

Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake, *Seminatrix pygaea*

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Abstract The causes and consequences of body size and sexual size dimorphism (SSD) have been central questions in evolutionary ecology. Two, often opposing selective forces are suspected to act on body size in animals: survival selection and reproductive (fecundity and sexual) selection. We have recently identified a system where a small aquatic snake species (*Seminatrix pygaea*) is capable of surviving severe droughts by aestivating within dried, isolated wetlands. We tested the hypothesis that the lack of aquatic prey during severe droughts would impose significant survivorship pressures on *S. pygaea*, and that the largest individuals, particularly females, would be most adversely affected by resource limitation. Our findings suggest that both sexes experience selection against large body size during severe drought when prey resources are limited, as nearly all *S. pygaea* are absent from the largest size classes and maximum body size and SSD are dramatically reduced following drought. Conversely, strong positive correlations between maternal body size and reproductive success in *S. pygaea* suggest that females experience fecundity selection for large size during non-drought years. Collectively, our study emphasizes the dynamic interplay between selection pressures that act on body size and supports theoretical predictions about the relationship between body size and

survivorship in ectotherms under conditions of resource limitation.

Keywords Cost of reproduction · Natural selection · Prey abundance · Sexual selection · Tradeoffs

Introduction

Body size is one of the most obvious characteristics of any organism and plays an important ecological role by influencing nearly all physiological and life history attributes, which in turn influence reproduction and survival (Peters 1983; Stearns 1992; Schmidt-Nielsen 1997). As a result, ecologists and evolutionary biologists have long studied the determinants and consequences of body size. A recurring theme is that the optimal body size for any given organism is context dependent and is often shaped by multiple, sometimes antagonistic forces (e.g., Darwin 1871; Case 1978; Wikelski 2005; Cox et al. 2007). In particular, two broad categories of selection act on body size: survival selection and selection for reproductive success, including sexual selection and fecundity selection (Preziosi and Fairbairn 1997; Wikelski and Trillmich 1997; Bonnet et al. 2000). Species that exhibit sexual size dimorphism (SSD)—sexual differences in body size—are of particular interest in this regard, because they provide the opportunity to explore the causes and consequences of different body sizes within a single species or population.

Ultimately, the direction and magnitude of SSD are determined by the ratio of different selection pressures on body size between each of the sexes (Arak 1988; Hedrick and Temeles 1989; Preziosi and Fairbairn 1997). Two dominant patterns of SSD are generally recognized, although more complex cases do exist (e.g., Madsen and

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Shine 1994). First, males are typically larger than females (male-biased SSD) in cases where the mating system is dominated by male-to-male combat (Darwin 1871; Clutton-Brock et al. 1977; Shine 1994). In this scenario, sexual selection for enhanced combat ability generally results in stronger selection for increased body size in males, compared to females. In contrast, females are usually larger than males (female-biased SSD) in populations with mating systems that do not involve male-to-male combat (Darwin 1871; Shine 1994). Female-biased SSD is often explained by the fecundity advantage hypothesis, whereby there is strong selection for large females because they are able to carry more or larger offspring than small females (Darwin 1871; Semlitsch and Gibbons 1982; Seigel and Ford 1987; Shine 1994). Thus, in the absence of stronger selection for large size in males, fecundity selection will lead to female-biased SSD (Shine 1994).

Although selection pressures that generate sexual divergence in body size have been identified for many organisms, relatively few studies have examined selection pressures that moderate or exaggerate SSD within or among populations. For example, decreased food availability and/or prey size is known to negatively influence survivorship of larger individuals of reptiles (e.g., Madsen and Stille 1988; Wikelski and Trillmich 1997; Beaupre 2002; Wikelski 2005) and has been correlated with the evolution of island dwarfism in snakes and lizards (e.g., Case 1978; Boback 2003; Keogh et al. 2005; Jessop et al. 2006). The cause is generally straightforward: absolute metabolic energy requirements are positively correlated with body size (Bennett and Dawson 1976; Bennett 1982). In other words, although the metabolic rate per gram of tissue is lower for larger individuals (Bennett and Dawson 1976; Bennett 1982), absolutely more energy is required for larger individuals to support maintenance energy requirements, compared to smaller individuals, all else being equal (McNab 1971; Beaupre and Duvall 1998; McNab 1999; Bonnet et al. 2000; Beaupre 2002; Madsen and Shine 2002). Thus, unless larger individuals are relatively more efficient at foraging, smaller individuals will experience higher survivorship during periods of resource shortage (Forsman 1996; Beaupre 2002). In such cases, natural selection for ecological traits that increase survivorship during food shortages (e.g., smaller body size) may be in direct conflict with reproductive selection pressures that favor large body size (Forsman 1996; Beaupre and Duvall 1998).

On the Galapagos Archipelago, Galapagos marine iguanas (*Amblyrhynchus cristatus*) provide an outstanding demonstration of the existence of this phenomenon (Wikelski and Trillmich 1997; Wikelski 2005). *Amblyrhynchus cristatus* exhibit male–male combat for females, resulting in sexual selection for larger males and male-biased SSD.

However, during periods of food shortage caused by El Niño–Southern Oscillation (El Niño) events, the largest adults within populations experience the lowest survivorship because of their higher absolute energy requirements. As a result of fluctuating selection pressures, for large male body size in some years and small body size in other years, the degree of male-biased SSD fluctuates and is greatly reduced following El Niños. Moreover, mean adult body size and the degree of SSD differ among islands within the Galapagos archipelago; islands with greater food resources have larger lizards and a greater degree of male-biased SSD (Wikelski and Trillmich 1997; Wikelski 2005).

Recently, we have identified a system where a small aquatic snake species, the black swamp snake (*Seminatrix pygaea*), is capable of surviving severe drought conditions by aestivating in dried wetlands (Winne et al. 2006b). Presumably, the general lack of aquatic prey during extreme droughts (Gibbons et al. 2006) poses significant survivorship pressures on *S. pygaea*, analogous to those experienced by *A. cristatus* during El Niño events. In contrast to *A. cristatus*, however, *S. pygaea* exhibit female-biased SSD and no male–male combat (Gibbons and Dorcas 2004; Winne et al. 2005). Thus, our study system provides a unique opportunity to test the generality of the hypothesis that an antagonism exists between survivorship and reproductive selection pressures that act on body size and SSD. In particular, we are able to examine temporal variation in body size structure, maximum body size, and SSD within a single *S. pygaea* population. We predicted that: (1) the largest *S. pygaea* would be absent from the population following prolonged, severe droughts; and that (2) female-biased SSD would be more extreme in years following high food availability, compared to years following drought-induced aestivation and a shortage of aquatic prey. In addition, we examine the influence of maternal body size on litter size and offspring characteristics in *S. pygaea* to demonstrate the potential for fecundity selection to counteract survivorship selection and, thus, maintain female-biased SSD within the population.

Materials and methods

Study organism

Seminatrix pygaea is a member of the cosmopolitan subfamily Natricinae and is endemic to aquatic habitats throughout a portion of the southeastern US Coastal Plain. It is the smallest semi-aquatic snake in North America, reaching a maximum recorded snout-to-vent length (SVL) of 485 mm (Gibbons and Dorcas 2004), and published interspecific comparisons of SSD among snakes indicate that *S. pygaea* may be less sexually dimorphic than most

other naticine species (e.g., see Appendix 1 in Shine 1994). Like other New World naticines, *S. pygaea* is viviparous (Sever et al. 2000), and mothers typically give birth in late July or early August (Seigel et al. 1995b; Winne et al. 2005). They rely upon an income breeding strategy to reproduce and nearly all adult females are reproductive in years when the wetland holds water through parturition (Winne et al. 2006b). *S. pygaea* is capable of feeding on a wide variety of aquatic prey (Gibbons and Dorcas 2004). However, both males and females have fed nearly exclusively (i.e., 99%; $n = 610$ prey items) on aquatic larvae and pedomorphs of the mole salamander (*Ambystoma talpoideum*) at our study site since the early 1990s. A positive correlation exists between the body size of *S. pygaea* and the size of *A. talpoideum* consumed ($n = 334$; $r^2 = 0.11$; $P < 0.001$). Adult *S. pygaea* have very high rates of evaporative water loss compared with sympatric semi-aquatic snakes (Winne et al. 2001; Moen et al. 2005) and, consequently, they rarely venture away from the water's edge (Gibbons and Dorcas 2004).

Study site

Ellenton Bay is an isolated freshwater wetland located on the U.S. Department of Energy's Savannah River Site (SRS) in the upper Coastal Plain of South Carolina, USA. Although the water level is extremely variable, the bay generally holds water year-round, and covers approximately 10 ha when full. During most years, Ellenton Bay is dominated by shallow water (<1 m deep) and relatively uniform distributions of emergent grasses (predominantly *Panicum* spp.), water lilies (*Nymphaea odorata*), and water shields (*Brasenia schreberi*). However, severe droughts have rendered Ellenton Bay dry on at least three occasions in the past three decades, most recently during 1987–1990 and 2000–2003 (Seigel et al. 1995a; Willson et al. 2006; Winne et al. 2006b). When dry, a thick (up to 0.5 m) organic crust covers the entire basin but subsurface areas remain moist and small, temporary (<2 months) open water areas are often present in the early spring when there has been sufficient precipitation (Fig. 1). However, these small, temporary pools provide only a brief source of *A. talpoideum* for *S. pygaea* to consume during extended droughts and the snakes are limited to only small (<4 g) prey (Fig. 1). This stands in sharp contrast to non-drought years, which provide a relatively continuous source of large (up to 8 g), pedomorphic *A. talpoideum* (Fig. 1).

The habitat surrounding Ellenton Bay is a mosaic of old-fields in various stages of succession and second-growth mixed pine-hardwood forest. In drought years, Ellenton Bay is the last non-permanent wetland to dry within the region (i.e., it has the longest hydroperiod). The only permanent

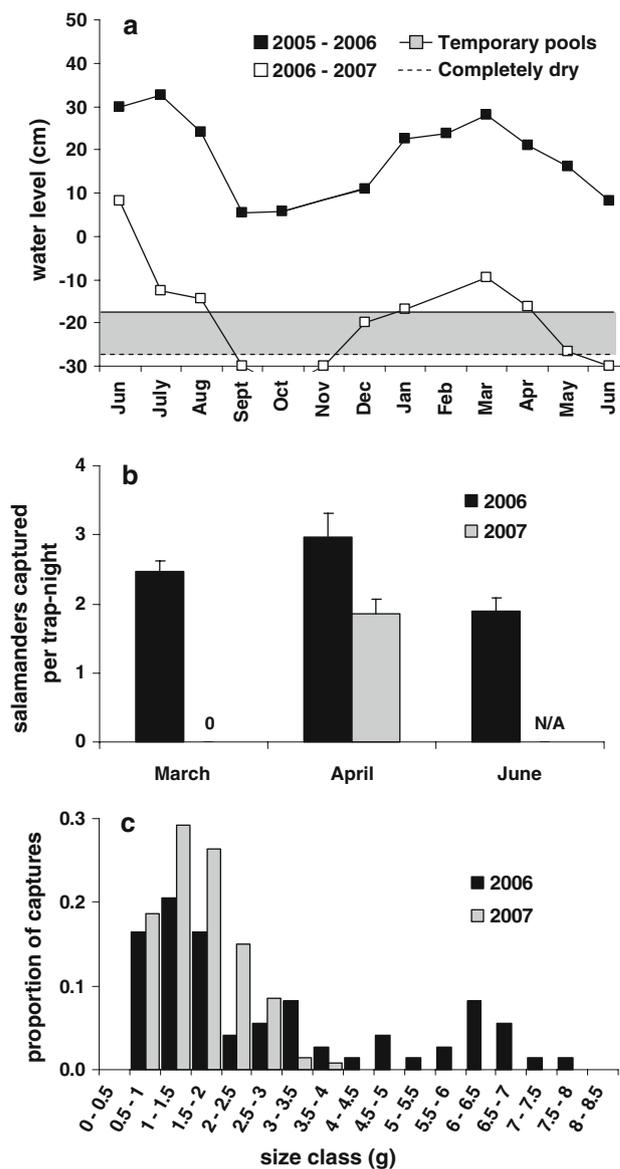


Fig. 1 Prey availability at Ellenton Bay in relation to drought. **a** Water level at Ellenton Bay in non-drought (2005–2006) and drought (2006–2007) years. **b** Mean (+SE) abundance of aquatic salamanders (larval and pedomorphic *Ambystoma talpoideum*) as measured by catch-per-unit effort in minnow traps in 2006 ($n = 227$ trap-nights) and 2007 ($n = 82$ trap-nights). **c** Size-frequency distributions of *A. talpoideum* captured in the first week of May 2006 ($n = 73$) and 2007 ($n = 140$). Note that in March 2007 no salamanders were captured, despite the presence of water within the wetland, and only small salamanders (<4 g) were available in April and early May 2007. By June 2007 the wetland was dry and no aquatic prey were available for the rest of the year

wetland within 1.4 km of Ellenton Bay is a small, manmade pond ca. 0.5 km from Ellenton Bay. However, no *S. pygaea* have been captured in the pond during aquatic trapping over many years (C. T. Winne, J. D. Willson, and J. W. Gibbons, unpublished data). In fact, the two closest known *S. pygaea* populations are 5.7 and 8.7 km from Ellenton Bay.

Consequently, the Ellenton Bay population is effectively isolated from all known populations of *S. pygaea* on the SRS. Ellenton Bay is currently fish-free but harbors a diverse assemblage of amphibians (24 species) and semi-aquatic reptiles (18 species) during most years (Gibbons and Semlitsch 1991; Gibbons et al. 2006).

Data collection

To assess post-drought changes in body size distributions of *S. pygaea* within Ellenton Bay, we conducted aquatic trapping during May and June of each of the following years: 1983–1987 (Seigel et al. 1995a; Seigel et al. 1995b), 1998 (Winne et al. 2005), and 2003 (Winne et al. 2006b). We used a combination of commercially available steel and plastic minnow traps (Willson et al. 2005) set approximately 2 m apart in transects along the margin of the bay amidst emergent vegetation. Although we did not purposefully bait the traps, they naturally accumulated amphibian larvae between daily trap checks and we left these in the traps (Seigel et al. 1995a; Winne 2005). All captured snakes were returned to the laboratory where we recorded SVL (nearest mm), body mass (nearest 0.1 g using an electronic balance), and sex (by visual inspection or probing). We marked each snake with a unique code by scale-clipping (1983–1987, 1998) or heat-branding (2003; Winne et al. 2006a). We released all snakes the following day (1983–1987, 2003) or at the end of each 5-day trapping period (1998). Additionally, we used a terrestrial drift fence that completely encircled Ellenton Bay to document the body sizes of any *S. pygaea* that moved into or out of the wetland during 2003 (for details see Willson et al. 2006; Winne et al. 2006b).

To determine maternal-litter relationships for *S. pygaea* from Ellenton Bay, we collected 16 pregnant females from 21 May to 30 July 2003 and housed them under laboratory conditions until parturition. We housed snakes individually in plastic 5-l shoeboxes, fitted with paper towels as a substrate and a large water dish that allowed snakes to fully submerge. We placed all cages in an environmental chamber at 25°C with a 14-h:10-h light:dark photoperiod. We changed water and towels 2–3 times per week, and offered all snakes live salamander larvae (*A. talpoideum*) totaling 40–60% of the snake's mass every 7–10 days. During late July and August we examined cages once or twice daily for the presence of neonates. All pregnant females gave birth from 3 to 25 August 2003. We measured the SVL and mass of mothers and neonates within 24 h of parturition. We also incorporated maternal and litter size data (determined by palpation) collected at Ellenton Bay from 1983 to 1987 ($n = 70$; for details of these methods see Seigel et al. 1995b; Winne et al. 2006b) into our analyses of maternal-litter relationships.

Statistical analyses

We compared size-frequency distributions of *S. pygaea* among three time intervals to assess drought-associated changes in population size structure. Snake captures from 1983 to 1987 were combined and represent historical size-frequency distributions, which occurred prior to a major drought that began in autumn 1987 and ended in 1990 (Seigel et al. 1995a). Captures from 1998 constitute the population size structure immediately prior to the recent drought (September 2000–February 2003) that is the focus of this paper. Snakes captured during 2003 comprise the drought survivors and, thus, yield estimates of post-drought size structure. We have recently documented that aquatic minnow traps cannot reliably capture *S. pygaea* smaller than 200 mm SVL (Willson et al. 2008). Therefore, we excluded individuals smaller than 200 mm SVL from all figures and analyses. We also excluded recaptured snakes within each year category (i.e., 1983–1987, 1998, 2003) to avoid pseudoreplication.

We compared maximum body size among years using the largest 10% of individuals of each sex captured in a given year category (1983–1987, $n = 107$; 1998, $n = 120$; 2003, $n = 68$) as our indicator of maximum body size. We used a two-way ANOVA (independent factors: year and sex, dependent factor: SVL) to examine the effects of year, sex, and year-by-sex interactions. Subsequently, we used Tukey's honestly significant difference test for post-hoc comparisons. We also calculated an index of SSD for each year, using the difference between the ratio of female to male SVL (based on the largest 10% of individuals in each sex) and one (Shine 1994). Following the methods of Forsman (1991) and Wikelski and Trillmich (1997), we verified that using the largest 10% of individuals for each sex/year category was a robust estimate of maximum body size for our study. To do this, we calculated maximum body size of each sex (for each year category) using eight different metrics: the SVL of the single largest individual and the mean SVL of the two, three, four, five, or ten largest individuals, and also the mean SVL of the largest 5% of the population and largest 10% of the population. We found that indices of maximum body size were all highly correlated (Kendall's coefficient of concordance: males, $W = 0.89$, $P < 0.001$; females, $W = 1$, $P < 0.001$), indicating that annual comparisons of maximum body size in *S. pygaea* are insensitive to the number of individuals used in the calculation (Forsman 1991; Wikelski and Trillmich 1997).

We used linear regression (on natural log-transformed variables) to describe the relationships between maternal SVL and mean litter characteristics. To assess the effect of maternal length on relative post-partum body condition, we regressed mass against SVL and plotted the best fit linear

line. We used the STATISTICA for Windows (1998) software package (StatSoft 1998; StatSoft, Tulsa, Okla) for all tests. All means are presented ± 1 SE.

Results

We observed dramatic differences in size-frequency distributions of *S. pygaea* captured before (1983–1987, 1998) and after (2003) prolonged drought (Fig. 2). In pre-drought years, a large proportion (25–32.7%) of individuals was larger than 325 mm SVL (Fig. 2a, b). However, following the 2000–2003 drought only one individual (1.5% of the population), a female, was larger than 325 mm SVL (Fig. 2c). Hence, both males and females from these larger size classes (i.e., ≥ 325 mm SVL) were noticeably absent. Inspection of the size-frequency histograms indicates that females (typically the larger of the two sexes) experienced a greater shift toward smaller size than did males following the drought. After the drought, only nine *S. pygaea* entered Ellenton Bay (throughout all of 2003) and all of these animals were similar in size to those captured contemporaneously within the wetland (one female, 234 mm SVL; eight males, SVLs 250–315 mm).

We found significant variation in maximum body size among years ($F_{2,24} = 16.55$; $P < 0.001$) and between the sexes ($F_{1,24} = 31.88$; $P < 0.001$). There was no significant interaction between year and sex ($F_{2,24} = 0.90$; $P = 0.418$). Temporal variation in maximum body size was due only to changes between pre- and post-drought comparisons ($P < 0.001$), as there were no statistical differences in maximum body size between the two pre-drought samples ($P = 0.542$). Comparisons of the SSD index revealed that SSD was greater in pre-drought years (1983–1987, SSD = 0.147; 1998, SSD = 0.161) than in 2003 (SSD = 0.095), indicating that compared with males, females experienced a greater reduction in maximum body size. Further evidence of a post-drought decrease in SSD is provided by year-by-sex independent contrasts, which demonstrated that maximum body size was significantly reduced following drought for females ($P \leq 0.001$), but not for males ($P \geq 0.271$). As expected, independent contrasts showed no significant differences in maximum body size between pre-drought years for males ($P = 0.998$) or females ($P = 0.865$). Overall, maximum body size and SSD were greater in pre-drought years and were dramatically reduced after the 2000–2003 drought (Fig. 3).

As expected, there was a significant positive relationship between maternal SVL and litter size in 2003 ($r^2 = 0.39$; $P = 0.010$) and in all years (1983–1987 and 2003; data not available for 1998) combined ($n = 86$ litters; $r^2 = 0.35$;

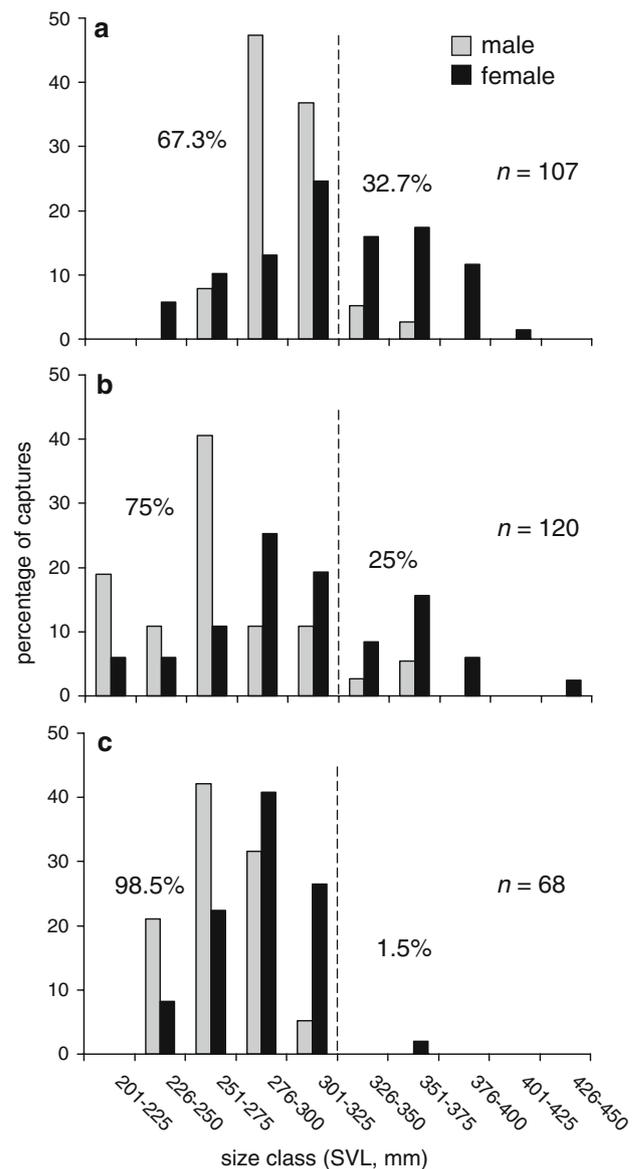


Fig. 2 Percentage of *S. pygaea* captures at Ellenton Bay by size-class (snout-to-vent length; SVL) in 1983–1987 (**a**; pre-drought), 1998 (**b**; pre-drought), and 2003 (**c**; post-drought). Prior to the onset of the 2000–2003 drought (**a**, **b**), females were significantly larger than males and 25–32.7% of the population was larger than 325 mm SVL. In contrast, immediately following the drought (**c**) sexual size dimorphism (SSD) was reduced, and only one snake (1.5% of captures) was larger than 325 mm SVL. Individuals smaller than 200 mm SVL were excluded from figure (see “Materials and methods”). All snakes were captured in May or June

$P < 0.001$; Fig. 4a). Also, longer mothers gave birth to longer (SVL: $r^2 = 0.24$; $P = 0.051$; Fig. 4b) and heavier ($r^2 = 0.24$; $P = 0.054$; Fig. 4c) offspring. Regressing post-partum mass on maternal body length (SVL) demonstrated that mid-sized females had greater masses for their length (i.e., were less emaciated) compared to small and large adult females (Fig. 4d).

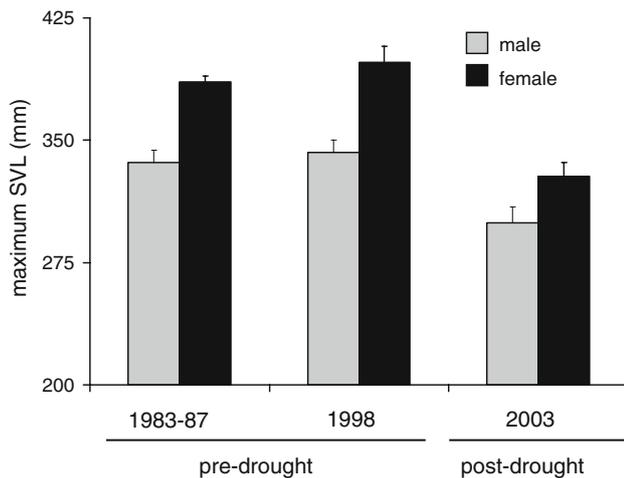


Fig. 3 Maximum body size (SVL) of *S. pygaea* at Ellenton Bay. Maximum body size and SSD were greatest in pre-drought years and were significantly reduced in 2003, after the 2000–2003 drought ($P < 0.001$). All snakes were captured in May or June

Discussion

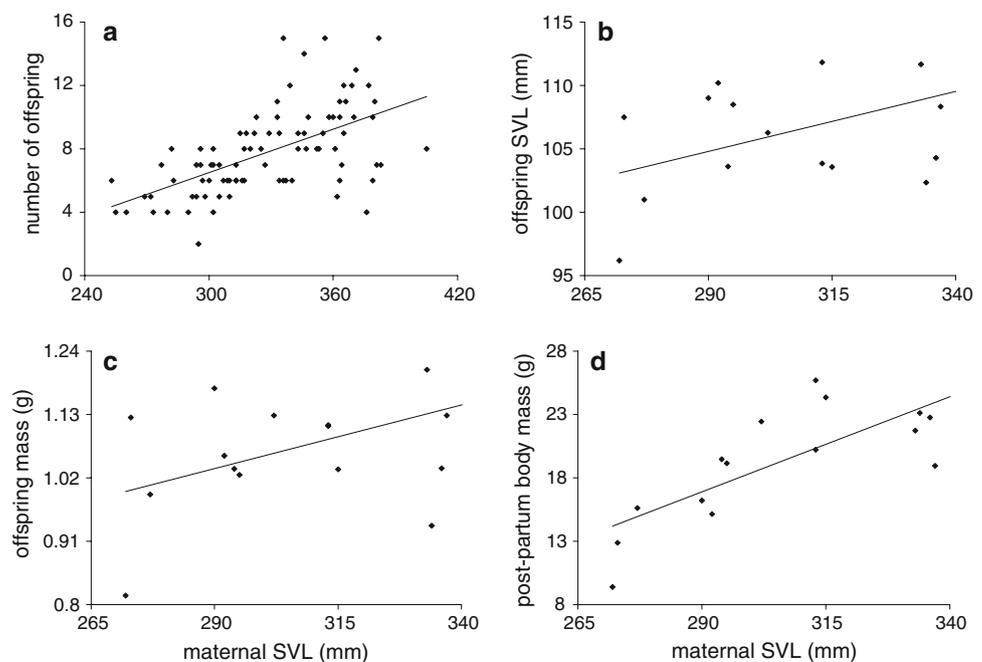
Drought-induced mortality

We predicted that extreme drought, such as the 2000–2003 drought that left Ellenton Bay effectively dry and relatively devoid of amphibian prey for multiple years, would pose significant hardships to *S. pygaea*. In particular, we predicted that larger *S. pygaea* would suffer greater mortality during the drought-induced prey shortage, analogous to the survivorship patterns observed for *A. cristatus* during El

Niño-induced resource shortages on the Galapagos archipelago (Wikelski and Trillmich 1997; Wikelski 2005). Aestivation ultimately allowed a substantial proportion of *S. pygaea* to survive the drought (Winne et al. 2006b), unlike many sympatric species of semi-aquatic snakes that do not aestivate and which experienced precipitous declines or local extirpations (Willson et al. 2006). Nevertheless, we observed substantial shifts in the demography of *S. pygaea* following the drought that were indicative of differential survival among individuals. Both average and maximum body size were significantly reduced after the drought, results that support our hypothesis and fit expected changes in body size of reptiles experiencing prolonged food scarcity. Simply put, in reptiles larger individuals have higher absolute metabolic rates and energy requirements (Bennett and Dawson 1976; Bennett 1982), making resource scarcity potentially more costly for larger individuals (e.g., Madsen and Stille 1988; Wikelski and Trillmich 1997; Beaupre 2002; Madsen and Shine 2002).

We observed a larger demographic shift in female than male *S. pygaea* following the drought. Typically, female *S. pygaea* attain larger maximum body size than males and few males grow larger than 325 mm SVL. Thus, one likely reason that females experienced greater post-drought decline in body size is that, being larger, more of them exhausted energy reserves before the drought ended. However, an additional reason is that costs associated with female reproduction may have left females with reduced energy reserves prior to the drought and contributed to lower survivorship following parturition and the onset of drought (Madsen and Shine 1993a; Luiselli et al. 1996;

Fig. 4 Relationships between maternal body size (SVL) and reproductive characteristics in *S. pygaea* at Ellenton Bay. There was a significant positive relationship between maternal SVL and **a** litter size ($P < 0.001$), **b** mean offspring SVL ($P = 0.051$), and **c** mean offspring body mass ($P = 0.054$). Plotting the relationship between **d** maternal SVL and post-partum body mass demonstrates that mid-sized females are relatively fatter (above best-fit line) than the longest females, which were extremely emaciated following parturition



Brown and Weatherhead 1997; Shine 2003). For example, female water pythons (*Liasis fuscus*) that allocate more energy to reproduction experience lower survival rates (Madsen and Shine 2000a). At Ellenton Bay *S. pygaea* are income breeders and most females reproduce every year if there is standing water (Winne et al. 2006b). The majority of *S. pygaea* give birth in late July or August (Seigel et al. 1995b; Winne et al. 2005). These months coincide with the beginning of the driest season in the region and in 2000 parturition occurred approximately 1 month before Ellenton Bay dried completely, from 2000 to early 2003. Adult females, therefore, would have had little, if any time to recover from the depletion of energy reserves allocated to reproduction before entering aestivation. Although all female *S. pygaea* typically invest a majority of their lipid reserves into reproduction (C. T. Winne, unpublished data), mid-sized females (ca. 295–315 mm SVL) were less emaciated after parturition than larger females, suggesting that they had greater post-partum energy reserves. This corresponds with our observation that the largest females had the lowest survivorship during the drought.

Three alternative interpretations of our results include: (1) selective emigration of large *S. pygaea* prior to the drought, (2) disproportionate shrinking of large individual *S. pygaea*, and (3) large *S. pygaea* of both sexes dying of old age. The available evidence does not support any of these hypotheses. First, we found that little overland migration occurred in *S. pygaea* following the 2000–2003 drought (Willson et al. 2006; Winne et al. 2006b). Only nine *S. pygaea* entered Ellenton Bay in 2003 and all were shorter than 325 mm SVL, indicating that our samples were based on the resident population and that no larger individuals survived. Furthermore, previous studies of *S. pygaea* have demonstrated that neonates and juveniles move overland far more frequently than adults (Dodd 1993; Winne et al. 2005). Also, because no *S. pygaea* have ever been captured in nearby wetlands (the closest *S. pygaea* occurrence is 5.7 km away; C. T. Winne and J. D. Willson, unpublished data), it is unlikely that the largest *S. pygaea* survived the drought by emigrating to nearby wetlands. Second, long-term studies spanning periods of severe food shortage suggest that significant shrinkage does not occur in individual snakes (Madsen and Shine 2001; Luiselli 2005). We observed no evidence of shrinking by any *S. pygaea* during our study, but we note that snakes were not permanently marked prior to the drought. Nonetheless, despite the ability of Galapagos marine iguanas to shrink up to 20% in body length during El Niños (Wikelski and Thom 2000), the largest iguanas still suffered disproportionate starvation-induced mortality. Third, in reptiles, survivorship generally increases with age or is independent of age after the first year (Turner 1977; Parker and Plummer 1987). Age and body size are often not highly

correlated in adult reptiles because of substantial individual variation in growth trajectories (Madsen and Shine 2000b; Blouin-Demers et al. 2002). Thus, although we were not able to age adult *S. pygaea* in our population, it is unlikely that all of the largest individuals were also the oldest individuals. Additionally, evidence from another reptile demonstrates that when resources are limited, natural selection against large body size occurs independently of age (Wikelski and Trillmich 1997; Wikelski 2005).

Shifting SSD

Traditionally, SSDs have been treated as species-specific traits. More recently, a few studies have demonstrated that SSD can vary among populations (e.g., Forsman 1991; Madsen and Shine 1993c; Pearson et al. 2002) or among age classes (King et al. 1999) and have attempted to understand the ecological causes of this variation using comparative techniques. We predicted that, compared to pre-drought years, SSD would be reduced following periods of prolonged food shortage, such as the 2000–2003 drought. As predicted, we observed significant annual variation in SSD within a single population, with both maximum body size and SSD being reduced immediately following a severe drought. More broadly, the annual pattern of variation in SSD that we observed for *S. pygaea* supported our prediction that the larger sex of sexually dimorphic species should be most adversely affected by resource limitation, thus reducing maximum body size and the degree of SSD.

One obvious question that arises from our results is: if *S. pygaea* undergo periodic, drought-induced selection for reduced body size, then what are the potential mechanisms that maintain female-biased SSD in *S. pygaea*? That is, why do *S. pygaea* ever grow larger than a size capable of surviving prolonged droughts, and why do females grow even larger than males? The prevalence of female-biased SSD has been well documented in natricine snakes (Shine 1994; King et al. 1999) and there is strong theoretical and empirical evidence that fecundity selection generally favors large body sizes in female snakes (Semlitsch and Gibbons 1982; Shine 1994; Shine and Wall 2005). In *S. pygaea*, we found strong positive relationships between female body size and several measures of reproductive success, including litter size, offspring length, and offspring mass. The production of a greater number of offspring has obvious evolutionary advantages, but producing larger offspring is also beneficial because it can increase offspring survivorship (Saint Girons and Naulleau 1981; Kissner and Weatherhead 2005). Together these reproductive advantages to large mothers are suspected to be the evolutionary driving force behind female-biased SSD in natricines, including *S. pygaea* (e.g., Semlitsch and Gibbons 1982; Shine 1994).

Our data suggest that selection for increased reproductive output during non-drought years favors female *S. pygaea* that are too large to survive prolonged food shortages such as those occurring during severe droughts. There may be less selection pressure for large body sizes in male *S. pygaea*. For example, there is no evidence of male–male combat in aquatic natricine snakes, including *S. pygaea*, and therefore no strong reason to expect selection pressure to result in larger body sizes in males than females (Shine 1994). Additionally, genetic evidence demonstrates that adult male size does not influence reproductive success in wild populations of another aquatic natricine, *Nerodia sipedon* (Weatherhead et al. 2002). Nonetheless, larger male size can improve reproductive success in some circumstances for *N. sipedon* (Kissner et al. 2005) and other natricine species (Madsen and Shine 1993b; Shine et al. 2000). No data regarding the effect of body size on reproductive success of male *S. pygaea* are currently available, but we suspect that most male *S. pygaea* forgo becoming large under conditions of resource limitation and follow the low-energy, low-growth strategy employed by male *N. sipedon* (Weatherhead et al. 2002), at least partly as a means to remain small enough to persist through periodic droughts via aestivation.

Conclusion

By taking advantage of the temporally dynamic nature of our isolated wetland study site, we documented shifting selection pressures acting on body size in a population of *S. pygaea*. We found that *S. pygaea* experienced significant reductions in maximum body size and SSD following prolonged drought-induced prey shortages and that the demographic shifts were greater in females, the larger sex. We attribute these patterns to differential mortality of snakes that were too large to support their basal maintenance requirements under resource limitation and/or that were depleted in energy stores (due to costs of reproduction) prior to the onset of the drought. Conversely, we found strong positive correlations between maternal size and several measures of reproductive success in *S. pygaea*, indicating that larger females are likely favored by fecundity selection during years of high food abundance (i.e., non-drought years). Our study emphasizes the dynamic interplay between selection pressures that act on body size in *S. pygaea* and is analogous to broader patterns predicted by theory (e.g., Beaupre 2002; Forsman 1996) and observed in other wild reptile populations (e.g., Madsen and Stille 1988; Forsman 1996; Wikelski and Trillmich 1997; Beaupre 2002). Ultimately, *S. pygaea* are better able to persist during droughts than sympatric natricine watersnakes that do not aestivate (Willson et al. 2006; Winne et al. 2006b), but our study suggests that the strategy of aestivation may come at the cost of reduced body size and SSD in

S. pygaea. These results are particularly interesting given that *S. pygaea* is the smallest semi-aquatic snake in North America (Gibbons and Dorcas 2004) and one of the least sexually dimorphic natricine water snake species. Future comparative studies across populations of aquatic snakes inhabiting wetlands with differing hydroperiods and prey dynamics may be informative as to the effects of aestivation and prey availability on body size evolution in *S. pygaea* and other species.

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References

- Arak A (1988) Sexual dimorphism in body size: a model and a test. *Evolution* 42:820–825
- Beaupre SJ (2002) Modeling time-energy allocation in vipers: individual responses to environmental variation and implications for populations. In: Schuett GW, Höggren M, Douglas ME, Greene HW (eds) *Biology of the vipers*. Eagle Mountain Publishing, Eagle Mountain, pp 463–481
- Beaupre SJ, Duvall D (1998) Variation in oxygen consumption of the western diamondback rattlesnake (*Crotalus atrox*): implications for sexual size dimorphism. *J Comp Physiol B* 168:497–506
- Bennett AF (1982) The energetics of reptilian activity. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, vol 12. Academic Press, New York, pp 155–199
- Bennett AF, Dawson WR (1976) Metabolism. In: Gans C (ed) *Biology of the reptilia. Physiology A*, vol 5. Academic Press, London, pp 127–223
- Blouin-Demers G, Prior KA, Weatherhead PJ (2002) Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. *J Zool* 256:1–10
- Boback SM (2003) Body size evolution in snakes: evidence from island populations. *Copeia* 2003:81–94
- Bonnet X, Naulleau G, Shine R, Lourdais O (2000) Reproductive versus ecological advantages to larger body size in female snakes, *Vipera aspis*. *Oikos* 89:509–518
- Brown GP, Weatherhead PJ (1997) Effects of reproduction on survival and growth of female northern water snake, *Nerodia sipedon*. *Can J Zool* 75:424–432
- Case TJ (1978) General explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18
- Clutton-Brock TH, Harvey PH, Rudder B (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* 269:797–800
- Cox RM, Butler MA, John-Alder HB (2007) The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Székely T (eds) *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford University Press, Oxford, pp 38–49
- Darwin C (1871) *The descent of man and selection in relation to sex*. Murray, London

- Dodd CK Jr (1993) Population structure, body mass, activity, and orientation of an aquatic snake (*Seminatrix pygaea*) during a drought. *Can J Zool* 71:1281–1288
- Forsman A (1991) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *J Anim Ecol* 60:253–267
- Forsman A (1996) Body size and net energy gain in gape-limited predators: a model. *J Herpetol* 30:307–319
- Gibbons JW, Dorcas ME (2004) North American watersnakes: a natural history. University of Oklahoma Press, Norman
- Gibbons JW, Semlitsch RD (1991) Guide to the reptiles and amphibians of the Savannah River Site. University of Georgia Press, Athens, GA
- Gibbons JW, Winne CT, Scott DE, Willson JD, Glaudas X, Andrews KM, Todd BD, Fedewa LA, Wilkinson L, Tsaliagos RN, Harper SJ, Greene JL, Tuberville TD, Metts BS, Dorcas ME, Nestor JP, Young CA, Akre T, Reed RN, Buhlmann KA, Norman J, Croshaw DA, Hagen C, Rothermel BB (2006) Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. *Conserv Biol* 20:1457–1465
- Hedrick AV, Temeles EJ (1989) The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol Evol* 4:136–138
- Jessop TS, Madsen T, Sumner J, Rudiharto H, Phillips JA, Ciofi C (2006) Maximum body size among insular Komodo dragon populations covaries with large prey density. *Oikos* 112:422–429
- Keogh JS, Scott IAW, Hayes C (2005) Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. *Evolution* 59:226–233
- King RB, Bittner TD, Queral-Regil A, Cline JH (1999) Sexual dimorphism in neonate and adult snakes. *J Zool* 247:19–28
- Kissner KJ, Weatherhead PJ (2005) Phenotypic effects on survival of neonatal northern watersnakes *Nerodia sipedon*. *J Anim Ecol* 74:259–265
- Kissner KJ, Weatherhead PJ, Gibbs HL (2005) Experimental assessment of ecological and phenotypic factors affecting male mating success and polyandry in northern watersnakes, *Nerodia sipedon*. *Behav Ecol Sociobiol* 59:207–214
- Luiselli L (2005) Snakes don't shrink, but 'shrinkage' is an almost inevitable outcome of measurement error by the experimenters. *Oikos* 110:199–202
- Luiselli L, Capula M, Shine R (1996) Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. *Oecologia* 106:100–110
- Madsen T, Shine R (1993a) Costs of reproduction in a population of European adders. *Oecologia* 94:488–495
- Madsen T, Shine R (1993b) Male mating success and body size in European grass snakes. *Copeia* 1993:561–564
- Madsen T, Shine R (1993c) Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* 47:321–325
- Madsen T, Shine R (1994) Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution* 48:1389–1397
- Madsen T, Shine R (2000a) Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecol* 25:670–675
- Madsen T, Shine R (2000b) Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *J Anim Ecol* 69:952–958
- Madsen T, Shine R (2001) Do snakes shrink? *Oikos* 92:187–188
- Madsen T, Shine R (2002) Short and chubby or long and slim? Food intake, growth and body condition in free-ranging pythons. *Austral Ecol* 27:672–680
- Madsen T, Stille B (1988) The effect of size dependent mortality on colour morphs in male adders, *Vipera berus*. *Oikos* 52:73–78
- McNab BK (1971) On the ecological significance of Bergmann's rule. *Ecology* 52:845–854
- McNab BK (1999) On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. *Physiol Biochem Zool* 72:642–644
- Moen DS, Winne CT, Reed RN (2005) Habitat-mediated shifts and plasticity in the evaporative water loss rates of two congeneric pit vipers (Squamata, Viperidae, *Agkistrodon*). *Evol Ecol Res* 7:759–766
- Parker WS, Plummer MV (1987) Population ecology. In: Seigel RA, Collins JT, Novak SS (eds) *Snakes: ecology and evolutionary biology*. Blackburn Press, Caldwell, pp 253–301
- Pearson D, Shine R, Williams A (2002) Geographic variation in sexual size dimorphism within a single species (*Morelia spilota*, Pythonidae). *Oecologia* 131:418–426
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- Preziosi RF, Fairbairn DJ (1997) Sexual size dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: lifetime fecundity selection on female total length and its components. *Evolution* 51:467–474
- Saint Girons H, Naulleau G (1981) Poids des nouveau-nés et stratégies reproductrices de vipères européennes. *Terre Vie* 35:597–616
- Schmidt-Nielsen K (1997) *Animal physiology: adaptation and environment*, 5th edn. Cambridge University Press, Cambridge
- Seigel RA, Ford NB (1987) Reproductive ecology. In: Seigel RA, Collins JT, Novak SS (eds) *Snakes: ecology and evolutionary biology*. Macmillan, New York, pp 210–249
- Seigel RA, Gibbons JW, Lynch TK (1995a) Temporal changes in reptile populations: effects of a severe drought on aquatic snakes. *Herpetol* 51:424–434
- Seigel RA, Loraine RK, Gibbons JW (1995b) Reproductive cycles and temporal variation in fecundity in the black swamp snake, *Seminatrix pygaea*. *Am Midl Nat* 134:371–377
- Semlitsch RD, Gibbons JW (1982) Body size dimorphism and sexual selection in two species of water snakes. *Copeia* 1982:974–976
- Sever DM, Ryan TJ, Morris T, Patton D, Swafford S (2000) Ultrastructure of the reproductive system of the black swamp snake (*Seminatrix pygaea*). II. Annual oviducal cycle. *J Morphol* 245:146–160
- Shine R (1994) Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346
- Shine R (2003) Reproductive strategies in snakes. *Proc R Soc B* 270:995–1004
- Shine R, Wall M (2005) Ecological divergence between the sexes in reptiles. In: Ruckstuhl KE, Neuhaus P (eds) *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge University Press, Cambridge, pp 221–253
- Shine R, Olsson MM, Moore IT, LeMaster MP, Mason RT (2000) Body size enhances mating success in male garter snakes. *Anim Behav* 59:F4–F11
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Turner FB (1977) The dynamics of populations of squamates, crocodylians, and rhynchocephalians. In: Gans C, Tinkle DW (eds) *Biology of the reptilia*, vol 7. Academic Press, London, pp 157–264
- Weatherhead PJ, Prosser MR, Gibbs HL, Brown GP (2002) Male reproductive success and sexual selection in northern water snakes determined by microsatellite DNA analysis. *Behav Ecol* 13:808–815
- Wikelski M (2005) Evolution of body size in Galapagos marine iguanas. *Proc R Soc B* 272:1985–1993
- Wikelski M, Thom C (2000) Marine iguanas shrink to survive El Niño. *Nature* 403:37–38

- Wikelski M, Trillmich F (1997) Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* 51:922–936
- Willson JD, Winne CT, Fedewa LA (2005) Unveiling escape and capture rates of aquatic snakes and salamanders (*Siren* spp. and *Amphiuma* means) in commercial funnel traps. *J Freshwater Ecol* 20:397–403
- Willson JD, Winne CT, Dorcas ME, Gibbons JW (2006) Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: insights on different strategies for persistence in a dynamic habitat. *Wetlands* 26:1071–1078
- Willson JD, Winne CT, Keck MB (2008) Empirical tests of biased body size distributions in aquatic snake captures. *Copeia* 2008:401–408
- Winne CT (2005) Increases in capture rates of an aquatic snake (*Seminatrix pygaea*) using naturally baited minnow traps: evidence for aquatic funnel trapping as a measure of foraging activity. *Herpetol Rev* 36:411–413
- Winne CT, Ryan TJ, Leiden Y, Dorcas ME (2001) Evaporative water loss in two natricine snakes, *Nerodia fasciata* and *Seminatrix pygaea*. *J Herpetol* 35:129–133
- Winne CT, Dorcas ME, Poppy SM (2005) Population structure, body size, and seasonal activity of black swamp snakes (*Seminatrix pygaea*). *Southeast Nat* 4:1–14
- Winne CT, Willson JD, Andrews KM, Reed RN (2006a) Efficacy of marking snakes with disposable medical cautery units. *Herpetol Rev* 37:52–54
- Winne CT, Willson JD, Gibbons JW (2006b) Income breeding allows an aquatic snake *Seminatrix pygaea* to reproduce normally following prolonged drought-induced aestivation. *J Anim Ecol* 75:1352–1360