

Income breeding allows an aquatic snake *Seminatrix pygaea* to reproduce normally following prolonged drought-induced aestivation

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Summary

1. Capital breeding is an ideal reproductive strategy for many ectotherms because it provides a disassociation between feeding and reproduction, a necessary requirement for animals that become anorexic during pregnancy. Among ectotherms, some viviparous snakes (e.g. Viperidae) exemplify the capital breeding strategy because many species (i) do not feed during pregnancy due to behavioural conflicts between reproduction and foraging, and (ii) take more than one season to accumulate sufficient energetic stores for reproduction.

2. Isolated wetlands often exhibit extreme annual fluctuations in environmental conditions with prolonged droughts periodically leaving wetlands completely dry and devoid of prey. Following droughts, however, wetlands can be extremely productive, rendering prey resources virtually unlimited for some species.

3. This study examines drought survival strategy and reproductive ecology of a small aquatic snake *Seminatrix pygaea* (Cope) in an isolated wetland. *Seminatrix pygaea* are atypical from most sympatric snake species in that (i) their small body size, reliance on aquatic prey, and high rates of evaporative water loss make them ill-suited to overland movement, and (ii) they may not be subject to costs typically associated with feeding during pregnancy.

4. We hypothesized that *S. pygaea* would survive periodic multiyear droughts by aestivating within the dried wetland, a survival strategy heretofore undocumented in snakes. Further, we hypothesized that if *S. pygaea* rely on 'typical' snake reproductive strategies of 'adaptive anorexia' and capital breeding, reproductive output would be reduced in the first wet year following drought.

5. By encircling a 10-ha wetland with a continuous drift fence before it refilled we were able to demonstrate that *S. pygaea* were present within the dried wetland prior to the onset of spring rains that refilled the wetland in 2003. Our results suggest that *S. pygaea* are capable of surviving multiyear droughts by aestivating within the dried wetland.

6. Despite having presumably depleted energy reserves during the drought, *S. pygaea* reproduced with the same frequency and fecundity during the first season following refilling of the wetland as in pre-drought years.

7. The ability of *S. pygaea* to rebound rapidly from the stresses of prolonged drought is due in part to their reproductive ecology. *Seminatrix pygaea* readily feed throughout pregnancy and consequently can rapidly translate high prey abundances into reproductive output through income breeding.

Key-words: climatic variation, foraging ecology, migration, reproductive allocation, reptile

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Introduction

Coping with climatic variation and associated fluctuations in resource levels is one of the greatest challenges to organisms in many ecosystems. Extreme drought, in particular, is among the most powerful selective forces and has been implicated in the evolution of numerous character traits and life-history attributes (e.g. Grant & Grant 1989, 1996; Grant 1999). For aquatic organisms inhabiting isolated wetlands, droughts pose an obvious challenge to population stability and persistence. For example, severe droughts can result in osmotic stress, heat stress, increased predation risk, and decreased prey abundance (Bennett, Gibbons & Franson 1970). In turn, these stressors can reduce survivorship and reproduction, and even cause local extinction (Seigel, Gibbons & Lynch 1995a; Willson *et al.*, in press). Consequently animals have evolved numerous drought-survival strategies.

Two prevalent drought-survival strategies are migration and aestivation. Studies of drought effects on semi-aquatic snakes are limited, but suggest that many species migrate to other habitats to escape drought conditions. For example, banded watersnakes *Nerodia fasciata* may leave isolated wetlands when wetlands dry (Seigel *et al.* 1995a) and return once wetlands refill (Willson *et al.*, in press). Similarly, in response to wet-dry cycles of tropical Australia, water pythons *Liasis fuscus* and Arafura filesnakes *Acrochordus arafurae* migrate between habitats to take advantage of rainfall-mediated changes in prey abundances (Shine & Lambek 1985; Madsen & Shine 1996). In other taxa, smaller, more aquatic species are often ill-suited to overland travel and rely on aestivation, rather than migration, to abide drought (Chessman 1984). For example, in turtles, large-bodied emydids (e.g. *Trachemys scripta*, *Pseudemys floridana*) generally migrate to other water bodies during drought, while smaller or more aquatic species (e.g. *Deirochelys reticularia*, *Kinosternon subrubrum*, *Sternotherus odouratus*) generally remain at the wetland, either aestivating within the wetland itself, or burying in adjacent uplands (Gibbons, Greene & Congdon 1983; Buhlmann & Gibbons 2001).

In addition to direct effects of drought on survival of wetland organisms, stochastic variation in rainfall affects organisms indirectly through fluctuations in resource abundance. Indeed, prey resources within wetlands often vary widely between abundant and absent. Under such conditions, organisms are generally expected to exhibit large-scale variation in reproductive output among 'good' and 'bad' years (Seigel & Fitch 1985; Shine & Madsen 1997; Madsen & Shine 2000). For example, during severe droughts Florida snail kites *Rostrhamus sociabilis* suffer from reduced prey availability and experience decreased survivorship and reproductive output (Mooij *et al.* 2002). Similarly, in tropical Australia, Arafura filesnakes *A. arafurae* and water pythons *L. fuscus* show strong negative responses (e.g. decreased growth, reproductive output and number

of reproductive females) to decreases in prey abundance that are driven by rainfall patterns (Shine & Madsen 1997; Madsen & Shine 2000).

Animals have evolved alternative reproductive strategies to cope with temporal fluctuations in resource availability. Capital breeding is a strategy whereby animals accumulate energy ('capital') during periods of high productivity and allocate that energy towards reproduction once a threshold of stored energy has been met (e.g. Bonnet, Bradshaw & Shine 1998; Bonnet *et al.* 2002). Functionally, this permits reproductive output to be independent of resource availability at the time of reproduction. Aspic vipers *Vipera aspis*, for example, can rely on stored energy to reproduce during years when mothers do not catch a single prey item (Lourdais *et al.* 2003). In contrast, income breeding is a strategy that relies on recently ingested energy ('income') to fuel reproductive output (Bonnet *et al.* 1998). In many vertebrate ectotherms, however, females do not eat during pregnancy, which can limit their ability to use income breeding and translate high resource abundance into viable offspring on a short time-scale (Bonnet *et al.* 1998).

Many snake species either do not feed or drastically reduce foraging during pregnancy (e.g. Gregory & Skebo 1998; Gregory, Crampton & Skebo 1999; Shine 2003; Brown & Shine 2004; Gregory & Isaac 2004), whereas other species continue to eat throughout pregnancy (e.g. Brown & Weatherhead 1997; Aldridge & Bufalino 2003; Shine *et al.* 2004). In many cases, optimal habitats and behaviours for gestation are incompatible with feeding (Gregory & Skebo 1998; Gregory *et al.* 1999). For example, females suffer from reduced locomotor speeds during pregnancy, which presumably reduces foraging efficiency and increases predation risk (Shine 1980; Seigel, Huggins & Ford 1987; Brown & Shine 2004; Webb 2004). Also, many females thermoregulate at higher temperatures and with greater precision during pregnancy (e.g. Charland & Gregory 1990), otherwise they risk longer gestation times and improperly developed offspring (Peterson, Gibson & Dorcas 1993; Arnold & Peterson 2002). Such precise thermoregulation may not be compatible with foraging behaviour. Consequently, for some species, the inability or unwillingness to feed during pregnancy may be a form of 'adaptive anorexia' that reduces conflicts between feeding and thermoregulation during pregnancy (Mrosovsky & Sherry 1980; Gregory & Skebo 1998; Gregory *et al.* 1999).

In this study, we examined the ecology of a small, aquatic snake, the black swamp snake *Seminatrix pygmaea* (Cope), inhabiting an isolated freshwater wetland (Ellenton Bay) that is subject to periodic extreme droughts. Because their small body size, reliance on aquatic prey, and high rates of evaporative water loss make them ill-suited to prolonged overland movement, we hypothesized that *S. pygmaea* remain within the dried wetland and rely on aestivation to survive drought. Further, if *S. pygmaea* become anorexic during pregnancy

and rely on a capital breeding strategy to fuel reproduction, we predicted that in the first season following drought the necessity to replenish depleted resources would preclude successful reproduction. To test these hypotheses, we (1) used aquatic and terrestrial capture methods in the first wet year following a prolonged drought to assess the drought-survival strategy of *S. pygaea*; (2) assessed reproduction during and after drought and compared these periods with pre-drought conditions using historical data; and (3) examined the propensity of this species to feed during pregnancy.

Materials and methods

STUDY SPECIES

Seminatrix is a monotypic genus of the cosmopolitan subfamily Natricinae and is endemic to a portion of the south-eastern US Coastal Plain. *Seminatrix pygaea*, the smallest aquatic snake in North America, is viviparous, and typically reproduces annually (Seigel, Loraine & Gibbons 1995b; Sever *et al.* 2000; Winne, Dorcas & Poppy 2005). Although capable of feeding on a wide variety of aquatic prey (Gibbons & Dorcas 2004), *S. pygaea* at our study site have fed nearly exclusively on aquatic larvae and pedomorphs of the salamander *Ambystoma talpoideum* (Holbrook) since the early 1990s (unpublished data). Adult *S. pygaea* have high rates of evaporative water loss compared with sympatric semi-aquatic snakes (Winne *et al.* 2001; Moen, Winne & Reed 2005), rarely venture away from the water's edge (Gibbons & Dorcas 2004), and are abundant in some isolated wetlands, making them ideal for long-term investigations of population-level responses to drought.

STUDY SITE

Ellenton Bay, an isolated freshwater wetland in South Carolina, USA, has been the focus of numerous long-term herpetological studies (Gibbons 1990). The regional climate consists of hot, humid summers and mild, wet winters (mean annual precipitation *c.* 100 cm). Two multiyear droughts (1987–90, 2000–03) have occurred at Ellenton Bay since 1975 (Fig. 1). We initiated the current study in February 2003 at the end of the second drought.

Ellenton Bay is currently fish-free but harbours a diverse assemblage of amphibians (24 species) and semi-aquatic reptiles (18 species) during most years (Gibbons & Semlitsch 1991; Gibbons *et al.* 2006). Ellenton Bay has the longest hydroperiod of nonpermanent wetlands in the region. The only permanent wetland within 1.4 km of Ellenton Bay is a small, man-made pond *c.* 0.5 km from Ellenton Bay. No *S. pygaea* have ever been captured in the pond during extensive aquatic trapping over many years (unpublished data). The Ellenton Bay basin is approximately 10 ha when full, but water surface area and depth are extremely

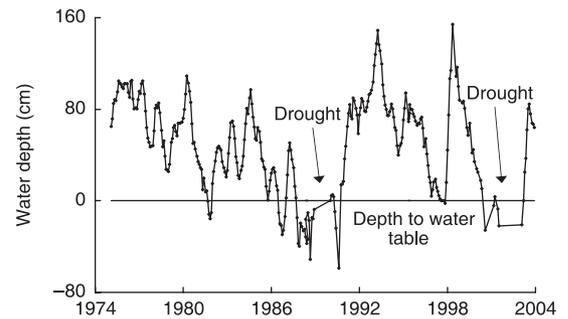


Fig. 1. Mean monthly water depth at Ellenton Bay. During most droughts the depth to the top of the water table was determined by digging below the soil surface (represented by horizontal line); however, this depth was not determined between August 2001 and January 2003.

variable (Fig. 1), ranging from no water to a maximum depth of approximately 2 m. During droughts, a thick (up to 0.5 m) organic crust covers the entire basin but subsurface areas remain moist and up to 1 ha of viscous mud surrounds small open water areas during shorter dry spells. However, during the 2000–03 drought, no standing water remained. Gibbons (1990) and Gibbons *et al.* (2006) provide further study site details.

SNAKE CAPTURES

From 1 February 2003 to 31 January 2004, Ellenton Bay was completely surrounded by a 1230-m long, 40-cm high, aluminium flashing drift fence, buried 6–10 cm into hard-packed soil (Gibbons & Semlitsch 1982). We installed 164 evenly spaced traps (82 19-L buckets, 42 2.3-L buckets, 40 wooden box funnel traps) in pairs on opposite sides of the fence, allowing captures to be judged as entering or leaving the bay (Gibbons *et al.* 2006). Pitfall and funnel traps were checked a minimum of once daily. Captures of thousands of fossorial amphibians and reptiles, including salamanders, anurans and snakes (Gibbons *et al.* 2006; Willson *et al.* in press; unpublished data) strongly suggest that animals were seldom able to burrow under the drift fence and thus pass into the wetland undetected.

Aquatic trapping with minnow traps was conducted at Ellenton Bay from 1983 to 1987 (Seigel *et al.* 1995a,b) and May to June 1998 (Winne *et al.* 2005). Aquatic trapping was also conducted monthly from May to August 2003 (4788 trap nights), immediately following the 2000–03 drought. Traps were spaced approximately 2 m apart in transects along the margin of the bay, among emergent vegetation and checked at least once daily for snakes.

Sex, snout–vent length (SVL), tail length, body mass and reproductive state were recorded for all captured snakes. Reproductive states of females were determined by palpating them for the presence of enlarged ova or developing embryos (Seigel *et al.* 1995b). Additionally, in some years (1983–87), the presence or absence of prey items was identified by forced regurgitation

(Fitch 1987). Each snake was marked with a unique code by clipping (1983–98; Fitch 1987) or branding (2003; Winne *et al.* 2006) ventral scales before release at its capture location.

FEEDING TRIALS AND MATERNAL-LITTER RELATIONSHIPS

To examine feeding rates of snakes in the laboratory, pregnant ($n = 16$) and nonpregnant ($n = 7$) females were collected between 21 May and 30 July 2003 and housed under laboratory conditions until parturition. Snakes were kept individually in plastic 5-L shoeboxes fitted with paper towels as a substrate and a large water dish (737 mL) that allowed snakes to fully submerge. Cages were placed within an environmental chamber at 25 °C with a L : D 14 : 10 photoperiod. Water and towels were changed two to three times per week, and all snakes were offered live *A. talpoideum* larvae totalling 40–60% of the snake's mass every 7–10 days. Approximately 12 h after feeding, all remaining prey were removed and weighed to determine the amount of prey consumed. During late July through August cages were examined once or twice daily for the presence of neonates. All pregnant females gave birth between 3 and 25 August 2003. Mass, SVL, and tail length of mothers and neonates were measured within 24 h of parturition.

STATISTICAL ANALYSES

A contingency table analysis was used to determine if frequencies of reproductive females were statistically different among years and to detect differences in frequencies of individuals containing food items among sexes and reproductive classes. Both Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA; with maternal SVL as the covariate) were used to test whether litter size varied among years; data were natural log-transformed prior to analyses. The relationship between maternal SVL and litter size was determined using linear regression on natural log-transformed data. To compare feeding rates of pregnant and nonpregnant females, the Kruskal–Wallis test was used in lieu of a one-way ANOVA because the assumption of homogeneous variances could not be met. All tests were performed by hand (asymmetric contingency table analysis) or using the STATISTICA for Windows software package (StatSoft, Inc., Tulsa, OK, USA 1998). Data were examined prior to each analysis and all statistical assumptions were met. Statistical significance was recognized at $\alpha = 0.05$. All means are presented as ± 1 standard error.

Results

DROUGHT SURVIVAL STRATEGY

Ellenton Bay was completely encircled with a terrestrial drift fence prior to the onset of rains in early

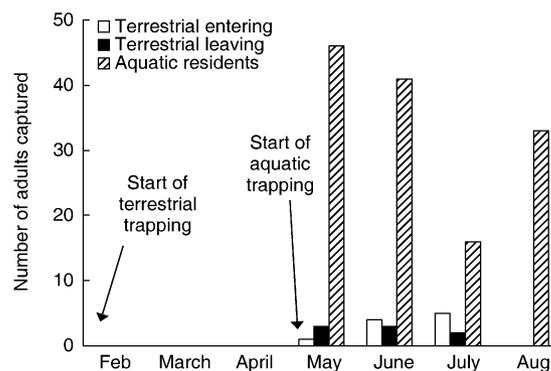


Fig. 2. Terrestrial and aquatic captures of individual adult *Seminatrix pygaea* at Ellenton Bay in 2003. A drift fence served as a barrier to potential *S. pygaea* migrants and was operational in February, prior to the onset of rains that refilled the wetland. This allowed us to enumerate immigrant ('terrestrial entering') and emigrant ('terrestrial leaving') *S. pygaea* before and after the wetland refilled. Aquatic trapping began in May and revealed a large population of *S. pygaea* resident within the wetland ('aquatic residents') after heavy rains refilled the wetland.

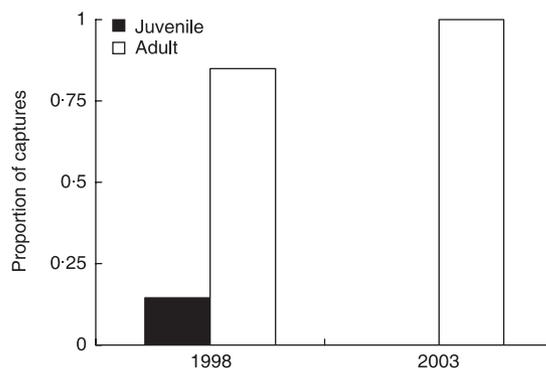


Fig. 3. Proportion of juvenile *Seminatrix pygaea* captured at Ellenton Bay in 1998 and 2003. The lack of juveniles in 2003 suggests that no successful reproduction occurred during the 2000–03 drought.

February 2003 that refilled the wetland, which reached peak water level in August (Fig. 1). This allowed us to detect any potential immigrants to the wetland prior to wetland refilling. None the less, *S. pygaea* were not captured entering or exiting Ellenton Bay from 1 February 2003 through April 2003. During May three adults were captured leaving the bay at the drift fence (6, 18 and 21 May), and only one adult was captured entering (21 May). Despite the previous drought (Fig. 1) and the paucity of immigrants to Ellenton Bay (Fig. 2), aquatic trapping revealed that a substantial population of adult *S. pygaea* was resident within Ellenton Bay after it refilled (Fig. 2). However, in comparison with 1998, the population was highly skewed towards adults in 2003 ($\chi^2 = 19.24$; $P < 0.001$), with no juveniles captured in 2003 (Fig. 3). Thus, it appears that adult *S. pygaea* were able to survive within the dried wetland throughout the 2.5-year drought but that no recruitment (and probably no reproduction) occurred.

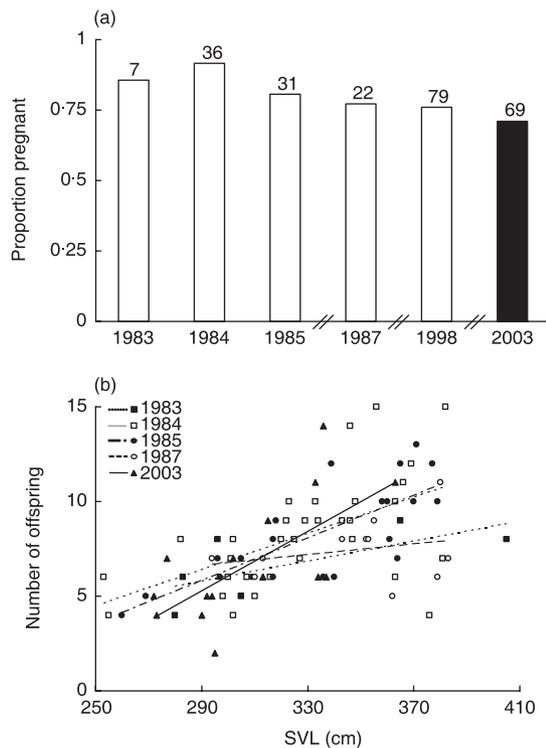


Fig. 4. Reproductive ecology of *Seminatrix pygaea* at Ellenton Bay during pre- and post-drought years. (a) Proportion of adult female *S. pygaea* that were pregnant in pre-drought (white) and post-drought (black) years. The number of adult females captured is given above each bar. (b) Maternal–litter relationships among years.

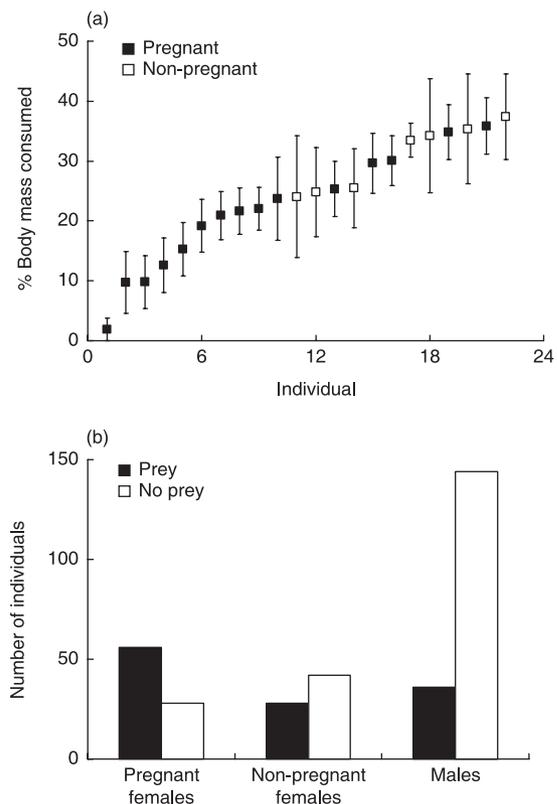


Fig. 5. Effect of pregnancy on feeding in *Seminatrix pygaea* from Ellenton Bay. (a) Mean (± 1 SE) per cent body mass consumed in the laboratory presented in order of increased prey consumption. (b) Frequency of field-captured snakes containing food items.

POST-DROUGHT REPRODUCTION

Sixty-nine individual females were captured in the aquatic habitat from May to August 2003. Of these, 49 (71%) were pregnant during one or more months, which is similar to the percentage (76%) pregnant in 1998 (Winne *et al.* 2005) and in the 4 years sampled during the 1980s (Seigel *et al.* 1995b; Fig. 4a). Despite notable changes in water level and the severe drought of 2000–03 no significant differences in the frequency of reproductive females were found among these 6 years (contingency table; $\chi^2 = 6.2$; $P = 0.267$; Fig. 4a).

Litter size did not vary significantly among years (ANOVA, $F_{4,81} = 1.69$, $P = 0.160$; Fig. 4b), even after accounting for maternal length (ANCOVA, SVL as covariate, $F_{4,80} = 1.21$, $P = 0.314$). As expected, a significant positive relationship (slope = 3.43) existed between natural log-transformed maternal SVL and litter size in 2003 ($r^2 = 0.39$; $P = 0.01$). The slope of the regression was not significantly different from the slopes observed by Seigel *et al.* (1995b) in previous years (ANCOVA test for difference in slope, SVL as covariate, $F_{4,76} = 1.44$, $P = 0.229$; Fig. 4b).

LACK OF ANOREXIA DURING PREGNANCY

Most *S. pygaea* readily consumed large meals (20.8 \pm 2.5% of their body mass per feeding) during pregnancy

(Fig. 5a). The average per cent body mass consumed by six of the pregnant females (range: 24–36%) was similar to consumption by nonpregnant females (range: 24–37%; Fig. 5a). Meal sizes were large for some pregnant females, with several consuming prey items totaling 40–57% of their pre-partum body mass during single feeding events. Nonpregnant females consumed proportionally more prey, on average (30.7 \pm 2.1% of their body mass), than pregnant females (Kruskal–Wallis; $H_{1,22} = 5.58$; $P = 0.018$; Fig. 5a), but field captures demonstrate that pregnant females readily feed during pregnancy in the wild. Records of adult females (84 nonpregnant, 70 pregnant) from June 1983 to August 1987 show that pregnant females were the most likely demographic to contain prey items: 67% of pregnant females contained one or more prey items, whereas only 40% of nonpregnant females contained prey items (Fig. 5b). Proportions of pregnant and nonpregnant females containing prey items ($\chi^2 = 2.230$; $P = 0.135$) did not vary significantly. Of 180 males, only 25% contained prey items, significantly less than the proportion of pregnant females with food ($\chi^2 = 10.6$; $P = 0.001$), but not statistically less than the proportion of nonpregnant females containing prey ($\chi^2 = 2.4$; $P = 0.122$). In accordance with our laboratory results, meal sizes of field-captured pregnant females were large. For example, one pregnant female captured in the field regurgitated

two *A. talpoideum* larvae with a combined mass equaling 32% of the female's pre-partum body mass.

Discussion

DROUGHT SURVIVAL STRATEGY

We documented the number of *S. pygaea* returning to Ellenton Bay as it refilled after being dry for over 2 years, as well as the relative abundance of snakes within the wetland after the water had returned to normal levels. None immigrated to the wetland prior to the refilling of the bay and only a few returned after the wetland refilled. None the less, a substantial population of adult *S. pygaea* was resident within the wetland as soon as it refilled. Thus, despite their highly aquatic habits, *S. pygaea* appear well-adapted to survive multi-year droughts.

Although *S. pygaea* is the smallest aquatic snake species at Ellenton Bay (and thus least likely to trespass over the drift-fence), it accounted for only 0.8% of the snakes captured entering the wetland during spring 2003. None the less, it was the most abundant snake within the aquatic habitat both before (1998; 69.7% of snake captures) and after (2003; 89.1% snake captures) the drought. Additionally, drift fence captures of adult and neonate *S. pygaea* during summer 2003 (see fig. 6 in Winne *et al.* 2005) and in other drift fence studies, both at Ellenton Bay (Seigel *et al.* 1995a) and elsewhere (Dodd 1993), demonstrate that *S. pygaea* are readily captured in drift fences. Consequently, we conclude that *S. pygaea* captured within the aquatic habitat after Ellenton Bay refilled in 2003 must have been inside the drift fence, within the dried basin of the bay, when the drought ended. Opportunistic searches and the use of artificial coverboards within the Ellenton Bay basin during the drought resulted in no *S. pygaea* captures (C. Winne, pers. obs.). Presumably, *S. pygaea* survived the multiyear drought by aestivating beneath the dried surface of the wetland, a phenomenon documented in a diversity of other taxa, including invertebrates (Dietz-Brantley *et al.* 2002), fish (Fishman *et al.* 1986; Sturla *et al.* 2002), amphibians (Loveridge & Withers 1981; Etheridge 1990; Withers 1993), and turtles (Grigg *et al.* 1986; Kennett & Christian 1994; Ligon & Peterson 2002), but not previously reported in snakes. Comparisons of relative abundance (snakes per trap night) within the aquatic habitat attest to the success of this strategy. Relative abundance of *S. pygaea* was similar between pre-drought (1998) and post-drought (2003) years, whereas sympatric semi-aquatic natricines (*Nerodia fasciata* and *N. floridana*) that did not aestivate experienced precipitous declines during the drought (Willson *et al.* in press).

Despite unequivocal evidence from our study that a sizable portion of the *S. pygaea* population had aestivated within the wetland, data are not available to know what proportion of the population, if any, emigrated during the drought itself. Likewise, previous

evidence for how *S. pygaea* survive droughts has been contradictory. Two studies suggested that they migrate between wetlands in response to drought (Dodd 1993; Seigel *et al.* 1995a). Seigel *et al.* (1995a) documented adult *S. pygaea* emigrating from Ellenton Bay in response to an earlier drought (1987–90). Seigel *et al.* (1995a) did not monitor immigration or resident population levels immediately after the drought but noted that 'despite the large number of individuals leaving the bay, many [others] did not emigrate', which suggests that some *S. pygaea* may have relied upon aestivation during that drought. Matthew J. Aresco (pers. comm.) found *S. pygaea* aestivating within a dried wetland in Florida during a severe drought. Similarly, Archie Carr (1940) noted that *S. pygaea* in Florida burrow deep (60 cm) into sphagnum and mud during winter. Thus, *S. pygaea* appears to be capable of adopting different drought-avoidance strategies in different situations, a phenomenon that has been noted for at least one species of amphibian (Lampert & Linsenmair 2002).

POST-DROUGHT REPRODUCTIVE ECOLOGY

Drought is energetically challenging for many animals, in part because food availability is often reduced or absent. To survive, nonmigratory animals must rely on stored energy that might have otherwise been allocated to reproduction. Thus, many animals do not reproduce during drought and reproductive output is often reduced immediately following drought, until energy reserves are replenished. The conflicting requirements between reproduction and survival are evident in Galapagos marine iguanas *Amblyrhynchus cristatus* exposed to periodic food shortages caused by the El Niño–Southern Oscillation (ENSO) cycle. During ENSO events, *A. cristatus* allocate all of their stored energy to survival and do not reproduce (Laurie 1990; Wilkelski & Thom 2000). Moreover, following an ENSO event, few females are able to gather enough resources to reproduce during the first season; thus, successful reproduction does not occur until 2 years following drought (Laurie 1990).

In contrast, *S. pygaea* reproduced in the same frequency and with the same fecundity in the first season following extreme drought as in pre-drought years. How did *S. pygaea* fuel reproduction following the drought? In 2003, we began aquatic trapping in May when most females already contained enlarged ova or embryos. We were therefore unable to directly estimate post-drought body condition, and, by extension, the amount of energy stores ('capital') available for reproduction (Bonnet *et al.* 2001; Gignac & Gregory 2005) for our population. None the less, two lines of evidence indicate that *S. pygaea* began 2003 with little or no energy for capital reproduction. First, aestivation by *S. pygaea* during the drought and the absence of amphibian prey (Gibbons *et al.* 2006) suggest that feeding opportunities were limited or absent. Lack of successful reproduction during the drought, as evidenced by

the absence of juveniles immediately following the drought, further supports the supposition that for *S. pygaea* to survive the drought, they would have been forced to rely upon energy stores primarily for maintenance metabolism. In addition, compared with pre-drought years, significantly fewer large individuals remained within the wetland immediately following the drought (unpublished data). For reptiles, the largest individuals within a population are generally the most vulnerable to energetic deficiencies: larger individuals have greater total metabolic demands and are more likely to be selected against during times of food shortage (Wilkelski & Thom 2000; Beaupre 2002). The cumulative evidence suggests that *S. pygaea* were energetically constrained at the beginning of 2003 and relied primarily upon food consumed during vitellogenesis and/or pregnancy (i.e. income) to fuel reproduction. Such income breeding is considered rare for snakes (Bonnet *et al.* 1998; Gregory *et al.* 1999) but seems fitting for the ecology of *S. pygaea*.

Bonnet *et al.* (1998) stated that capital breeding is best suited to organisms for which simultaneous energy acquisition and expenditure is unlikely to be feasible. Thus, for many snakes capital breeding is an ideal strategy because it provides a disassociation between feeding and reproduction, a necessary requirement for snakes that become anorexic during pregnancy (Bonnet *et al.* 1998). Unlike many snakes, *S. pygaea* are not constrained to a capital breeding strategy because they do not exhibit 'adaptive anorexia', but instead feed readily throughout pregnancy.

What allows *S. pygaea* to continue to feed during pregnancy? A possible explanation is that *S. pygaea* are not subject to the costs typically associated with feeding. For example, unlike most natricines, *S. pygaea* seldom bask out of the water and rarely leave the aquatic habitat (Gibbons & Dorcas 2004). Therefore, because pregnant *S. pygaea* are always in close proximity to prey, no obvious spatial conflicts arise between foraging and thermoregulation. Additionally, aquatic locomotion in *S. pygaea* is less impaired by pregnancy than terrestrial locomotion (Winne & Hopkins, in press), thus, selective pressures to reduce activity (e.g. Brodie 1989) may be lower in aquatic habitats compared with terrestrial habitats (Brown & Weatherhead 1997). Finally, the nearly exclusive use of heavily vegetated subsurface habitats, both during foraging and gestation, may reduce overall predation pressure on pregnant *S. pygaea* (compared with more exposed foragers) and therefore remove selective pressures to reduce foraging activity during pregnancy. These hypotheses certainly warrant further study but are supported by recent evidence that other aquatic snake species (e.g. *Emydocephalus annulatus*, *Nerodia sipedon*) also continue to feed during pregnancy (Brown & Weatherhead 1997; Aldridge & Bufalino 2003; Shine *et al.* 2004).

In addition to a lack of anorexia, aestivation may contribute to the ability of *S. pygaea* to reproduce in the first season following drought. By aestivating within the

wetland, *S. pygaea* were able to emerge as soon as the wetland refilled and take immediate advantage of extraordinarily high abundances of explosively breeding amphibian prey (Gibbons *et al.* 2006). Aestivation also allowed *S. pygaea* to exploit this abundant resource with virtually no competition because most other semi-aquatic snake and turtle species that inhabit Ellenton Bay either did not survive the drought or slowly immigrated to the wetland after it refilled (Gibbons *et al.* 1983; Willson *et al.*, in press). Consequently, prey availability was likely unlimited for *S. pygaea* immediately following the drought.

Conclusions

Our findings demonstrate that *S. pygaea* possess a distinctive suite of life-history traits that permit them to survive and reproduce in isolated wetlands subject to periodic droughts and dramatic fluctuations in prey abundance. In contrast to snake species that leave aquatic habitats in response to drought, *S. pygaea* at Ellenton Bay apparently survived a multiyear drought by aestivating within the dried wetland. Furthermore, they reproduced at normal levels in the first season after the wetland refilled. The ability to rebound rapidly from the stresses of prolonged drought is due in part to *S. pygaea*'s reproductive ecology. As opposed to many ectotherms that exhibit capital breeding and 'adaptive anorexia', *S. pygaea* readily feed throughout pregnancy, rapidly translating high prey abundance into reproductive output through income breeding. Collectively, these characteristics make *S. pygaea* well-adapted to isolated wetlands and an important model organism for future studies of reproductive ecology.

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