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Evaluating the functional importance of secretive species: A case study of aquatic snake predators in isolated wetlands

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Abstract

Although the need to prioritize limited conservation resources has prompted increased interest in understanding the functional importance of species within ecosystems, species that are infrequently observed are often written off as being unimportant. In this study, we use aquatic snakes as a case study for examining the importance of secretive predators. Most snakes are extremely cryptic and secretive, traits that not only lead to the perception that they are rare, and of minor importance, but also impede attempts to quantify densities. We used high sampling effort and robust-design capture–recapture analyses to estimate density of aquatic snakes inhabiting an isolated 5.4-ha wetland in South Carolina, USA. We assessed snake diets and coupled field measurements of growth rates with laboratory-derived data on mass conversion efficiency to estimate prey consumption by snakes over a 1-year period. We found a peak density 171 snakes ha^{-1} of wetland habitat, corresponding to a standing biomass of 7.77 kg ha^{-1}. We calculated that snakes within the wetland consumed a total of over 200 kg (>55 000 individuals) of amphibian prey annually, translating into >150 000 kJ ha^{-1} of energy flow from secondary to tertiary consumers within the wetland food web. Further, because many amphibians are primarily terrestrial as adults and are consumed by aquatic snakes only when they return to wetlands to breed, snakes can be responsible for substantial transfer of energy and biomass between terrestrial and aquatic habitats. Our study is one of the first comprehensive evaluations of the importance of snakes as predators and underscores the need to consider snakes in initiatives aimed at preserving overall ecosystem integrity.

Introduction

Recognition of the magnitude and diversity of effects that human activities have on the environment has prompted increased interest in understanding the functional importance of species within ecosystems (e.g. Lyons & Schwartz, 2001; Vanni *et al.*, 2002). Predators are known to be particularly important, and their contributions to ecosystem function have been demonstrated in a variety of ecosystems (e.g. Estes *et al.*, 2011). Major groups of predatory vertebrates include mammals, birds, fish, amphibians and reptiles. Among these groups, reptiles have been largely overlooked. Particularly, although all snakes are strictly carnivorous and many are secondary or tertiary carnivores (Greene, 1997), our knowledge of the importance of snakes as ecosystem components is extremely limited.

Often, a necessary first step in evaluating the functional importance of species is to measure their abundance. Thus, we have gleaned much of our knowledge of the effects of community structure on ecosystem processes from studies of species that are easy to survey, such as grassland plants or sessile invertebrates (e.g. Paine, 1966; Tilman *et al.*, 1997). Conversely, the importance of secretive species remains largely unknown, and in many cases, infrequent observation prompts a perception of rarity and lack of importance. Reptiles and amphibians are well-known for their cryptic habits (Gibbons *et al.*, 2000; Mazerolle *et al.*, 2007). In recent years, however, field and analytical techniques have been developed that improve researchers' abilities to accurately estimate abundance of species with low recapture probabilities (Dorcas & Willson, 2009). For example, Bailey, Simons & Pollock (2004) used robust-design capture–recapture models to demonstrate that during any given sampling period, 58–87% of terrestrial salamanders were unavailable for capture due to temporary use of subterranean refuges. Due, in part, to advances in field and analytical techniques, several studies have examined the importance of amphibians as ecosystems components (e.g. Burton & Likens, 1975; Regester, Lips & Whiles, 2006).

Among the terrestrial vertebrates, snakes are one of the most difficult groups to study due to their cryptic behavior and low or sporadic activity (Dorcas & Willson, 2009). Although they are seldom conspicuous, snakes can occur at high densities [e.g. >1200 ha^{-1} for crayfish snakes *Regina alleni* and black swamp snake *Seminatrix pygaea* in Florida wetlands (Godley, 1980); >1000 ha^{-1} for ringneck snakes *Diadophis punctatus* in Kansas (Fitch, 1975); 102 ha^{-1} for dog-faced water snakes *Cerberus schneiderii* in mangrove habitats in Singapore (Chim & Doiong, 2013)]. At such high densities, snakes may be important predators, but our overall knowledge of the effects of snake predation on prey populations is minimal (Gragg *et al.*, 2007; Nowak, Theimer & Schuett, 2008).

In this study, we used aquatic snakes in an isolated, fishless wetland as a case study for examining the functional importance of secretive predators. We used high sampling effort and robust-design capture–recapture models to estimate density of two species of aquatic snakes. We then coupled measurements of diet and growth rates in free-ranging snakes with laboratory data on mass conversion efficiencies to estimate prey consumption by snakes over a 1-year period. Our results shed light on the importance of snakes as predators in this ecosystem.

Materials and methods

Study site

Ellenton Bay is an isolated Carolina bay freshwater wetland located on the US Department of Energy's Savannah River Site (SRS) in the Upper Coastal Plain of South Carolina, USA. It is characterized by shallow water (<1 m deep) and relatively homogeneous expanses of emergent vegetation. The wetland is semipermanent and the surface area remained relatively constant (5.4 ha) during this study. Ellenton Bay is devoid of fish, crayfish and giant salamanders (*Siren* and *Amphiuma*), providing a relatively simple food web in which amphibians and reptiles are the numerically dominant vertebrate predators.

Study species

Although seven species of semiaquatic snakes inhabit Ellenton Bay, two species dominate the community (>94% of snake captures): the banded water snake *Nerodia fasciata* and black swamp snake *S. pygaea*. *Nerodia fasciata* (hereafter *Nerodia*) is larger [maximum snout–vent length (SVL) in our population = 893 mm, maximum total length (TL) = 1033 mm] and is abundant and ubiquitous in aquatic habitats of the southeastern US. *Seminatrix pygaea* (hereafter *Seminatrix*) is much smaller (maximum SVL = 476 mm, maximum TL = 550 mm) and is endemic to the southeastern Coastal Plain. Both species are viviparous (parturition in July–August) and virtually all mature females reproduce annually (Winne, Willson & Gibbons 2006b; J.D. Willson and C.T. Winne, unpublished data).

Snake sampling

We captured snakes at Ellenton Bay over 1 year (May 2005 to May 2006) using a temporal pattern of sampling to fit Pollock's (1982) robust design. Robust-design analysis requires widely spaced primary sampling intervals, each consisting of a series of short secondary samples, within which demographic closure is assumed. We sampled snakes monthly (primary samples) from May to October 2005 and March to April 2006 for 6–10 consecutive nights (secondary samples). Specific sampling dates were 18–28 May, 18–28 June, 18–28 July, 18–28 Aug, 18–28 September, 18–24 October 2005; and 29 March to 4 April and 18 April to 4 May 2006. During each sampling period, we set 465 unbaited plastic minnow traps (N.A.S Incorporated, Marblehead, OH, USA), spaced approximately 2 m apart in a continuous transect around the aquatic periphery of the wetland and checked traps each morning. Following capture, we recorded sex, SVL (nearest mm by stretching along a meter stick) and mass (nearest 0.01 g on an electronic balance), identified recently ingested prey items by forced regurgitation up to once per year per individual, marked each snake with a unique code by branding ventral scales (Winne *et al.* 2006a), and released it at its capture location on the day of capture. We excluded from all analyses the mass for any snake with palpable prey that was not regurgitated.

We estimated the importance of snakes at Ellenton Bay in terms of prey consumption using data on snake density, diet, growth rates and mass conversion efficiency. We divided snakes into three demographic groups per species: males, females and juveniles. *Nerodia* grew rapidly at this site, often reaching sexually mature body size in their second summer. Thus, the juvenile group for *Nerodia* included only young born during the study (i.e. 2005 young-of-year). Because very small *Seminatrix* can escape through the mesh of aquatic traps (Willson, Winne & Keck, 2008), the 'juvenile *Seminatrix'* group included individuals from the size at which they first become catchable in traps (200 mm SVL; 5 g) to the minimum size at maturity for females in this population (259 mm SVL). We assessed snake population sizes, diets and growth rates on a seasonal basis, by subdividing the year into four biologically relevant periods – late spring (May–June), summer (July–August), fall/winter (September–February) and early spring (March–April).

Snake density

We used the robust-design format in Program MARK to construct mark-recapture models. We based our population estimation procedure on models that garnered the most support in a previous study that systematically evaluated factors influencing capture probability using this dataset (Willson, Todd & Winne, 2011). Based on Willson *et al.* (2011), models for both species allowed for behavioral responses to traps (i.e. 'trap-happiness') and allowed capture and recapture probabilities to vary among primary sampling periods. Capture and recapture probabilities were set equal for both sexes of *Nerodia* and for all demographic groups of *Seminatrix*. Willson *et al.* (2011) did not consider juveniles, but unpublished models conducted under the same framework showed strong support for low capture and recapture probabilities of juvenile *Nerodia*. Thus, we allowed these parameters to vary from adult parameters. We constrained survivorship to be constant over time but allowed it to vary among demographic groups. Because there was little support for random temporary emigration in *Nerodia* (Willson *et al.*, 2011), we fixed the temporary emigration parameter at zero. For *Seminatrix*, however, we allowed constant random temporary emigration that differed between demographic groups (Willson *et al.*, 2011). We estimated population size for both species at each of the four seasonal time periods (i.e. we used a single population size parameter for each month within seasons), but only estimated population size of juvenile *Nerodia* over one interval, fall–spring. Because *Seminatrix* exhibited temporary emigration, we estimated the total population size (i.e. superpopulation size; Kendall, Nichols & Hines, 1997) for each demographic group of *Seminatrix* during each season ($N_{\text{super,season}}$) by correcting our population estimate (sampled population, $N_{\text{sampled,season}}$) for temporary emigration ($\text{TE}_{\text{season}}$) using the formula:

$$N_{\text{super,season}} = \frac{N_{\text{sampled,season}}}{(1 - \text{TE}_{\text{season}})}$$

Snake diets

We evaluated diets of *Nerodia* and *Seminatrix* directly using gut contents manually regurgitated from snakes. We corrected diet proportions for prey mass by multiplying the number of prey items (grouped by genus or life-stage: *Ambystoma*, adult *Hyla*, adult *Rana*, *Acris*, newly metamorphosed *Rana* and tadpoles) recorded in snake's diets by the mean mass of prey within each group. Prey genera were lumped into functional groups (*Ambystoma talpoideum*, post-metamorphic anurans and tadpoles) to ease visualization in figures.

Snake growth and mass conversion efficiency

We calculated seasonal, species and group-specific growth rates from individual capture-recapture data. We calculated growth (mass) for each individual snake captured in at least two primary periods (months) within a season by dividing the change in mass by the number of days elapsed between captures. Because captures of *Seminatrix* were very low in March, we assessed growth in this species during only three periods (late spring, summer and fall–early spring). Due to parturition and mass loss over winter, some groups occasionally exhibited negative seasonal growth rates. In such cases, we set growth rate at zero for the season, rather than using a negative prey consumption value.

We measured mass conversion efficiency of *Nerodia* feeding on amphibians in the laboratory. We used 21 captive-born *N. fasciata* (8–68 g) fed a diet of frozen/thawed *A. talpoideum* collected from Ellenton Bay. Snakes were maintained communally in 75.7 L aquaria, lined with paper towels and provided with large water bowls, hide boxes and basking lamps. Every 6 d snakes were individually offered 35% of their body mass in *A. talpoideum*. After 48 d, snakes were fasted to ensure post-absorptivity (6 d; the approximate duration of the digestive response in *N. fasciata*; Willson & Hopkins, 2011) and weighed. Mass conversion efficiency was calculated by dividing the mass gained by the cumulative wet mass of prey consumed. Because *Seminatrix* often refused to feed in the laboratory, we did not measure mass conversion for this species. Instead, we assumed that mass conversion efficiencies were similar for both species. Likewise, because *A. talpoideum* comprised the vast majority of the diet of both species (see Results), we used mass conversion efficiency values for *A. talpoideum* to assess consumption of other amphibian prey.

Prey consumption by snakes

We calculated prey consumption for each snake demographic group within each season using the formula:

$$\text{Prey consumed (g group}^{-1}\text{season}^{-}1) = \frac{G_{t,\text{group}} \times N_{t,\text{group}}}{\substack{\text{MCE} \\ \text{days in season}}}$$

where $N_{\text{t,group}}$ = population size during each season, $G_{\text{t,group}}$ = mean seasonal growth rate (g snake^{-1} day^{-1}) and MCE = mass conversion efficiency (g gained g consumed^{-1}).

We then summed prey consumption across seasons and demographic groups to calculate total mass of prey consumed. We converted prey mass into energetic equivalents using published values of energy content for *A. talpoideum* (4.06 kJ g^{-1} wet mass; Willson & Hopkins, 2011). We subdivided prey consumption among prey taxa by multiplying the total prey mass consumed within each season by the proportion of diet (by mass) represented by each prey taxon within that season. We then divided the total mass of each prey taxon consumed by the mean mass of prey within that group to estimate the number of individual prey of each type consumed.

Results

Snake density

Sixty-eight days of sampling yielded 1571 captures of 528 individual *Nerodia* and 1286 captures of 495 individual *Seminatrix* (Fig. 1). Despite strong seasonal variation in capture rates, estimated abundances of adult *Nerodia* (220–270) and *Seminatrix* (214–322) were relatively constant over time (Fig. 2). Total estimated population size of *Nerodia* nearly doubled in the fall, when females gave birth to an estimated 222 neonates. Peak total population sizes of both species occurred in the fall, at which time an estimated 919 snakes inhabited Ellenton Bay, representing a density of 171 snakes ha^{-1} and a mean standing biomass of 7.77 kg ha^{-1}.

Snake diet

We recorded a total of 1504 and 518 diet items for *Nerodia* and *Seminatrix*, respectively. The diet of both species was dominated by larval and pedomorphic *A. talpoideum* (Fig. 3a). *Seminatrix*, particularly, specialized on *Ambystoma*, with only 7 instances of other prey (small anurans). *Nerodia* included more tadpoles and post-metamorphic anurans in their diet (91 and 47 records, respectively), in the spring (Fig. 3b). Stable isotope studies in this system confirmed that both snake species feed predominantly on *Ambystoma*, but that *Nerodia* opportunistically feed on seasonally available adult anurans and tadpoles in the spring (Willson *et al.*, 2010).

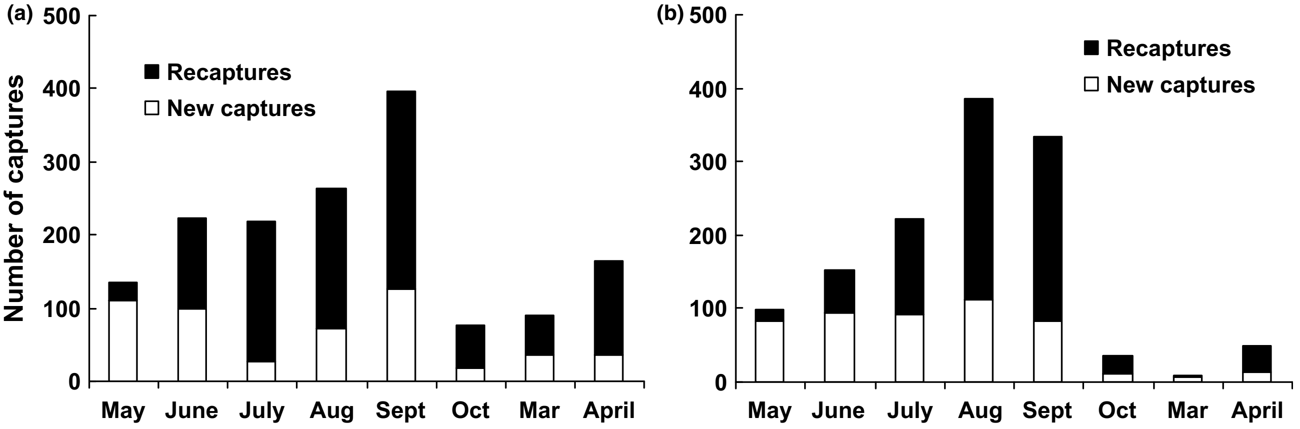

Figure 1 Seasonal distribution of captures of (a) *Nerodia fasciata* and (b) *Seminatrix pygaea* at Ellenton Bay from May 2005 to April 2006. During each season, snakes were captured using 465 aquatic funnel traps set in a continuous transect around the periphery of the wetland. Bars represent total captures over 10 consecutive days of trapping from May to September 2005 and 6 consecutive days of trapping in October 2005 and April and May 2006.

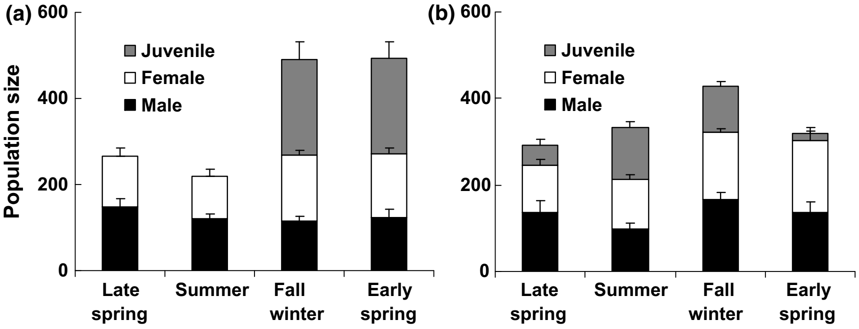

Figure 2 Population size estimates (±1 SE) of (a) *Nerodia fasciata* and (b) *Seminatrix pygaea* at Ellenton Bay from May 2005 to April 2006. Population sizes were estimated using robust-design analysis in program MARK. Models included time varying and independent (i.e. allowing for a behavioral response to traps) capture and recapture probabilities for both species and group-specific constant random temporary emigration for *S. pygaea*. Thus, population estimates for *S. pygaea* represent superpopulation size (i.e. population size corrected for temporary emigration).

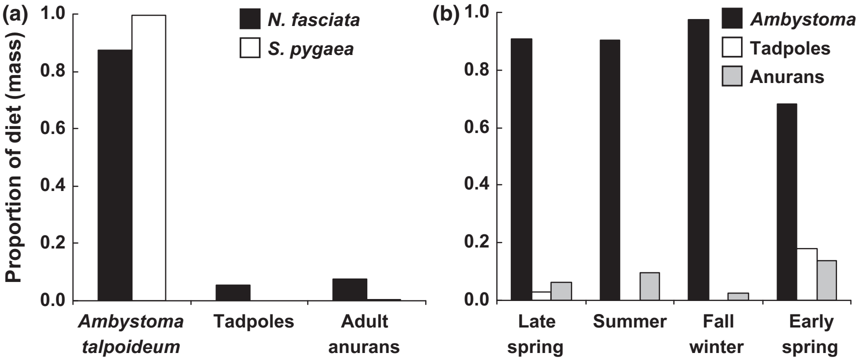

Figure 3 Diet composition of *Nerodia fasciata* and *Seminatrix pygaea* at Ellenton Bay from May 2005 to April 2006. Overall mass-corrected diet composition for *N. fasciata* and *S. pygaea* (a) was derived from a total of 1504 and 518 diet items, respectively. Mass-corrected seasonal diet composition for *N. fasciata* (b) demonstrates seasonal diet shifts in this species.

Snake growth and mass conversion efficiency

Nerodia showed strong seasonal variation in growth, but adult females generally grew faster than adult males and juveniles (Fig. 4a). Growth rates were highest in spring, with rates approaching 1 g per day in females. Due to their smaller size, *Seminatrix* exhibited much lower absolute growth rates (Fig. 4b). Female *Seminatrix* grew rapidly from fall

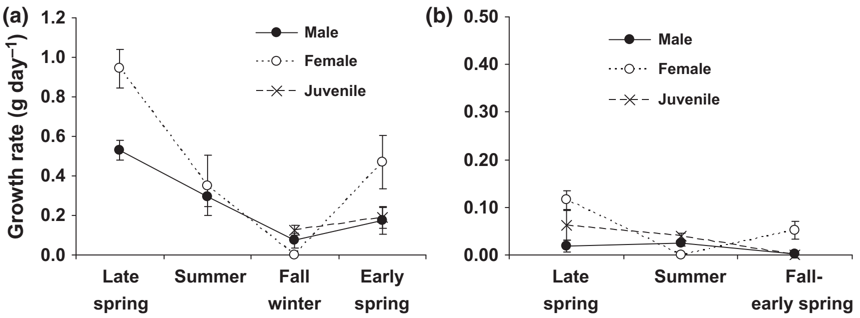

Figure 4 Mean (±1 SE) seasonal growth rates of (a) *Nerodia fasciata* and (b) *Seminatrix pygaea* at Ellenton Bay from May 2005 to April 2006. In cases where snakes lost mass between capture intervals (due to females giving birth or snakes losing some mass over winter), growth rate was set at zero. Thus, if mass change was negative, we conservatively assumed no prey consumption rather than negative prey consumption.

through late spring, but lost mass in summer as a result of parturition. Juvenile and adult male *Seminatrix* exhibited slow growth in spring and summer and negligible growth over the winter. On average, *Nerodia* gained 0.16 ± 0.01 g of wet body mass per gram of amphibian prey consumed in the laboratory.

Prey consumption by snakes

We estimated that snakes consumed 213.35 kg (37 kg ha^{-1}) of amphibian prey at Ellenton Bay annually (Table 1). Prey consumption was highest in the late spring, primarily as a result of high consumption rates by female *Nerodia*. *Nerodia* contributed substantially more to total prey consumption than *Seminatrix,* and females consumed more prey biomass than males in both species. When translated into energetic equivalents, we estimated that snakes consumed a total of 866 186 kJ (161 301 kJ ha^{-1}) of amphibian prey at Ellenton Bay annually.

Ambystoma accounted for the majority of individual prey consumed (90%); *Nerodia* and *Seminatrix* consumed over 53 000 individual *Ambystoma* in 1 year (Table 2). Although they represented a relatively minor component of snake diets, tadpoles and adult anurans were also consumed in large numbers (3493 and 1777 individuals, respectively).

Discussion

Because snakes are often encountered with a frequency that belies their true abundance, they have historically been undervalued as ecosystem components. For example, the 1953 edition of the *Golden Guide to Reptiles and Amphibians* stated: 'as a group [reptiles] are neither "good" nor "bad," but are interesting and unusual, although of minor importance. If they should all disappear, it would not make much difference one way or the other' (Zim & Smith, 1953). Even in cases when snakes are frequently encountered, capture rates are often poor indicators of density. For example, research on invasive brown treesnakes *Boiga irregularis* has found no correlation between visual counts and population density estimated using mark-recapture (Rodda *et al.*, 2005). Snakes have been shown to exhibit time- and group-dependent (e.g. sex or age) capture and recapture probabilities, behavioral responses to traps and temporary emigration (Tyrrell *et al.*, 2009; Willson *et al.*, 2011), all of which can bias estimates of abundance. Due, in part, to the difficulties associated with accurately measuring density, the importance of snakes as predators in most ecosystems remains unknown.

The most dramatic evidence of the potential impacts of snake predation arises from situations where non-native snakes

Table 1 Estimated consumption of amphibian prey by snakes at Ellenton Bay between May 2005 and May 2006

	Prey consumption (kg)					
	Late spring	Summer	Fall/winter	Early spring	Total (kg)	Total (kJ)
N. fasciata						
♂	29.89	13.72	9.69	8.19	61.49	249 655
♀	42.58	13.76	0.00	26.18	82.52	335 023
Juvenile	0.00	0.00	30.87	15.89	46.76	189 851
Total	72.47	27.48	40.56	50.26	190.77	774 529
S. pygaea						
♂	0.98	0.94	0.24	0.07	2.23	9038
♀	4.91	0.00	9.22	3.35	17.48	70 966
Juvenile	1.10	1.77	0.00	0.00	2.87	11 652
Total	6.99	2.71	9.46	3.41	22.58	91 656
Grand total	79.46	30.19	50.02	53.68	213.35	866 186

Prey consumption was calculated using mean seasonal growth rates for each snake demographic group, mass conversion efficiency, and population size estimates. Prey mass was converted into energetic equivalents using published values for energetic content of *Ambystoma talpoideum*.

Table 2 Estimated distribution of prey consumption by snakes across prey taxonomic groups

	Prey consumption (individuals)		
	Ambystoma	Tadpoles	Anurans
N. fasciata			
Late spring	18 979	668	487
Summer	7171	0	284
Fall/winter	11 383	24	107
Early spring	9859	2801	766
Total	47 392	3493	1645
S. pygaea			
Late spring	1991	0	54
Summer	781	0	0
Fall/winter	2723	0	7
Early spring	952	0	71
Total	6446	0	132
Grand total	53 838	3493	1777

Prey consumption (# of individuals) was calculated by multiplying total prey mass consumed within each season (Table 1) by the proportion of diet (by mass) represented by each prey taxon within that season (Fig. 3) and dividing the result by the mean mass of prey within each group.

have invaded novel ecosystems. The accidental introduction of brown treesnakes to the Pacific island of Guam has caused suppression or extirpation of most birds, bats and lizards (Rodda & Savidge, 2007; Campbell *et al.*, 2012). More recently, invasive Burmese pythons *Python molurus* have been linked to severe declines of mammals in the Florida Everglades (Dorcas *et al.*, 2012). Many cases where native snake abundance or prey consumption has been quantified are difficult to interpret because the area occupied by foraging snakes is unknown. For example, Ineich *et al.* (2007) estimated that approximately 1400 sea kraits (*Laticauda* spp.) which congregated at 6-ha islet in the South Pacific consumed over 36 000 eels (972 kg) from surrounding reefs annually. Although their results clearly show that snakes are important predators in coral reef ecosystems, this predation pressure may have been spread over as much as 130-ha of reef habitat (Ineich *et al.*, 2007). Conversely, in his classic study of the striped crayfish snake *R. alleni*, Godley (1980) used systematic sampling to estimate snake density and prey (crayfish and odonate naiad) consumption in exotic water hyacinth communities in Florida. He calculated that the mean standing crop of *R. alleni* was 30.79 kg ha^{-1} (1289 snakes ha^{-1}) and estimated that during the fall, snakes consumed 9.6% and 90.7% of the standing biomass of crayfish and odonate naiads, respectively.

Our results support the idea that snakes exist at high densities and are important predators in aquatic ecosystems. At peak density, 171 snakes ha^{-1} (7.77 kg ha^{-1}) inhabited Ellenton Bay, and these snakes consumed over 37 kg ha^{-1} of amphibians annually. Our estimates of prey consumption by snakes are higher than annual consumption rates of voles by mammalian and avian predators in Sweden (1.37 kg ha^{-1}; calculated from Erlinge *et al.* (1983), assuming an average vole mass of 35 g), and approach rates of fish and squid consumption (48–57 kg ha^{-1}) by cetaceans inhabiting Georges Bank in the Northwest Atlantic (Kenney *et al.*, 1997). Our estimates are well within the range of prey consumption rates by spiders in ruderal ecosystems in the US and Europe (1–60 kg ha^{-1}), but lower than those of spiders in European woodlands (~100 kg ha^{-1}) and Atlantic salt marshes (~200 kg ha^{-1}) (Nyffeler, 2000). Ellenton bay is somewhat unusual in that its isolation has led to a relatively simplified food web, lacking many aquatic predators (e.g. crayfish and fish). However, snakes are abundant in a wide array of aquatic habitats worldwide. Examples include gartersnakes *Thamnophis atratus* that reach densities of 58–131 km^{-1} in California streams (Lind, Welsh & Tallmon, 2005), northern water snake *N. sipedon* densities up to 1107 km^{-1} of shoreline in the US Great Lakes (King, Queral-Regil & Stanford, 2006), and up to 100 filesnakes *Achrocordus arafurae* ha^{-1} (>50 kg ha^{-1}) in Australian billibongs (Shine, 1986). Of particular note are the diverse and highly aquatic homolopsid snakes of southeast Asia, which often occur at extraordinarily high densities in fresh, brackish and saltwater habitats (Brooks, Allison & Reynolds, 2007; Chim & Doiong, 2013). As a testament to their abundance, Brooks *et al.* (2007) estimated that 6.9 million of these snakes are commercially harvested annually from a single large lake in Cambodia. Thus, it is likely that snakes are important ecosystem components across diverse aquatic ecosystems world-wide.

The high snake densities we observed, and their important contributions to biomass and energy flow, may be due, in part, to characteristics of the amphibian prey community at Ellenton Bay. As ectotherms, amphibians efficiently transfer biomass and energy through food webs and occur at high densities in many ecosystems (Davic & Welsh, 2004). Burton & Likens (1975) demonstrated that the average biomass of salamanders (1.77 kg ha^{-1}; 2950 individuals ha^{-1}) in a New Hampshire forest was more than twice that of breeding birds and comparable to the biomass of small mammals. Fishless wetlands are recognized as hotspots of amphibian biodiversity and productivity (Semlitsch, 1998; Gibbons *et al.*, 2006). Further, aquatic salamanders may represent ideal prey for aquatic snakes because their elongate morphology allows snakes to consume large meals with minor impediments to crawling speed (Willson & Hopkins, 2011). Thus, it is likely that high abundances of amphibians, particularly *A. talpoideum*, are important in fueling high snake biomass in Ellenton Bay and other fishless wetlands.

Despite the fact that snakes at Ellenton Bay preyed primarily on *A. talpoideum*, we estimated that snakes also consumed nearly 1800 adult anurans annually. Many anurans are primarily terrestrial as adults and are consumed by aquatic snakes only when they return to wetlands to breed (Willson *et al.*, 2010). Thus, snakes are responsible for the annual transfer of up to 15 kg of biomass or 61 000 kJ of energy from surrounding uplands to Ellenton Bay. Because many amphibians exhibit complex life histories, they are thought to be important contributors to energy and nutrient flow between aquatic and terrestrial systems (Davic & Welsh, 2004; Gibbons *et al.*, 2006; Regester *et al.*, 2006). Our results demonstrate that snakes may also link terrestrial and aquatic food webs by sequestering biomass of migratory adult amphibians when they arrive at wetlands to breed.

The catastrophic global decline of amphibians has received much recent attention, and studies have highlighted the effects that loss of amphibians may inflict on ecosystems (e.g. Whiles *et al.*, 2006). In fact, one hypothesized result of amphibian declines is subsequent declines of tertiary predators, including snakes (Todd, Willson & Gibbons, 2010). Although they have garnered less public attention, reptiles are also declining worldwide (Gibbons *et al.*, 2006; Todd *et al.*, 2010). Our study demonstrates the importance of snakes as predators in some ecosystems and highlights the fallacy that infrequently encountered species are necessarily rare or of minor ecological importance.

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