POST-DROUGHT RESPONSES OF SEMI-AQUATIC SNAKES INHABITING AN ISOLATED WETLAND: INSIGHTS ON DIFFERENT STRATEGIES FOR PERSISTENCE IN A DYNAMIC HABITAT

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Abstract: Most aquatic habitats are temporally dynamic, and selection has favored diverse strategies to persist in the face of fluctuating environmental conditions. Isolated wetlands in the southeastern United States harbor high diversities of aquatic and semi-aquatic organisms. However, drought may render these wetlands temporarily unsuitable for many species, sometimes for years at a time. We studied the movement patterns and demography of seven species of semi-aquatic snakes at Ellenton Bay, an isolated 10-ha freshwater wetland in the Upper Coastal Plain of South Carolina, following complete drying of the bay during a drought from 2000 to 2003. Behavioral and population responses varied markedly among species. Cottonmouths (*Agkistrodon piscivorus*) migrated to and from the wetland annually, fared well, and reproduced during the drought. Banded watersnakes (*Nerodia fasciata*) suffered a dramatic population decline and apparently did not reproduce, while eastern green watersnakes (*N. floridana*) were locally extirpated. Black swamp snakes (*Seminatrix pygaea*) aestivated within the wetland and were less affected by the drought than *Nerodia*. Interspecific differences in response to drought demonstrate that conservation measures may affect species differently and highlight the importance of terrestrial habitat around wetlands for semi-aquatic reptiles.

Key Words: *Agkistrodon piscivorus*, drought, *Farancia abacura*, *Farancia erytrogramma*, metapopulation dynamics, *Nerodia erythrogaster*, *Nerodia fasciata*, *Nerodia floridana*, *Seminatrix pygaea*, wetland conservation

INTRODUCTION

Organisms inhabiting temporally dynamic habitats face a unique set of selective forces. Variability in environmental conditions can lead to periods of high productivity (e.g., Gibbons et al. 2006) punctuated by predictable (i.e., periodic or seasonal) or unpredictable periods of low productivity or unfavorable environmental conditions (e.g., Seigel et al. 1995a, Polis et al. 1997, Madsen and Shine 2000a, b, Brown et al. 2002). To capitalize on periods of abundance, animals must either stay and be able to survive unfavorable conditions or leave to seek refuge in other habitats until favorable conditions return.

Migration may involve directed movement to known refugia or undirected dispersal in which encountering favorable territory is serendipitous. In either case, migration incurs multiple costs, including the energetic and physiological demands of movement (e.g., energy and water loss), increased susceptibility to predation, and the costs associated with establishing a new home range. The decision to migrate involves weighing the costs of migration against the benefits of leaving an unfavorable habitat for a better one (Alexander 1998, 2002). Theoretical models suggest that migration costs are minimized for larger animals and those that swim or fly (Alexander 1998, 2002), and the long-distance migrations of birds, marine mammals, and terrestrial ungulates are well-known. On a smaller scale, snakes such as water pythons (*Liasis fuscus* Peters, 1873) and filesnakes (*Acrochordus arafurae* McDowell, 1979) in tropical Australia undertake annual migrations between habitats in response to seasonal changes in prey abundance (Shine and Lambeck 1985, Madsen and Shine 1996). In temperate regions, many snakes make yearly migrations between summer foraging or gestation areas and winter dens (e.g., Gregory and Stewart 1975, Gregory 1984, Glaudas et al. 2007). However, non-seasonal, irregular migrations of snakes in response

to detrimental environmental conditions are poorly documented.

Animals that remain within habitats during periods of low productivity may reduce activity levels (e.g., aestivate or hibernate) or rely on stored energy reserves to persist without modifying their activity. The low energy requirements of ectotherms (Pough 1980) make them well-suited to activity-reducing strategies such as aestivation, a strategy used by many ectothermic organisms including invertebrates, fish, amphibians, and some reptiles to escape seasonally inhospitable or unproductive conditions (e.g., McClanahan 1966, Bemis et al. 1987, Dietz-Brantley et al. 2002, Ligon and Peterson 2002). Alternatively, the low-energy lifestyles of some ectothermic vertebrates may allow them to build up sufficient energy reserves during productive periods to survive periods of shortage. For example, female aspic vipers [*Vipera aspis* (Linnaeus, 1758)] can rely on stored energy to reproduce during years in which they do not capture a single prey item (Lourdais et al. 2003).

Isolated wetlands in the southeastern United States harbor diverse assemblages of organisms (Semlitsch and Bodie 1998). In particular, the ovoid, isolated wetlands known as Carolina bays that occur along the Atlantic Coastal Plain from Virginia to Florida are among the most productive and species-rich habitats in the region (Sharitz 2003). Reptiles and amphibians are major predators and prey in these ecosystems and constitute a significant portion of both biomass and species diversity (Sharitz 2003, Gibbons et al. 2006). Within Carolina bays and other wetlands, the population and community dynamics of both amphibians and reptiles are often highly dependent on hydroperiod, with periods of extreme productivity (Pechmann et al. 1991, Gibbons et al. 2006) punctuated by droughts when wetlands become unsuitable for most aquatic organisms.

In this study, we examined the responses of seven species of semi-aquatic snakes inhabiting an isolated wetland in the Upper Coastal Plain of South Carolina to a severe drought. We used recolonization patterns following the drought and compare changes in relative abundance and demographics before and after the drought to infer survival strategies and the impacts of drought on the snake community.

MATERIALS AND METHODS

Study Site

Ellenton Bay is an isolated Carolina bay on the Department of Energy's Savannah River Site (SRS)
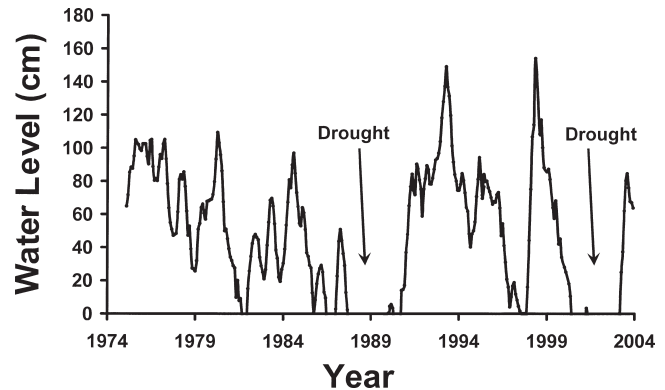

Figure 1.   Water level at Ellenton Bay in the years 1974 – 2004. Note severe droughts in 1987 -1990 and 2000 – 2003. Water depth was measured at a point in the interior of the wetland that represented general maximum basin depth, although a few isolated deeper holes existed in the muddiest central sections of the wetland.

in the Upper Coastal Plain of South Carolina, USA. Although water levels are extremely variable (Figure 1), the bay generally holds water year-round and when full covers approximately 10 ha. 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 (Figure 1). Ellenton Bay is currently fish-free [*Gambusia holbrooki* Girard, 1859 were present until the drought in 1987] and harbors a diverse assemblage of semi-aquatic amphibians (24 species) and reptiles (18 species; Gibbons and Semlitsch 1991). The habitat surrounding Ellenton Bay is a mosaic of old-fields in various stages of succession and second-growth mixed pine-hardwood forest. Ellenton Bay has hosted several long-term studies of the effects of drought on reptiles and amphibians (Gibbons et al. 1983, Seigel et al. 1995a, 1995b, Gibbons et al. 2006, Winne et al. 2006). It is inhabited by seven semi-aquatic snake species, thus providing an excellent opportunity to examine interspecific differences in drought-avoidance strategies and their subsequent short- and long-term impacts on snake populations.

Methods

In February 2003, we erected a continuous terrestrial drift fence (Gibbons and Semlitsch 1981) that completely encircled Ellenton Bay and was equipped with pitfall and funnel traps. Serendipitously, we began monitoring the fence and traps three days before the start of a long period of rain that began to refill the wetland after the 2.5-year drought. We monitored the fence from 1 February 2003 to 31 January 2004 and therefore were able to document the numbers of snakes entering and

exiting the wetland for one year. By April, the wetland held substantial standing water (> 4 ha surface area), and the maximum water level was reached in August.

The drift fence was constructed of aluminum flashing (1230 m long, 40 cm high) and buried several cm into the soil. Along the fence, we installed 41 pairs of 19-L pitfall traps (plastic buckets), spaced approximately every 30 m along the fence with one trap on each side of the fence (Gibbons and Semlitsch 1981). Beginning 27 February 2003, 20 pairs of wooden box funnel traps were placed along the drift fence between every other pair of buckets, such that funnel trap pairs were spaced equally around the bay, 60 m apart. Traps were rectangular, measuring 92.5 × 32.5 × 28.5 cm, with treated plywood sides and 0.6 cm hardware cloth funnels, extending 28 cm into the trap, with a square 3.5 × 3.5 cm funnel opening. Funnel traps were removed for several nights in May to avoid mortality of tens of thousands of metamorphosing amphibians emigrating from the bay (Gibbons et al. 2006). Captured snakes were judged as entering or leaving the bay based on the side of the fence where they were captured (Seigel et al. 1995a).

Pitfall and funnel traps were checked at least once daily (0700 – 0900 h). On days warm enough for snakes to be active, traps were checked again in the late afternoon (1700–2000 h). In the laboratory, we recorded the snout-vent length (SVL) and tail length (nearest mm), body mass (nearest 0.1 g using an electronic balance), and sex (by probing) of all captures. Each snake was marked with a unique code by branding (Winne et al. 2006). Snakes were returned to the bay within three days and released on the opposite side of the drift fence where they were captured.

The drift fence was also operational in the spring of 1986 (31 December 1985 – 1 July 1988; Seigel et al. 1995a) when 246 5-L pitfall traps and 40 – 50 hardware cloth terrestrial funnel traps (Fitch 1987) were placed along the fence and checked daily (Seigel et al. 1995a). Captured snakes were processed as above but were marked by scale clipping (Brown and Parker 1976).

To assess changes in relative abundance of aquatic snakes within Ellenton Bay, aquatic trapping was conducted using comparable techniques and effort from 31 May to 5 June 1998 (Winne et al. 2005) and 5 – 20 May 2003 (Willson et al. 2005). Trapping in 1998 was conducted using 93 commercially available plastic minnow traps (465 trap-nights) and in 2003 using 30 plastic minnow traps (450 trap-nights). An additional 900 trap-nights of sampling was conducted in May 2003 using other trap types (steel and nylon mesh minnow traps; Willson et al. 2005).

Traps were set approximately 2 m apart in transects along the margin of the bay, amidst emergent vegetation. Although traps were not purposefully baited, they readily accumulated amphibian larvae between trap checks (Keck 1994, Winne et al. 2005). Traps were checked once (2003) or twice (1998) per day, at which time all captured animals were removed from traps. Captured snakes were processed as described above and returned the following day (2003) or at the end of the trapping period (1998).

Data Analyses

Rayleigh's test of uniformity ($\alpha = 0.05$) was used to test spatial movement patterns during the March–May recolonization period against the null hypothesis that snakes immigrated to Ellenton Bay non-directionally following drought.

We compared aquatic funnel trap snake captures in early summer 1998 and 2003 to assess changes in the aquatic snake community at Ellenton Bay following the drought in 2000 - 2003. Recaptured snakes were not included in capture totals, and capture rates were standardized to sampling effort by dividing the number of snakes captured by the number of trap nights and multiplying by 100.

To assess reproduction during the drought, we compared size-frequency distributions of snakes captured entering Ellenton Bay in 1986 (a non-drought year) with snakes captured entering the bay during the same time period in 2003 (after prolonged drought). Snakes were judged to have been born in the previous year by visual inspection of size-frequency distributions, published data on snake sizes at birth and growth rates (Gibbons et al. 1977, Semlitsch et al. 1988, Ernst and Ernst 2003, Gibbons and Dorcas 2004), and unpublished data for thousands of snakes captured on the SRS.

RESULTS

Terrestrial Movements Following Drought

Captures of snakes in the drift fence in 2003 indicate that recolonization of the wetland primarily occurred from March to May, when most snakes were captured moving towards the bay (Figure 2A). Interspecific differences were apparent in timing, orientation, and magnitude of recolonization. Thirty cottonmouths [*Agkistrodon piscivorus* (Lacepède, 1789)] arrived at the bay in March, with fewer individuals arriving later in spring (Figure 2B). A few banded and red-bellied watersnakes [*Nerodia fasciata* (Linnaeus, 1766) [N=12] and *N. erythroga-ster* (Forster, 1771) [N=8]], mud snakes [*Farancia*
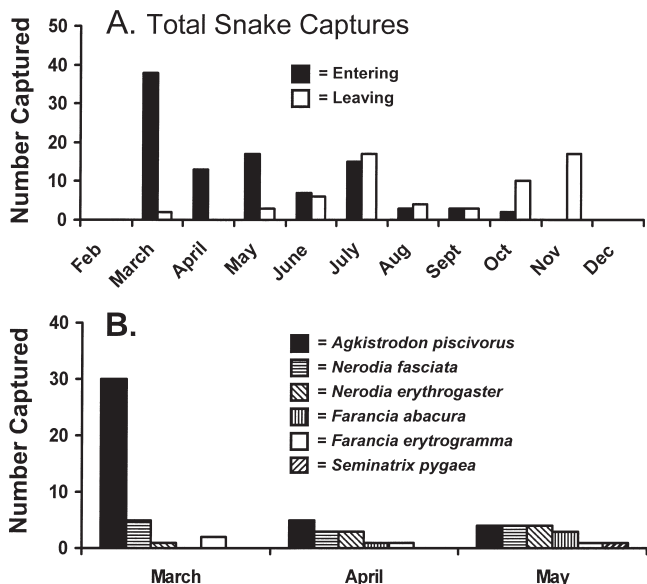
Figure 2. A) Captures of semi-aquatic snakes in the drift fence encircling Ellenton Bay in 2003 following a prolonged drought, excluding young snakes born in 2003. B) Species composition of semi-aquatic snakes captured entering Ellenton Bay during recolonization following drought.

abacura (Holbrook, 1836); N=4], and rainbow snakes [*F. erytrogramma* (Palisot de Beauvois, 1801); N=4] were captured sporadically during the spring (Figure 2B). No eastern green watersnakes [*N. floridana* (Goff, 1936)] and only one black swamp snake [*Seminatrix pygaea* (Cope, 1871)] were captured entering the bay during this period (Figure 2B). Large numbers of snakes leaving the bay in the fall (Figure 2A) were primarily *A. piscivorus*. No adult *Nerodia* and only one *F.*

erytrogramma were captured leaving the bay during October and November.

Directionality of *A. piscivorus* movement during the March – May recolonization period differed significantly from random (Rayleigh's test; P = 0.01; Figure 3A). Most *A. piscivorus* captures were made on the southwest and northeast sides of the bay, corresponding to the direction to the Savannah River swamp and Bulldog Bay, respectively, the nearest permanent aquatic habitats. Although sample sizes for the remaining species were small, no significant directionality was detected for *N. fasciata* (P = 0.38; Figure 3B), *N. erythrogaster* (P = 0.40; Figure 3B), *F. abacura* (P = 0.30; Figure 3C), or *F. erytrogramma* (P = 0.58; Figure 3C).

Reproduction during Drought

In 1986 (following several years of normal water levels), 17 *N. fasciata*, 17 *F. abacura*, and 8 *F. erytrogramma* captured entering the bay in the spring were judged to be the previous year's offspring (Figure 4A–C). Trapping in 2003, following the severe drought, yielded few young of these species (*N. fasciata* [N=1], *F. abacura* [N=0], *F. erytrogramma* [N=1]; Figure 4A-C). In contrast, 13 (39%) of the *A. piscivorus* captured entering the bay in the spring of 2003 were identified as being born the previous fall (Figure 4D).

Effects of Drought on Relative Abundances of Semi-Aquatic Snake Species

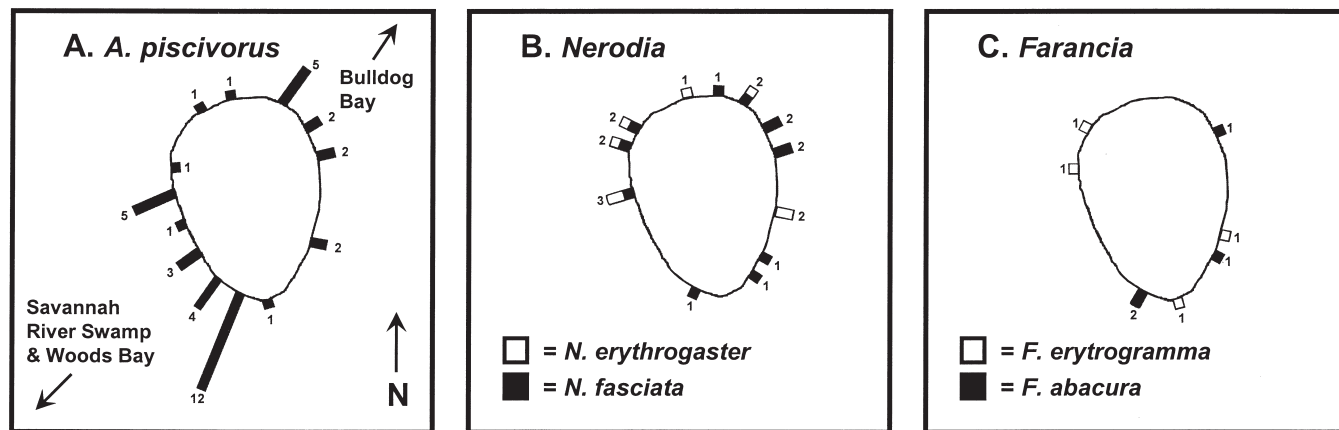Although *N. fasciata* (N=18) accounted for nearly half of the aquatic funnel trap captures in

Figure 3. Spatial patterns of snake recolonization of Ellenton Bay following extreme drought. Bars outside the boundary of the edge of the bay represent individuals captured entering the bay between 1 February and 30 May 2003; bars inside represent snakes captured leaving the bay during this period. Large numbers of *A. piscivorus* A) immigrated from the direction of the other aquatic habitats (e.g., Savannah River swamp, Woods Bay, and Bulldog Bay). *Nerodia* B) and *Farancia* C) did not show significant directionality.
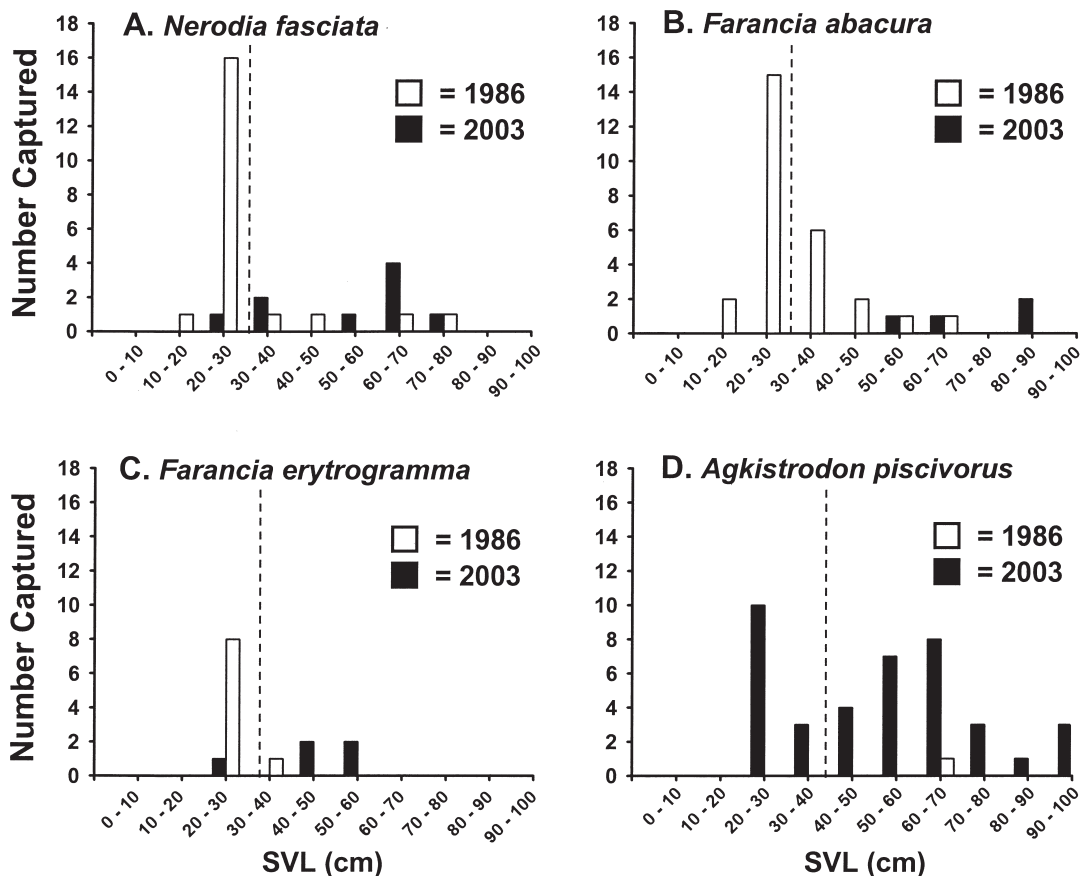
Figure 4. Size-frequency histograms of snakes captured entering Ellenton Bay in 2003, following drought, compared to a non-drought year, 1986. Dotted lines indicate sizes (SVL) below which snakes were judged to be young from the previous year. Juvenile size class is greatly reduced or absent in 2003 for *N. fasciata*, *F. abacura*, and *F. erytrogramma*, but is present in *A. piscivorus*. Because of differences in trapping methods, direct comparisons of numbers of adult snakes entering the bay between years is not possible, but all young snakes entering the bay were likely captured in both years.

1998, we did not capture any in spring 2003 (Figure 5). *Nerodia floridana*, detected at Ellenton Bay in 1998 (N=5), were not captured in 2003 (Figure 5). *Seminatrix pygaea* were captured with similar frequency in both years (Figure 5). Although no *F. abacura* were captured in 1998, we captured two in aquatic traps in 2003 that had not been captured in the drift fence while entering the bay (Figure 5). Additional trapping in May 2003 using other trap types yielded additional *S. pygaea* (N=18) and *F. abacura* (N=4) but no *N. fasciata* or *N. floridana*.

Overall, aquatic snake capture frequencies in 2003 were reduced by about 40% compared to 1998 (Figure 5). A similar but more dramatic reduction in aquatic snake capture rates was seen following the extreme drought that lasted from 1987 to 1990 (Figure 5).

DISCUSSION

To capitalize on the productivity of dynamic habitats, organisms must evolve strategies to escape
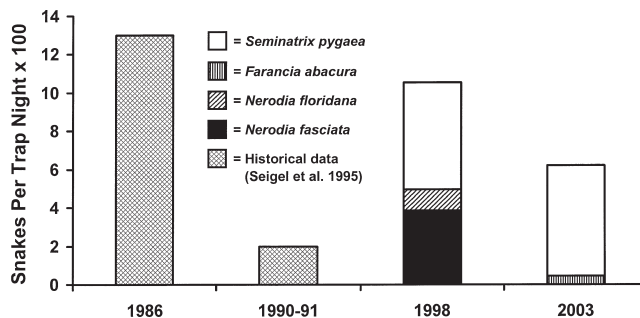

Figure 5. Relative abundance of snakes within Ellenton Bay as measured by aquatic trapping success in 1986 and 1998 (pre-drought years) and 1990–91 and 2003 (post-drought years). Data from 1998 and 2003 represent individual snakes captured per 100 trap nights. Historical data (Seigel et al. 1995a) represents overall number of snakes captured per 100 trap nights and does not specify species composition.

or survive periods of low resource abundance or unfavorable environmental conditions. Our examination of seven species of semi-aquatic snakes inhabiting an isolated wetland subjected to periodic extreme droughts revealed that these species adopt different drought-survival strategies and consequently are affected differentially by extended drought.

Strategies for Inhabiting a Dynamic Environment

We captured relatively large numbers of *A. piscivorus* entering Ellenton Bay as it refilled following over two years of extreme drought. The majority entered in March and arrived at the bay in near straight-line directions from the nearest permanent aquatic habitats. In October and November, many *A. piscivorus* (including many adults that had been marked entering in the spring) exited the bay along the same corridors, strongly suggesting that *A. piscivorus* undertake annual migrations to capitalize on the seasonally-productive ecosystem and/or to overwinter in other habitats (Glaudas et al. 2007). Migration apparently allows *A. piscivorus* to fare well during drought, based on the abundance condition of adults in 2003 and the presence of juveniles born the previous summer in drift fence captures. The ability of *A. piscivorus* to migrate, and its apparent success during droughts, may be enhanced by low rates of evaporative water loss in comparison to other semi-aquatic snakes (Winne et al. 2001, Moen et al. 2005), as well as its large body size, generalist feeding preferences, and potent venom for defense.

Seigel et al. (1995a) found that *N. fasciata* emigrated directionally towards other aquatic habitats in response to drying of Ellenton Bay in the fall of 1986. Our data indicate that this species fared poorly at Ellenton Bay during the 2000–2003 drought. Few *N. fasciata* were captured returning to the bay following the drought, and relative abundance was considerably reduced compared to predrought years. Additionally, the lack of juveniles immigrating to the bay in 2003 is evidence that there was either little successful reproduction or high juvenile mortality for this species during the drought. Although the exact cause for decline of *N. fasciata* is unclear, high rates of evaporative water loss (Winne et al. 2001), dependence on aquatic prey, and a paucity of nearby wetlands that held water during the drought could lead to high mortality for this species after emigrating from the bay as it dried. Alternatively, snakes that dispersed to other aquatic habitats to escape the drought may not have returned to Ellenton Bay once it refilled

because the costs of the return journey may have outweighed the benefits of retuning to the wetland.

As in previous droughts (Seigel et al. 1995a), the drought of 2000 – 2003 appears to have resulted in local extirpation of *N. floridana* at Ellenton Bay. However, the high reproductive potential of this species and *N. fasciata* (maximum litters of 101 and 57 young, respectively; Gibbons and Dorcas 2004) may enhance repopulation following drought. Indeed, Seigel et al. (1995a) noted that *N. floridana* populations had recovered substantially seven years after they were locally extirpated by drought in 1988. *Nerodia erythrogaster* have not been particularly common at Ellenton Bay over the last three decades (J. W. Gibbons, pers. obs.), but capture rates in 2003 suggest that this species declined less than *N. fasciata* during the drought. The apparent resilience of *N. erythrogaster* to drought may be partially because this species normally travels more extensively between wetlands than other watersnakes (Roe et al. 2003).

Seminatrix pygaea possess traits, including small size, high rates of evaporative water loss (Winne et al. 2001), and defensive behaviors that are ineffective outside of aquatic habitats (Gibbons and Dorcas 2004), that make them ill-suited to extensive terrestrial activity. Although *S. pygaea* have been suggested to migrate between wetlands in some situations (Dodd 1993, Seigel et al. 1995a), data from the 2000 – 2003 drought suggest that a sizeable proportion of the *S. pygaea* population aestivated within Ellenton Bay during the drought rather than leaving the bay for other aquatic habitats (Winne et al. 2006). Aestivation appears to have allowed *S. pygaea* to fare better than other species during the drought, as relative abundance of this species (indicated by catch per unit effort of aquatic trapping) was similar in 1998 and 2003.

Sample sizes for *Farancia* were too small to draw definitive conclusions, but the capture of several *F. abacura* within the bay that had not been captured in the drift fence suggests that at least a few of these snakes also remained within the bay during the dry period. Aestivation has been noted in this species and *S. pygaea* in Florida wetlands during drought (M. Aresco, pers. comm.). Young of both *Farancia* species are known to inhabit temporary wetlands, including Ellenton Bay, with young snakes entering the wetland in the spring after presumably overwintering in terrestrial nests (Gibbons et al. 1977, Semlitsch et al. 1988). The absence of young-of-the-year *Farancia* immigrants in 2003 suggests that these species did not successfully reproduce in the vicinity of Ellenton Bay during the drought. Adult *Farancia*, although never abundant at Ellenton Bay, did not

appear to be dramatically reduced in comparison to predrought periods.

Long-Term Changes in the Ellenton Bay Aquatic Snake Community

Shifts in snake relative abundance and substantial changes in species composition have been observed at Ellenton Bay during more than two decades of study. Most notable has been the proliferation of cottonmouths, which were rarely observed until the late 1980s (J. W. Gibbons, unpublished data) and have since become the second most commonly-encountered snake after *S. pygaea*. One hypothesis for this change is that succession around the bay (from old-field to second-growth forest; Gibbons et al. 2006) has allowed cottonmouths to colonize this productive habitat and now permits this species to make yearly migrations to Ellenton Bay from terrestrial hibernacula or other more permanent but less productive habitats.

Of the species examined, *N. fasciata* and *N. floridana* appear to be most vulnerable to local extinctions during drought. *Nerodia floridana* has apparently become locally extinct twice in 20 years, and *N. fasciata* experienced dramatic population reductions in years following drought. Both species, however, appear to recover after a sufficient period following drought, possibly due in part to the high fecundity of these species.

Interestingly, *S. pygaea* continues to be extremely abundant in this wetland, despite the recent extreme droughts and extirpation of a major prey item (*Gambusia holbrooki*) in the 1980s. Apparently *S. pygaea*'s ability to aestivate within the bay during drought and take immediate advantage of high post-drought amphibian prey abundances (Winne et al. 2006) have facilitated its continued success in this isolated wetland habitat.

Implications for Conservation of Isolated Wetland Fauna

The range of interspecific differences in drought-avoidance strategies of semi-aquatic snakes at Ellenton Bay reveals that land management may have different impacts on species. For species that rely on migration between wetlands to survive drought (e.g., *A. piscivorus*), maintenance of corridors between wetlands may be crucial for species persistence, and migration barriers such as highways or large expanses of cleared land may leave these species without refugia during drought (Roe et al. 2003, 2004). Alternatively, for species such as *S. pygaea* that are highly adapted to isolated seasonal wetlands such as Ellenton Bay, conservation of the delimited wetland itself, even when dry, is necessary. Finally, species that are apparently highly sensitive to drought (e.g., *N. fasciata* and *N. floridana*) may rely on metapopulation (Levins 1969) or source-sink (Pulliam 1988) dynamics to persist, necessitating the preservation of wetland complexes large enough to support several sub-populations connected by periodic dispersal events (Roe et al. 2003, 2004). Clearly, to maintain diverse assemblages of species that respond differently to climatic variability, conservation of multiple wetland types that vary in size, hydroperiod, and proximity to other wetlands is critical (Semlitsch and Bodie 1998). Additionally, terrestrial habitats surrounding wetlands are vital as refuges or migration corridors for many aquatic species during droughts (Gibbons 2003). The various drought avoidance strategies used by local species must all be considered when decisions are made about how to develop wetlands and surrounding terrestrial habitats.

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