al. 1995, Weatherhead and Brown 1996). However, these studies only examined mating effort in terms of the number of aggregations participated in, and did not measure mate-searching effort.

My first objective in this chapter was to test the hypothesis that smaller males have a reproductive advantage

due to better mate-searching ability. I predicted that if small males have an energetic or locomotory advantage over large males they could cover a larger area in search of receptive females. I further predicted that the larger the area searched during the breeding period, the more mating opportunities and potential mates a male would acquire.

A second objective of the present chapter is to explore further the hypothesis developed in Chapters one and three that males attempt to increase their survivorship after the mating season. In Chapter one I speculated that males may adopt a survival strategy in the latter half of the activity season to compensate for high levels of mortality during the mating season. If this is the case, selection may favour small male size because of lower maintenance costs. Thermoregulation data in Chapter three offered some support for this hypothesis. Compared to females, males selected cooler temperatures and thus may be more secretive during the latter half of the activity season. Here, I compare home range areas and rates of movements of transmitter-equipped males and females over the activity season. I predicted that during the mating season, males would be more active than females and have larger home ranges. I also predicted that following the mating season, movement and home range size of males would decrease.

Methods

Mating and location observations

During the mating period (late April to early June) both study sites were surveyed at least once per day. Snakes were captured by hand or in minnow traps and then measured, marked with a unique combination of dots of non-toxic acrylic paint and released the following day. I estimated percentage body fat of males using the equation provided by Weatherhead and Brown (1996) relating fat-free wet mass to SVL. To estimate the energetic costs of mating activity, I calculated rates of mass change over the mating period for a sample of males captured and weighed both during the early part of the mating season and the latter part or shortly after the end of the mating season. Each time a painted snake was observed, its identification, activity and location were recorded. When mating aggregations were observed the identities of participants were noted. Maps of both study sites were overlain with a reference grid scaled to divide the marshes into 20m X 20m quadrats. Each time a painted snake was sighted, the grid coordinate of its location was noted. At Barbs Marsh, location observations were made during the mating seasons from 1993 to 1996. At Beaver Marsh, location data were collected during the 1994 to 1996 mating seasons.

In addition to data gathered from opportunistic sightings, radio-transmitted snakes were regularly located

throughout the activity season and the grid coordinates of their locations recorded.

Home range calculations

I used a microcomputer software package (McPAAL, version 1.2, Smithsonian Inst., Va.) to construct and measure the area of snake home ranges, based on the x-y coordinates of their locations. Different methods of delimiting home ranges have different advantages and disadvantages (White and Garrot 1990). My objective was to compare mean home range areas among groups of individuals rather than to determine which single method best described the snakes' use of space. Therefore, I used three methods to delimit home ranges: convex polygons, concave polygons and harmonic means (see White and Garrot (1990) for a review and description of methodologies).

For transmittered snakes I calculated separate home ranges for the mating season (1 May - 14 June) and the post-mating season (15 June - 31 August) periods. I also calculated distances and rates of movement between consecutive locations for each transmittered snake during both periods. I measured distances between midpoints of the reference grids in which snakes were successively located. Snakes inhabiting the same grid on successive occasions were recorded as moving 0 m.

Measurement of true male mating success requires assessing the paternity of offspring produced in the

population. For this study, I indirectly estimated male mating success in three ways: 1) the number of mating aggregations in which he participated, 2) the number of different females with which he was observed in mating aggregations or 3) the number of males against which he competed in aggregations. The latter measure was used to estimate a male's ability to locate unaccompanied, sexually attractive females.

All analyses were performed using a micro-computer version of SAS. Significance was accepted at the 0.05 level, though marginally significant ($0.05 < p < 0.1$) results are discussed when deemed appropriate. Residuals for all parametric tests were inspected for violations of assumptions (Sokal and Rohlf 1981).

Results

I calculated the sizes of mating period home ranges for 51 females and 66 males in Barbs marsh and for 30 females and 31 males in Beaver Marsh. At both sites, transmitter-equipped males and females were located significantly more often than snakes seen opportunistically (all $t > 2.13$, all $p < 0.05$). Because home range size was positively correlated with the number of times an individual was located, it was inappropriate to pool home range data determined through radio-telemetry with those determined by opportunistic sighting.

Opportunistic sightings

At Barbs Marsh, I found evidence that male mating activity was associated with an increase in home range area. Reproductively active males (i.e., those seen in at least one mating aggregation) were observed more often than nonreproductive males and had significantly larger home range areas (Table 4.1). At Beaver Marsh, home ranges areas could only be calculated for two nonreproductive males, precluding a similar statistical comparison. Among females, reproductive individuals also tended to be seen more often than nonreproductive individuals (though this difference was significant only at Beaver Marsh) but home range areas did not differ at either marsh (Table 4.2).

Among nonreproductive individuals at Barbs Marsh there was no difference between males and females in the size of mating period home ranges (all $t < 0.5$, all $p > 0.62$). The paucity of data for nonreproductive males at Beaver Marsh again precluded a similar comparison at that site. Among reproductive individuals at Barbs Marsh, males had larger convex polygon ($t = 2.71$, $df = 39$, $p = 0.01$) and concave polygon ($t = 2.89$, $df = 36$, $p = 0.007$) home ranges than females. Harmonic mean home range areas differed at a marginally significant level ($t = 1.83$, $df = 39$, $p = 0.07$). At Beaver Marsh, reproductive males and females had similarly sized home ranges (all $t < 1.29$, all $p > 0.2$).

At Barbs Marsh there was some evidence of a positive

relationship between home range area and male mating success. The area of the convex polygon home range a male occupied during the mating period was significantly correlated with the number of different females he was observed courting ($r = 0.40$, $N = 29$, $p = 0.03$, Fig. 4.1). The area of concave polygon home range was positively correlated with both the number of different females a male courted ($r = 0.53$, $N = 29$, $p = 0.0031$, Fig. 4.2) and the number of mating aggregations in which he was observed to have participated ($r = 0.43$, $N = 29$, $p = 0.02$, Fig. 4.3). At Beaver Marsh there was no relationship between male home range size and mating success (all $r^2 < 0.09$, all $p > 0.17$).

The observed differences between study sites in the relationships between the male home range area and mating success may be due to the spatial distribution of receptive females. Sixty-four mating aggregations were observed in Barbs Marsh between 1993 and 1996. Map grid locations could be determined for 49 of these. At Beaver Marsh, 94 mating aggregations were observed between 1994 and 1996 and locations could be determined for 86. The spatial distribution of mating aggregations was much more clumped and predictable at Beaver Marsh than at Barbs Marsh (Fig. 4.4). The total area of Barbs Marsh comprised approximately 107 400-m² quadrats and mating was observed in 24% of them. Beaver Marsh covered approximately 75 400-m² quadrats and mating aggregations were observed in 13% of them. At Beaver

Marsh, however, 90% of the mating aggregations were located on the two beaver dams, which together covered only 4 grids. Thus, almost all the mating at Beaver marsh occurred in just 5% of the total area.

Although there was some evidence that larger home range area was related to increased mating success at Barbs Marsh (see above), with one exception, neither home range area nor mating success was related to male size or fat content. Measures of home range area were not related to male SVL (all $r^2 < 0.06$, all $p > 0.22$) or fat content (all $r^2 < 0.09$, all $p > 0.20$) at either marsh. Thus, smaller males did not search larger areas during the mating season, nor did males with higher fat content. Similarly, male body size and fat content were not related to the number of aggregations participated in, the number of different females that were courted or the number of other males competed against in aggregations (all $r^2 < 0.04$, all $p > 0.2$). At Barbs Marsh, there was a weakly significant relationship between male fat content and the number of other males competed against in aggregations ($r = 0.32$, $N = 43$, $p = 0.04$). However, the direction of this relationship is opposite to that predicted (i.e., that males with larger energy stores should face less mating competition).

Changes in male mass during the mating period

Mating activity did not appear to impose a heavy energetic

cost on males. At Barbs Marsh, nonreproductive males decreased mass at a mean rate of -0.06 g/day during the mating season. Reproductive males gained mass at a rate of 0.004 g/day over the same period. These growth rates were not significantly different ($t = 0.58$, $df = 28$, $p = 0.57$). At Beaver marsh nonreproductive and reproductive males increased mass at rates of 0.17 g/day and 0.02 g/day, respectively. Again, these growth rates were not significantly different ($t = 0.65$, $df = 27$, $p = 0.52$). At Barbs Marsh, weight change of reproductive males over the mating season was not related to either SVL ($r = 0.34$, $N = 13$, $p = 0.26$), fat content ($r = -0.41$, $N = 13$, $p = 0.17$) or home range area (all $r^2 < 0.16$, all $p > 0.2$). Similarly, at Beaver Marsh weight was not related to SVL ($r = -0.33$, $N = 23$, $p = 0.13$), fat content ($r = 0.03$, $N = 23$, $p = 0.91$) or home range area (all $r^2 < 0.32$, all $p > 0.09$).

Seasonal and sexual differences in home range size of radio-transmitted snakes

At Barbs Marsh there was a decline in the movements and home range areas of reproductive males following the mating season, but the decreases were not significant (Table 4.3). At Beaver Marsh, male movements and home range sizes tended to increase following the mating season, but again the changes were nonsignificant (Table 4.3). Among females, pregnant individuals at Barbs Marsh significantly decreased

rate of movement following the mating season ($t = 3.42$, $df = 6$, $p = 0.014$). Other measures of female movement and home range area did not differ between the mating and post-mating periods at either marsh (all $t < 1.86$, all $p > 0.14$).

During the mating season, movements and home ranges of reproductive males were much larger at Barbs Marsh than at Beaver Marsh (Table 4.3), though the differences were not significant (all $t < 1.58$, all $p > 0.21$). During the post-mating period, movements and home ranges of males were more equivalent between the sites (Table 4.3).

Table 4.1. Comparison of mating season home range areas (ha) and number of sightings of reproductive and nonreproductive adult male *N. sipedon* at Barbs Marsh. Values are means followed by sample size and standard error in parentheses.

	Nonreproductive	Reproductive	p
Sightings	5.9 (63, 0.68)	13.7 (43, 1.68)	<0.0001
Conv. Poly.	0.63 (28, 0.11)	1.14 (29, 0.12)	0.0023
Conc. Poly.	0.21 (23, 0.03)	0.51 (29, 0.09)	0.0045
Harm. Mn.	0.45 (28, 0.13)	1.43 (29, 0.2)	0.0002

Note: Home range methods are Convex Polygon, Concave Polygon and Harmonic Mean.

Table 4.2. Comparison of mating season home range areas (ha) and number of sightings of reproductive and nonreproductive adult female *N. sipedon* at Barbs and Beaver Marshes. Values are means followed by sample size and standard error in parentheses.

	Nonreproductive	Reproductive	p
<hr/>			
Barbs Marsh			
Sightings	5.5 (64, 0.7)	11.2 (19, 3.17)	0.10
Conv. Poly.	0.59 (23, 0.09)	0.53 (12, 0.21)	0.77
Conc. Poly.	0.24 (18, 0.03)	0.19 (9, 0.06)	0.44
Harm. Mn.	0.48 (25, 0.16)	0.75 (12, 0.3)	0.39
Beaver Marsh			
Sightings	4.7 (37, 0.84)	8.1 (29, 0.92)	0.009
Conv. Poly.	0.36 (9, 0.2)	0.4 (12, 0.08)	0.88
Conc. Poly.	0.08 (7, 0.04)	0.06 (8, 0.02)	0.71
Harm. Mn.	0.58 (10, 0.3)	0.56 (13, 0.12)	0.95
<hr/>			

Note: Home range methods are Convex Polygon, Concave Polygon and Harmonic Mean.

Figure 4.1. Relationship between the number of different females courted by male *N. sipedon* in Barbs Marsh and home range area delimited by the convex polygon method.

Figure 4.2. Relationship between the number of different females courted by male *N. sipedon* in Barbs Marsh and home range area delimited by the concave polygon method.

Figure 4.3. Relationship between the number of mating aggregations in which a male was observed to have participated in Barbs Marsh and home range area delimited by the concave polygon method.

Figure 4.4. Spatial distribution of observed mating aggregations at Beaver Marsh and Barbs Marsh. Aggregation locations are indicated by circles, numbers inside circles refer to how many aggregations were observed in that location.

100 m

Table 4.3. Comparison of mating season and post-mating season movements and home range areas (ha) of reproductive male *N. sipedon* equipped with radio-transmitters at Barbs and Beaver Marshes. Values are means followed by sample size and standard error in parentheses.

	Mating Season	Post-mating Season	p
<hr/>			
Barbs Marsh			
Rate of movement (m/day)	37.9 (4, 19.74)	21.8 (4, 7.58)	0.48
Total Distance Moved (m)	1186.4 (4, 643.0)	540.8 (4, 116.5)	0.39
Conv. Poly.	1.19 (4, 0.66)	0.75 (4, 0.50)	0.62
Conc. Poly.	0.59 (4, 0.32)	0.19 (4, 0.07)	0.30
Harm. Mn.	1.45 (4, 0.89)	0.91 (4, 0.59)	0.63
Beaver Marsh			
Rate of movement (m/day)	30.5 (7, 9.73)	11.7 (6, 2.13)	0.11
Total Distance Moved (m)	497.6 (7, 172.2)	682.5 (6, 142.2)	0.38
Conv. Poly.	0.29 (7, 0.14)	0.66 (6, 0.20)	0.15
Conc. Poly.	0.08 (7, 0.05)	0.16 (6, 0.06)	0.28
Harm. Mn.	0.52 (7, 0.33)	0.73 (6, 0.19)	0.61

Note: Home range methods are Convex Polygon, Concave Polygon and Harmonic Mean

Discussion

There have been numerous studies on the spatial ecology of snakes (reviewed by Macartney et al. 1988). However, many studies of reptile movements and home ranges are largely descriptive in nature and thus are of limited value (Macartney et al. 1988, Brown and Brooks 1993). Increasingly, though, investigators are using home range and movement data to address specific ecological or evolutionary hypotheses. Use of this approach has provided insight into the mating system of *N. sipedon*.

The results of this study confirm the casual observation that the activity and conspicuousness of reproductive males is elevated during the mating season. However, the extent to which male activity increases during the mating season may depend largely on the distribution of receptive females, which may in turn depend upon the physical characteristics of the habitat. Beaver Marsh consists largely of open water with few floating logs or other structures offshore. Water snake activity at this marsh is predominantly limited to shoreline areas, especially the beaver dams. In contrast, Barbs Marsh contains little open water and mainly consists of areas of dense willows, sedge clumps and large mats of floating vegetation. Water snakes appear preferentially to use such structures as basking sites (pers. obs.), and thus snakes are often found throughout the marsh as well as along the shoreline.

Although the two study ponds are beaver ponds located close to one another, differences in the habitat within each pond appears to produce very different demands on male mate-searching behaviour at the two sites. During the mating season, reproductive males at Barbs Marsh tend to move farther and have larger home ranges than males at Beaver Marsh. At Barbs Marsh, high levels of movement and large home ranges increase the number of receptive mates a male encounters and attempts to mate with. Since most receptive females at Beaver Marsh are located on dams, the best strategy for a male there may be to search a small area intensively.

The positive relationship between home range area and mating opportunity at Barbs Marsh is similar to that found by Madsen et al. (1993) in *V. berus*. They found that males that moved greater distances during the breeding season obtained more matings. Under certain conditions (e.g., if receptive females are widely or unpredictably distributed), mate-searching activity by males appears to be an important component of reproductive success. However, the factors that determine the level of mate-searching activity remain undetermined. Madsen et al. (1993) found that male movements were not related to body size. I found that movement and home range area were not related to either body size or energy reserves. Male mating activity corresponds to increased levels of plasma testosterone (Weil and Aldridge

1981, Bonnet and Nalleau 1996). Possibly, male water snakes with larger home ranges (and hence more mating opportunities) have higher testosterone levels. If this is the case, the important question is what factors cause differences in testosterone production among males? Although variation in body temperature affects the clearance rate of testosterone from the body of water snakes it is not known what factors affect its production (although energy reserves do not appear to be involved) (Weil and Aldridge 1979). Comparing testosterone levels between reproductive and nonreproductive males and determining what factors cause different levels of androgen production may be a useful area of future research. It may also help to clarify why all males do not appear to reproduce every year.

My finding that smaller males or males with larger energy stores did not participate in more mating aggregations than larger males is consistent with the findings of Weatherhead et al. (1995) and Weatherhead and Brown (1996). I also found that smaller males and males with higher relative energy reserves did not enjoy a mating advantage through mating with larger numbers of females nor were they more likely to locate unaccompanied females. Thus, it seems unlikely that the female-biased SSD in *N. sipedon* is maintained by selection favouring small male size through any increased ability to locate mates. It remains possible, however, that smaller males may be favoured through more subtle forms of

mating advantage (e.g., female choice, sperm competition).

Male mating activity at my study sites does not appear to be extremely expensive energetically. This appears to be in contrast to Feaver's (1977) data indicating that males forego feeding during the mating season and steadily lose weight. Males from my study populations will readily feed during the mating season and are often captured in minnow traps (presumably while foraging). The apparent differences in male energetics during the mating season could be related either to the density of prey or the density of females or rival males.

My results on the predicted decrease in male activity following the mating season are equivocal. Although data from transmitter-equipped males at Barbs Marsh suggests a decrease in activity following the mating season, consistent with the 'seasonal survival' hypothesis, the difference is not significant. However, the power of the statistical tests is low because of small sample sizes. My actual estimates of activity, movement and home range area, were also relatively crude. For instance, a male could move extensively within a single grid and yet would have low values of movement and home range size. It was not possible to quantify the activity of transmitter-equipped snakes based on observation because they would usually seek cover before visual contact was made. Radio-transmitters equipped with activity sensors would allow more accurate quantification of activity level.

This would provide a more decisive test of the trends observed in my study.

Summary and Conclusions

My goal in this study was to identify factors potentially influencing the evolution or maintenance of female-biased SSD in northern water snakes. In Chapter one, I determined that females delayed maturity and invested in growth for one year more than males. This is likely in response to the fecundity advantage associated with large body size. The success of this strategy is due to or enhanced by the concomitant increase in survivorship with body size among subadult females. I rejected the hypothesis that males remained small to decrease energy requirements as part of a 'survival strategy' because of the similarity between male and female annual survival rates and the lack of a decrease in male survivorship with body size. However, I hypothesized that a 'seasonal-survival strategy' could exist whereby selection favours the energetic advantage of smaller males during the latter half of the activity season.

In Chapter two, I described general thermal ecology of *N. sipedon*. Thermoregulatory indices indicated that the snakes were not especially careful thermoregulators and that during most of the activity season, the thermal environment provided ample opportunity for snakes to maintain their preferred body temperature. There was no evidence that snakes increased body temperature following feeding.

In Chapter three, I used body temperature data to test the seasonal-survival strategy. Differences in body

temperatures among males, nongravid females and gravid females were consistent with predictions based on the expected costs and benefits associated with thermoregulation for each category of snakes. Following the mating season, males showed a decrease in indices of thermoregulation, suggesting they were avoiding mortality costs associated with basking. This result was consistent with the seasonal-survival strategy hypothesis.

In Chapter four, I tested the hypothesis that small males could gain a reproductive advantage over large males through increased mate searching ability. Although the amount of area occupied by males snakes was correlated with mating success, it was not correlated with body size. Thus, small males do not appear to be more successful mate-searchers. I also used movement and home range data from transmitter-equipped males to test the seasonal-survival strategy. Although males appeared to dramatically decrease movement and home range size following the mating season at one marsh, because of the small sample size the differences were not significant.

In conclusion, although the selective advantage associated with large female size seems clear, the advantage of small male size is uncertain. However, there is evidence supporting the hypothesis that males attempt to decrease mortality costs following the mating season. Further study of seasonal size-specific patterns of male survival could

address whether smaller males do have a survival advantage after the mating season. It seems clear that small males do not have any advantage in finding receptive females during the mating period. It remains a possibility that smaller males enjoy a more subtle form of reproductive advantage through relatively larger sperm stores, sperm competition or female choice. Molecular studies assessing paternity could ascertain whether male reproductive success is related to body size and may provide insight into what the advantage might be.

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Appendix 1. Comparison of male and female body sizes at Barbs Marsh each year. Values are means followed by standard deviations in parentheses. Ranges are in parentheses beneath. t values refer to comparisons between male and female mean SVL each year. χ^2 values refer to sex ratio comparisons each year.

Year	FEMALE			MALE			t	χ^2
	N	SVL	MASS	N	SVL	MASS		
1988	27	56.3 (12.2) (32.7-74.2)	190.3 (109.9) (27-430)	57	45.5 (7.6) (29.4-60.6)	91.6 (41.0) (21-195)	4.22***	10.71**
1989	26	59.8 (12.1) (22.3-79.4)	208 (105.9) (8-510)	43	48.8 (7.8) (34.3-63.0)	100.4 (43.7) (30-188)	4.15***	4.19*
1990	38	59.4 (13.8) (27.2-86.3)	153.8 (82.9) (20-350)	49	51.3 (7.4) (31.1-71.0)	100.4 (37.2) (20-179)	3.27**	1.39
1991	33	60.5 (13.9) (35.2-81.7)	185.7 (107.6) (26.2-399)	43	52.4 (7.8) (35.5-68.3)	103.6 (36.0) (33-206)	3.0**	1.32

Appendix 1. (Continued)

Year	FEMALE			MALE			t	χ^2
	N	SVL	MASS	N	SVL	MASS		
1992	32	57.6 (16.2) (33.4-87.6)	155.1 (111.8) (34-388)	48	51.7 (8.0) (28.8-67.8)	104.4 (54.7) (21-351)	1.91	3.2
1993	56	55.0 (15.5) (26.0-88.6)	133 (101.0) (11-425)	53	47.2 (10.3) (25.7-69.8)	78.5 (42.5) (11-207)	3.14**	0.08
1994	53	56.0 (14.5) (16.5-82.1)	136.5 (96.5) (3.7-404)	56	47.2 (8.1) (26.0-68.0)	75.4 (38.7) (13-241)	3.9***	0.08
1995	56	57.1 (15.7) (25.0-83.2)	144.9 (110.5) (9-441)	48	49.1 (8.9) (28.3-73.3)	80.9 (41.3) (19-230)	3.25***	0.06
1996	48	58.5 (16.8) (20.1-86.8)	173.3 (136.5) (7-536)	41	46.7 (9.3) (22.2-62.8)	72.6 (35.9) (7.8-172)	4.15***	0.55
All	368	57.5 (14.8)	158.9 (109.4)	437	48.8 (8.7)	88.8 (41.2)	10.0***	

Appendix 2. Comparison of male and female body sizes at Beaver Marsh each year. Values are means followed by standard deviations in parentheses. Ranges are in parentheses beneath. t values refer to comparisons between male and female mean SVL each year. χ^2 values refer to sex ratio comparisons each year.

Year	FEMALE			MALE			t	χ^2
	N	SVL	MASS	N	SVL	MASS		
1990	25	67.6 (10.8) (45.8-87.4)	258 (132.3) (69-650)	20	53.8 (5.1) (43.3-60.2)	108.2 (30.6) (60-182)	5.66***	0.56
1991	6	71.4 (9.5) (57.5-82.5)	300.7 (135.1) (130-490)	9	56.6 (5.3) (48.4-64.6)	127.8 (46.5) (75-197)	3.89**	0.6
1992	11	73.9 (8.6) (60.8-85.5)	385.2 (115.0) (176-560)	9	54.1 (8.6) (36.6-62.9)	105.1 (35.8) (38-146)	5.13***	0.2
1993	12	73.9 (10.5) (49.4-87.1)	307.4 (122.5) (74-512)	14	50.8 (9.0) (25.6-62.2)	93.6 (33.3) (11-138)	6.07***	0.15

Appendix 2. (Continued)

Year	FEMALE			MALE			χ^2
	N	SVL	MASS	N	SVL	MASS	
1994	57	60.8 (16.3) (28.0-88.4)	195.1 (130.0) (18.5-580)	56	50.2 (10.3) (16.3-69.1)	93.2 (40.8) (3.6-191)	0.009
1995	56	61.1 (14.8) (23.5-86.9)	177.3 (100.9) (12.5-391)	50	48.6 (8.2) (29.5-64.9)	82.8 (36.7) (14-178)	0.34
1996	57	58.1 (16.7) (17.6-80.7)	182 (108.2) (5.1-311)	43	46.7 (8.1) (26.9-60.4)	75.7 (33.9) (14-151)	1.96
All	224	62.6 (15.4)	206.7 (126.5)	201	49.9 (8.8)	90.5 (38.7)	10.5***

Appendix 3. Comparison of von Bertalanffy growth equation parameters of male and female *N. sipedon* in Barbs Marsh over nine years. A is the asymptotic body size parameter, k is the characteristic growth constant, which indicates the rate of approach to the asymptote. Values are parameter estimates followed by 95% support plane confidence intervals in parentheses.

YEAR	SEX	N	A	k
1988	F	10	106.1 (60.4-151.8)	0.0016 (-0.0001-0.0033)
	M	27	61.2 (53.1-69.3)	0.0028 (0.0009-0.0047)
1989	F	12	77.2 (64.3-90.1)	0.0049 (0.0009-0.0089)
	M	27	62.4 (54.0-70.8)	0.0035 (0.0009-0.0061)
1990	F	28	85.6* (77.1-94.1)	0.0026 (0.0015-0.0037)
	M	34	64.2 (57.9-70.5)	0.0027 (0.0011-0.0043)
1991	F	14	86.7* (74.3-99.1)	0.0030 (0.0011-0.0049)
	M	24	62.3 (57.8-66.8)	0.0032 (0.0017-0.0047)
1992	F	21	85.6* (77.5-93.7)	0.0027 (0.0018-0.0036)
	M	23	64.3 (55.0-73.6)	0.0019 (0.0006-0.0032)
1993	F	32	91.0* (78.5-103.5)	0.0023 (0.0014-0.0032)
	M	37	62.0 (56.8-67.2)	0.0031 (0.0020-0.0042)
1994	F	60	92.5* (79.8-105.2)	0.0018 (0.0011-0.0025)
	M	54	66.4 (60.1-72.7)	0.0016 (0.0010-0.0022)
1995	F	47	90.9* (77.2-104.6)	0.0019 (0.0010-0.0028)
	M	31	58.6 (54.3-62.9)	0.0029 (0.0016-0.0042)
ALL	F	224	89.2* (84.8-93.6)	0.0022 (0.0019-0.0025)
	M	257	63.2 (60.9-65.5)	0.0025 (0.0021-0.0029)

* parameter estimates differ significantly between the sexes at $p < 0.05$

Appendix 4. Ages of male and female *N. sipedon* captured at Barbs Marsh each year. Age values are means with standard deviations in parentheses.

Year	N	Sex	Age	t	p
1988	27	F	3.1 (1.32)	-0.305	0.76
	57	M	3.2 (1.47)		
1989	26	F	3.4 (1.20)	-1.11	0.32
	43	M	3.8 (1.83)		
1990	38	F	3.3 (1.48)	-2.67	0.009
	49	M	4.4 (1.92)		
1991	33	F	3.6 (1.64)	-2.50	0.015
	43	M	4.7 (2.09)		
1992	32	F	3.5 (2.13)	-2.07	0.042
	48	M	4.5 (2.26)		
1993	56	F	3.2 (1.84)	-1.54	0.13
	53	M	3.8 (2.18)		
1994	53	F	3.0 (1.59)	-1.34	0.18
	56	M	3.5 (1.98)		
1995	56	F	3.5 (1.80)	-1.66	0.10
	48	M	4.1 (2.23)		
1996	48	F	3.6 (2.00)	-0.36	0.72
	41	M	3.7 (1.87)		

Appendix 5. Ages of male and female *N. sipedon* captured at Beaver Marsh each year. Age values are means with standard deviations in parentheses.

Year	N	Sex	Age	t	p
1990	25	F	4.7 (2.01)	-0.83	0.41
	20	M	5.2 (1.79)		
1991	6	F	4.8 (1.60)	-1.24	0.24
	9	M	6.2 (2.39)		
1992	11	F	5.7 (1.95)	-0.16	0.88
	9	M	5.9 (2.71)		
1993	12	F	6.1 (2.47)	1.92	0.07
	14	M	4.4 (1.91)		
1994	57	F	4.0 (2.26)	-1.37	0.17
	56	M	4.6 (2.69)		
1995	56	F	3.8 (1.82)	-0.50	0.62
	50	M	4.0 (2.22)		
1996	57	F	3.5 (1.77)	-0.31	0.76
	43	M	3.6 (1.61)		

Appendix 6. Jolly-Seber estimates of population size and survivorship of males and females in Barbs Marsh over the study period. Values are parameter estimates followed by standard errors and 95% confidence intervals (Manly 1984) in parentheses.

Year	Sex	Population Size	Survivorship
1988	F	\	0.52 (0.14) (0.29-0.90)
	M	\	0.54 (0.08) (0.39-0.75)
1989	F	42.0 (11.4) (28.2-69.9)	0.51 (0.11) (0.34-0.76)
	M	56.2 (6.7) (46.5-66)	0.71 (0.09) (0.56-0.91)
1990	F	41.2 (5.2) (38.0-55.5)	0.56 (0.09) (0.40-0.76)
	M	63.6 (7.5) (52.9-74.6)	0.62 (0.08) (0.48-0.80)
1991	F	36.1 (4.9) (33.1-46.7)	0.50 (0.11) (0.32-0.75)
	M	49.4 (6.0) (43.6-57.4)	0.53 (0.08) (0.39-0.70)
1992	F	44.4 (8.5) (33.8-62.8)	0.53 (0.09) (0.39-0.73)
	M	46.2 (4.3) (47.2-57.7)	0.43 (0.07) (0.31-0.59)
1993	F	54.3 (3.8) (56.4-68.7)	0.52 (0.07) (0.40-0.67)
	M	51.4 (3.8) (53.1-62.2)	0.71 (0.07) (0.58-0.86)

Appendix 6. (Continued)

Year	Sex	Population Size	Survivorship
1994	F	54.9 (4.6) (53.3-63.6)	0.71 (0.07) (0.58-0.85)
	M	62.5 (5.6) (57.9-72.7)	0.53 (0.07) (0.41-0.67)
1995	F	60.0 (7.2) (56.0-69.1)	\
	M	47.5 (5.9) (48.0-57.7)	\
MEAN	F	47.6 (3.33)	0.53 (0.03)
	M	53.8 (2.68)	0.58 (0.04)

Appendix 7. Jolly-Seber estimates of population size and survivorship of males and females in Beaver Marsh over the study period. Values are parameter estimates followed by standard errors and 95% confidence intervals (Manly 1984) in parentheses.

Year	Sex	Population Size	Survivorship
1990	F	\	0.82 (0.74) (0.26-2.70)
	M	\	0.64 (0.33) (0.27-1.51)
1991	F	35.9 (34.4) (10.8-135.6)	0.26 (0.22) (0.08-0.87)
	M	26.9 (15.1) (12.3-70.7)	0.43 (0.24) (0.17-1.06)
1992	F	10.3 (2.7) (12.2-17.2)	0.36 (0.15) (0.17-0.71)
	M	14.2 (6.0) (10.0-32.4)	0.96 (0.71) (0.30-2.96)
1993	F	10.4 (1.8) (14.4-15.5)	0.64 (0.15) (0.39-0.92)
	M	91.9 (100.4) (22.5-527.7)	0.24 (0.12) (0.10-0.57)
1994	F	50.8 (1.9) (64.9-75.8)	0.63 (0.10) (0.47-0.84)
	M	48.9 (4.1) (69.3-79.3)	0.50 (0.09) (0.36-0.71)
1995	F	72.0 (11.6) (59.3-92.8)	\
	M	56.4 (9.8) (50.0-80.8)	\
MEAN	F	35.9 (11.9)	0.54 (0.10)
	M	47.7 (13.4)	0.55 (0.12)

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