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Natural History of the One-toed Amphiuma, *Amphiuma pholeter*

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Abstract.—**The One-toed Amphiuma (*Amphiuma pholeter*) is endemic to the eastern Gulf Coastal Plain of the southeastern U.S. from Florida to Mississippi. Of the three-recognized species of *Amphiuma*, it is the least known; no comprehensive natural history of this rarely encountered species has been published. The objective of this study is to describe aspects of the morphology, behavior, life history, and ecology of *A. pholeter* based on collections of 427 individuals from 1969 to 2020. *Amphiuma pholeter* is most commonly encountered in deposits of fluid muck (saprist soils) that are maintained by seepage in small stream swamps. *Amphiuma pholeter* ranges in size from 89-314 mm total length and weighs 5–20 g, with no apparent sexual size dimorphism between males and females. Female *A. pholeter* have been found with enlarged ovarian eggs throughout the year. Examination of gut contents indicated that *A. pholeter* consume primarily small bivalve molluscs, aquatic arthropods and their larvae, and semi-aquatic earthworms. Although secretive and difficult to find, *A. pholeter* is likely not imperiled, as long as its seepage-dominated wetland habitats are left intact.**

Key Words.—diet; ecology; Florida; geographic distribution; Georgia; habitat; morphology; reproduction

Introduction

Large aquatic salamanders with reduced limbs of the family Amphiumidae (Bonnett et al. 2009) are found throughout the southeastern U.S. (Petranka 1998). Most of the ecological research on amphiumas has been restricted to the two larger and more widespread species, the Two-toed Amphiuma (*Amphiuma means*) and the Three-toed Amphiuma (*A. tridactylum*; Baker 1945; Johnson and Owen 2005; Boundy 2005). Based on allozymes, Karlin and Means (1993) found *A. means* and *A. tridactylum* to be closely related, whereas the One-toed Amphiuma (*A. pholeter*) was divergent and represented an ancient evolutionary offshoot. More recently, however, phylogenetic analysis of salamander families, based on widespread sampling of both nuclear and mitochondrial DNA sequences across the geographic distribution of the Amphiumidae, revealed three primary genetic lineages that correspond to the three recognized species with strong support for a sister relationship between *A. means* and *A. pholeter* (Weisrock et al. 2005; Bonnett et al. 2009).

Amphiuma means and *A. tridactylum* are large in size (up to 116 cm total length; Petranka 1998), regularly encountered in aquatic traps (Johnson and Barichivich 2004), and found in a variety of aquatic habitats that contain high amounts of submergent and emergent aquatic vegetation, leaf litter, and organic sediment, including permanent lakes, ephemeral ponds, wet prairies, marshes, bottomland swamps, bayous, cypress swamps, small streams, canals, and ditches (Johnson and Owen 2005; Boundy 2005). These large species consume nearly any animal they can overpower, including adult and larval aquatic invertebrates, especially crayfish, molluscs, annelids, and vertebrates, such as fishes, frogs, salamanders, small snakes, and turtles (Johnson and Owen 2005; Boundy 2005). They are preyed on by alligators, birds, fishes, aquatic snakes, larger conspecifics, and possibly mammals (Johnson and Owen 2005; Boundy 2005). A mark-recapture study of *A. means* indicated that this species can occur at high adult density (0.28 salamanders/m^2), though small individuals are rarely encountered in traps, and large individuals are relatively sedentary, tending to be recaptured within less than 10 m of original capture site (Sorensen 2004). *Amphiuma means* and *A. tridactylum* aestivate in burrows in organic sediment during drought periods when water levels are low (Cagle 1948; Knepton 1954). Both *A. means* and *A. tridactylum* lay eggs connected in a long string, and adults may brood eggs in a burrow in organic sediment (Gunzburger 2003).

In contrast with these larger species, relatively little is known about the ecology of *A. pholeter*. *Amphiuma pholeter* is small (up to 31.4 cm total length) and has a more restricted geographic range limited primarily to the Florida panhandle and adjacent Georgia, Alabama,

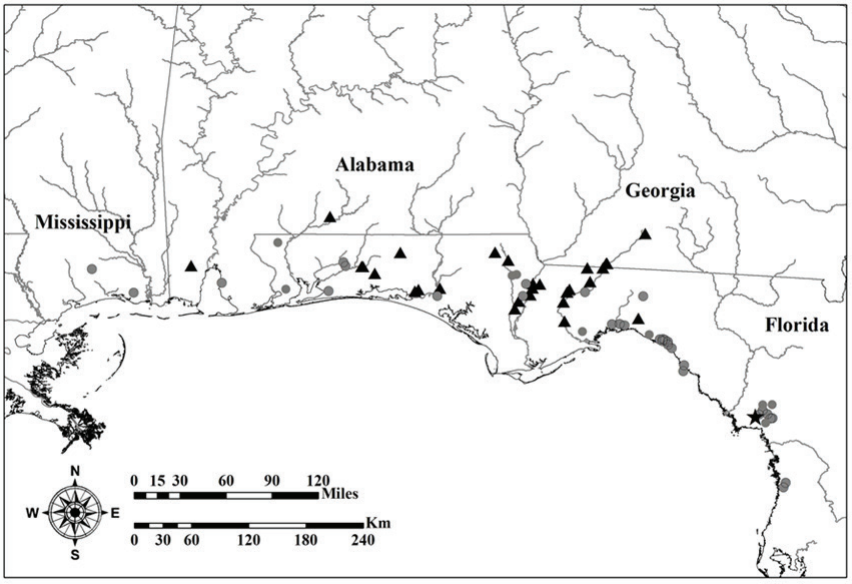

Figure 1. All known localities (in four states of southeastern USA) of *Amphiuma pholeter* (One-toed Amphiuma). Triangles are the sites we visited and gray dots are sites where *A. pholeter* were collected by others. The star (in Florida) is the type locality.

and Mississippi (Carey 1985; Floyd et al. 1998; Graham 2008; Brown and Lamb 2016; Means and Gunzburger Aresco 2019). Within this geographic range, it has a more restricted habitat occurrence compared with the other species of amphiumas, tending to be found in areas of organic sediment along seepage streams or in coastal lowland swamps (Means 1977). Since the description of *A. pholeter* (Neill 1964), most papers have been notes on the geographic range of the species (Stevenson 1967; Carey 1985; Floyd et al. 1998; Graham 2008; Brown and Lamb 2016). Only a few contributed natural history data (Means 1977, 2000). The objective of this study is to describe aspects of the morphology, behavior, life history, and ecology of *A. pholeter* from collections and observations that we made from 1969 to 2020.

Materials and Methods

From 1969 to 2020, we collected *Amphiuma pholeter* from 41 localities in Florida and three localities in Georgia, USA (Fig. 1). We also examined most of the specimens of this species in museums from 35 other localities collected from 1935 to 2020 in Alabama, Florida, and Mississippi, USA (Fig 1). Initially, we collected only one or a few individuals per locality on each visit during the first few years of this study because of the presumed rare status of *A. pholeter* (Means 1978, 1986, 1992). Two localities in Florida, Double Branch in Gadsden County and Big Sweetwater Creek in Liberty County, supported consistently large populations of *A. pholeter* because muck habitat was extensive and on more than a dozen visits to each locality, we raked up individuals readily. In comparison, at many other sites only one specimen was found. We selected these localities for more intensive collecting to obtain an adequate life-history series across all seasons. Muck is relatively easy to survey for *A. pholeter* by digging into it, and thus was the habitat mostly searched during this research. Other habitats, such as peat soils in floodplains under rooted vegetation are much more difficult to examine because of the stiff roots.

We followed Mitsch and Gosselink (1993) in broadly classifying wetland soils as saprists (mucks), fibrists (peats), or humists. Saprists are soils in which two-thirds or more of the material is decomposed into a pasty organic slurry in which less than one-third of plant fibers are identifiable. Fibrists are soils in which more than two-thirds of plant fibers are identifiable. Humists are intermediate between saprists and fibrists.

We collected specimens by hand or with a potato rake by raking through depressions of moist, mucky debris (Fig. 2) in the beds or along the sides of small streams fed by seepage. For each locality, we recorded habitat descriptions, including dominant vegetation, and any co-occurring vertebrate and invertebrate species that we could identify. We euthanized specimens by immersing them in 20% isopropanol for a few minutes, fixed them in 10% formalin for a few weeks or months, and then transferred them to 40% isopropanol for storage.

We observed 427 specimens in the field during this study and collected 206 individuals for detailed morphological and diet data. We performed Linear Regression analysis ($\alpha = 0.05$) to evaluate the relationship between survey effort (total hours spent at each site) and the total number of *A. pholeter* collected at that site. We measured and dissected 206 specimens after fixation in

Figure 2. Muck bed habitat from which *Amphiuma pholeter* (One-toed Amphiuma) were collected. (a) Sweetwater Creek, Liberty County, Florida, USA. (b) Ocklawaha Creek, Gadsden County, Florida, USA. (Photographed by D. Bruce Means).

formalin. We made measurements with dial calipers to the nearest 0.1 mm: SVL (snout to posterior angle of the vent), tail length (posterior angle of the vent to tail tip), snout to anterior base of forelimb, snout to center of gill cleft, posterior base of hindlimb to posterior angle of vent. We summed SVL and tail length to obtain total length (TL). We obtained weights before dissection to the nearest 0.1 g using a Mettler P-163 pan balance (Mettler Instrument Corp., Hightstown, New Jersey, USA) for 33 specimens (21 males, eight females, four sex not determined). We compared male and female weight and total length using *t*-tests ($\alpha = 0.05$).

We dissected specimens to determine their sex. For those females with developing ova, we recorded the number of ova and we measured the diameter of each ovum. We evaluated the relationship of number of ova and ovum diameter and female SVL using Linear Regression analyses ($\alpha = 0.05$). To observe oviposition, we maintained alive in captivity two females collected in May and June 1974 that appeared to contain mature ova. They were housed for a minimum of 120 d in 19 L (5 gallon) aquaria in which one half contained muck from the habitat in which they were collected and the other half contained *Sphagnum* moss on top of wet peat in which to burrow. We performed gut contents analysis for 96 specimens, scoring food or detritus from the stomach, intestines, and cloaca. Food items were removed and identified to the lowest taxonomic level possible, and we recorded the number of each prey item per gut.

Results

Habitat.—We recorded survey effort for 20 localities during 1970–2007. The total number of *A. pholeter* collected at each locality was significantly positively correlated with the survey effort for 20 localities for which survey effort was recorded ($r^2 = 0.94$, $F_{1,18} = 284.11$, $P = 0.006$; Fig. 3). Most of the 427 specimens we observed in the field were raked directly from within 30 cm under the surface of the muck, but some were as deep as up to 60 cm. We found 31 of these individuals under logs partially buried in muck. During drought when we excavated muck beds of Double Branch in Gadsden County, Florida, we found adults at the bottom of the moist organic sediments, on top of underlying sand, in burrows (apparently made by their own bodies) just above the interface between the distinct sandy substratum and the deep organic muck overlying it. Besides single individuals found in this manner (usually coiled loosely instead of lying stretched out), we also found very small young in two clusters, and we found four other groups ranging from two to six individuals of mixed sizes.

We found individuals of *A. pholeter* most commonly in wetland soils classed as saprists, or muck (Mitsch and Gosselink 1993). We rarely found *Amphiuma pholeter* in fibrist soils (peats). Occasionally, we found an individual in a humist soil, which was a saprist soil that was drying out and having no invading roots.

Most of the saprist muck sites in which we found *A. pholeter* were associated with seepage. Twenty-three (56%) of the sites were mucky depressions in the beds or along the sides of steephead streams in the Florida panhandle. Another 12 (29%) sites in the red clay hills of the Florida panhandle were associated with mucky depressions in small drainages fed by hillside seepages.

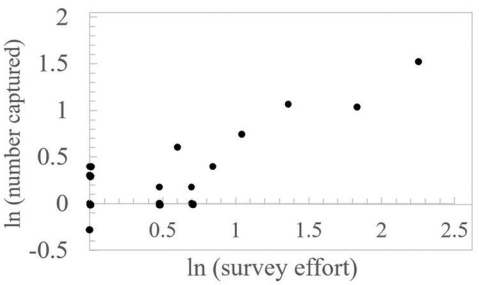

Figure 3. Number (natural log) of *Amphiuma pholeter* (One-toed Amphiuma) collected in relation to the natural log of cumulative survey effort (h) at 20 localities in Florida, USA.

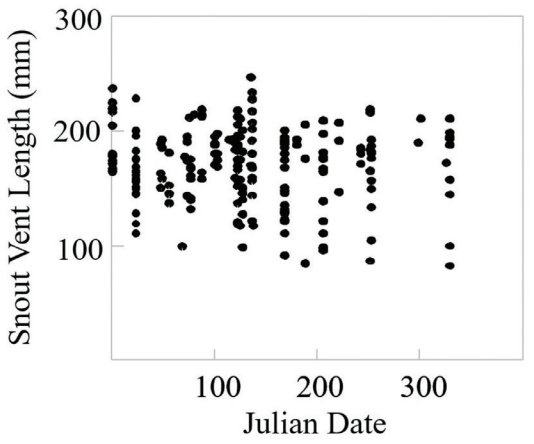

Figure 4. Snout-vent length (mm) of *Amphiuma pholeter* (One-toed Amphiuma; n = 206) in relation to Julian date when captured for 206 Florida, USA, specimens from the Liberty and Gadsden county sites.

Morphology.—*Amphiuma pholeter* collected during this study ranged in total length from 89 to 314 mm and in weight from five to 20 g (Table 1). We found no evidence of sexual size dimorphism; female and male *A. pholeter* were similar in body size and other morphological measurements (Table 1). We also found no significant difference in total length (t = -1.05, df = 190, P = 0.293) or weight (t = -1.175, df = 189, P = 0.241) between males and females. The smallest mature male was 125 mm TL and the smallest mature female was 122 mm TL. We collected *A. pholeter* of both sexes and all size classes throughout the year with no apparent seasonal pattern (Fig. 4). Hatchling size for *A. pholeter* is not known, but we collected the smallest sized individuals (< 10 cm) in this study throughout the year.

The dorsal coloration of *A. pholeter* ranged from uniformly dark reddish-brown to very faint purplish-brown. It was slightly different from the body coloration of *A. means* and *A. tridactylum*, which was dark brown dorsally, but lighter ventrally. Pigmentation was usually the same dorsally and ventrally in *A. pholeter* but occasional individuals had slightly lighter colored venters than their dorsa. In *A. pholeter* in the laboratory, we observed slight pigment intensity changes from day to night or after transfer from a dark container to a brightly lit one. We discovered two small albino *A. pholeter* from a population in southern Walton County, Florida, in 1972 next to a normally pigmented third individual of the same size (Fig. 5). On numerous occasions we observed individuals kept in plastic collecting bags secreting a colorless, white foam from secretory glands everywhere in the skin, visible in the albinos as yellow dots (Fig. 5). The secretion was not especially sticky or glutinous but was slightly bitter on

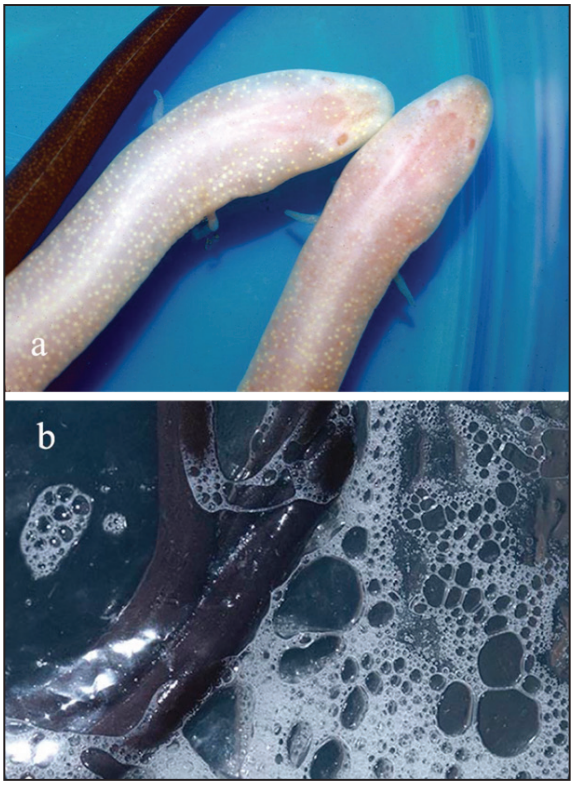

Figure 5. (a) Albino juveniles *Amphiuma pholeter* (One-toed Ampiuma) with normally pigmented individual collected together in Walton County, Florida, USA; note yellow skin glands. (b) Bitter and foamy skin secretion from an *A. pholeter* in a plastic collecting bag. (Photographed by D. Bruce Means).

Table 1. Means ± one standard deviation (Minimum-Maximum) of *Amphiuma pholeter* (One-toed Amphiuma) from study sites in Liberty and Gadsden counties, Florida, USA. Sample sizes for females and males was 115 and was 14 for salamanders of unknown sex for all measurements except weight: females (n = 8), males (n = 21), and unknown (n = 3). The abbreviation SVL = Snout-Vent-Length.

Measurement	Female	Male	Unknown
SVL (mm)	171 ± 33 (95–234)	175 ± 28 (98–247)	127 ± 41 (82–196)
Tail length (mm)	48 ± 10 (27–66)	50 ± 8 (27–67)	33 ± 14 (5–56)
Total length (mm)	219 ± 42 (122–299)	225 ± 35 (125–314)	160 ± 5 4 (89–252)
Weight (g)	14 ± 4 (8–20)	13 ± 4 (7–18)	7 ± 1 (5–8)
Snout-arm (mm)	16 ± 3 (10–23)	16 ± 2 (9–24)	12 ± 3 (9–18)
Snout-gill (mm)	14 ± 2 (9–19)	14 ± 2 (8–20)	11 ± 3 (7–15)
Legs-anus (mm)	6 ± 1 (3–8)	6 ± 1 (3–9)	5 ± 1 (3–7)

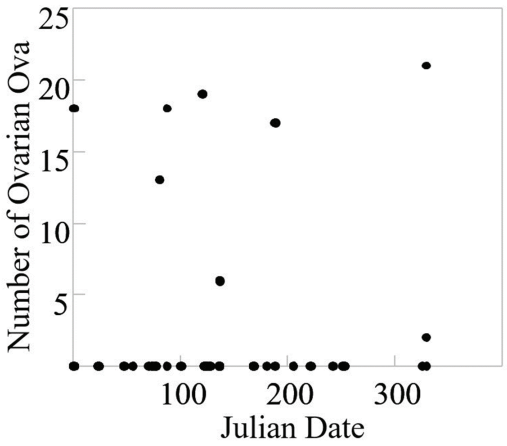

Figure 6. Number of ovarian eggs of eight female *Amphiuma pholeter* (One-toed Amphiuma) in relation to Julian date when captured.

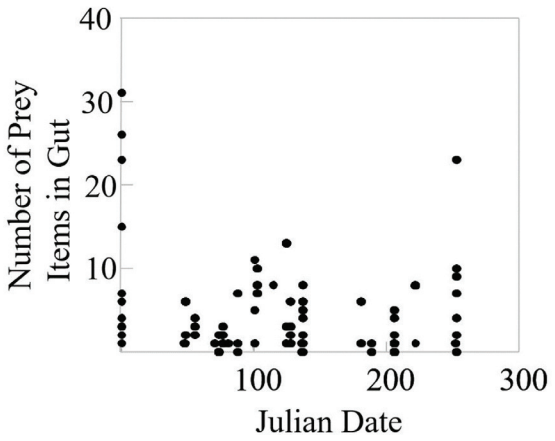

Figure 7. Number of diet items in gut of *Amphiuma pholeter* (One-toed Amphiuma) in relation to Julian date at time of capture.

the tongue when tasted.

Reproduction.—Eight of 77 female *A. pholeter* that we dissected contained developing ovarian eggs (Table 2). We found no apparent seasonality of females containing enlarged ovarian eggs (Fig. 6). The size of eggs at oviposition is not known, but the three females with the largest ovarian eggs (4–5 mm diameter) were collected in March, April, and July. In at least three cases, we observed large ovarian eggs through the abdominal body wall of living females. We kept two females that appeared to be gravid in captivity. After 120 d neither oviposited and appeared to have resorbed their ova. We did not find any eggs or larvae. Ovarian clutch size ranged from 2–21 eggs (Table 2) and there was no significant relationship between number of ova and ovum diameter ($F_{1,6} = 0.577$, $P = 0.476$) and also no relationship between female SVL and number of ova ($F_{1,6} = 0.356$, $P = 0.573$).

Habitat associates.—We occasionally found juvenile *A. means* of the same size or up to about twice as big as *A. pholeter* in the same muck beds with *A. pholeter* (nine of 101 site visits). Other vertebrates raked from the same muck beds on 101 site visits were adult and juvenile *Desmognathus auriculatus* (Southern Dusky Salamander; 31 times), larval *Eurycea cirrigera* (Southern Two-lined Salamander; 31), larval *E. guttolineata* (Three-lined Salamander; 19), larval and adult *Pseudotriton montanus* (Mud Salamander; 12), and *Siren* cf. *intermedia* (Lesser Siren: 10). The 31 occurrences of *D. auriculatus* with *A. pholeter* were recorded in the first 36 visits (86%) to *A. pholeter* sites from 1968 to 1973, making *D. auriculatus*, by far, the commonest muck habitat associate. The co-occurrences ceased abruptly in 1973, however, as *D. auriculatus* became extirpated from most of its geographic range (Dodd 1998; Means and Travis 2007; Graham et al. 2010; Maerz et al. 2015). In 70 visits we made to the remaining 45 known *A. pholeter* sites from 1974 to 2020, not a single *D. auriculatus* was found. We raked the following potential predators from the muck on 101 site visits: four Plain-bellied Water Snake (*Nerodia erythrogaster*), one Mud Snake (*Farancia abacura*), one Crayfish Snake (*Liodytes rigida*), three Eastern Mud Turtles (*Kinosternon subrubrum*), and two Common Snapping Turtles (*Chelydra serpentina*). We observed extensive damage to muck beds by feral pig rooting during seasonal drought five times at the Liberty County study site.

Diet.—In 96 *A. pholeter*, the gut contents were: 106 sphaeriid clams, 79 culicid mosquito larvae, 42 asellid isopods, 23 mayfly larvae (*Hexagenia* sp.), 43 adult and larval aquatic beetles (esp. *Cymbiodyta vindicata*), 15 subaquatic earthworms of the genera *Sparganophilus* and *Diplocardia*, 13 tipulid fly larvae, 11 gammarid amphipods, and a few other aquatic larval arthropods. Apparently, *Amphiuma pholeter* feed throughout the year because no relationship between the number of prey items in the gut and Julian day was evident (Fig.

Table 2. Julian date of unclear season of oviposition based on snout-vent length (mm), weight (mm), number of ova, and mean ovum diameter (MOD, mm) of eight female *Amphiuma pholeter* (One-toed Amphiuma) from counties in Florida, USA.

Locality	Julian Date	SVL (mm)	Weight (g)	# Ova	MOD (mm)
Gadsden E	1	219	13	18	2.8
Gadsden C	81	214	15	13	2.6
Gadsden D	88	213	13	18	4.5
Gadsden C	121	19	20	19	4.1
Gadsden E	138	211	12	6	1.4
Liberty A	189	206	15	17	5.0
Liberty A	330	211	16	21	2.0
Liberty A	330	195	14	2	3.4

7). A few *A. pholeter* guts contained minimal amounts of plant material. Annelids and ephemeropterans were consumed by all size classes. Frequency of amphipods, isopods, and dipteran larvae was highest in intermediate size *A. pholeter*. Sphaeriid clams were consumed with highest proportion by large *A. pholeter*. Male *A. pholeter* consumed more coleopterans, isopods, and sphaeriid clams than females. The digested soft tissues of earthworms (e.g. Sparganophilidae) were difficult to find in gut contents, but some were noted. In captivity, species of *Sparganophilus* were readily accepted. Parasites discovered in alimentary canals examined during the food study were predominantly nematodes, but we also found trematodes, cestodes, and acanthocephalans.

Discussion

We observed *Amphiuma pholeter* to be active year-round in the muck bed habitats we surveyed. Because these localities were swampy, mucky wetlands whose commercially valuable timber had been logged decades before our sampling, none of the sites were impacted mechanically during our survey period. We cannot deny, however, that water pollution from nearby agriculture and silviculture, nor from mosquito control or other aerial spraying, might have had an effect on water quality. Sampling of aquatic habitats by seine, dipnet, and large-mesh screen traps used for large *Siren* and other species of *Amphiuma* has not yielded *A. pholeter* specimens in museum collections as far as we have been able to ascertain from our experience, from communications with other biologists who have collected *A. pholeter*, and from accompanying field notes of museum specimens.

We found no indication of seasonal variation in reproductive activity (as indicated by maturity of ovarian eggs) or feeding behavior (as indicated by number of prey items in gut). We did not monitor the temperature of freshly captured *A. pholeter* nor the muck in which they were found, but the seepage provenience of muck may buffer extremes of seasonal air temperature fluctuations because the groundwater from which seepage issues year-round is the mean annual air temperature of the site (Darton 1920). When wet, muck habitats of *A. pholeter*, therefore, may be warm enough to permit activity and feeding at any season. The activity patterns of *A. pholeter* likely vary more based on water level in their habitat, with aestivation in burrows likely during dry conditions. No larval individuals or eggs were found during this study, so many aspects of the reproductive behavior of this species remain unknown.

Because of the difficulty of equitably censusing all the different types of wetland microhabitats in which *A. pholeter* might be found, we caution that our knowledge may be biased by the limitations of where humans are most easily able to search. It must be acknowledged, however, that humist and fibrist soils are more difficult to search, and adjacent clumps of rooted peat are usually not searched. If saprist soils (mucks) are truly preferred by *A. pholeter*, it probably has a lot to do with fibrist soils being composed of relatively undecomposed plant materials (leaves and woody litter) in which it would be difficult to locomote quickly and avoid predation. Also, invertebrate prey might be more abundant or more easily captured in the more fluid mucks.

We note here that all of the saprist muck beds in which we found most *A. pholeter* were heavily pimpled with the castings of species of the native subaquatic American earthworm family Sparganophilidae. These threadlike earthworms may be very important in converting humist and fibrist soils into saprist soils, and they may also be an important food source for the salamander. Seepage from large and small surficial aquifers is critically important in the ecological maintenance of *A. pholeter* sites. Steepheads form clear water streams by the spring sapping of surficial aquifers (Sellards and Gunter 1918) in deep sands and these streams rarely, if ever, dry out (Wolfe et al. 1988; Means 1975, 2000). Muck in the beds of small hillside seepage slopes was also the condition of the Alabama and Mississippi locations (Carey 1984, 1985; Floyd et al. 1998; Graham 2008; Brown and Lamb 2016). Saprist mucks readily dry out if dewatered and decompose. Their longevity, and suitable habitat for *A. pholeter*, depends on the perennial moisture provided by seepage.

Muck beds that depend on rainfall rather than seepage are common in the Lower Coastal Plain along the Big Bend of the upper peninsula of Florida, but they are subject to drying. *Amphiuma pholeter* are rarely captured from these habitats because their muck soils are usually fibrist, humic, and invaded by living roots of cypress and swamp hardwoods making the sites difficult to collect. Nevertheless, records for *A. pholeter* exist along the Florida Big Bend coast from movements observed during hurricanes (Neill 1954), drift fence operations (Enge and Wood 1998; 2000), and regular fieldwork (Paul Moler, pers. comm.). Likewise, a few individuals caught during drift fence operations at two sites in the Florida panhandle were hypothesized to be the result of flooding caused by Hurricane Georges (Enge 2002). Guy H. Means (pers. comm.), however, collected an adult *A. pholeter* while SCUBA diving in the spring-fed Wacissa River in open water (2 m deep), approximately 2 m from any organic material on the riverbank. The influence of water level on detectability of *A. pholeter* was not directly measured in this research, but it is likely that *A. pholeter* are easiest to collect when water levels are not too high (the muck becomes too liquid) or too low (the muck dries out and *A. pholeter* may

aestivate in burrows like other amphiumas).

Our gut contents data indicate that *Amphiuma pholeter* is a strict carnivore that feeds exclusively on invertebrates of its muck habitats. We found no vertebrates in its diet although juvenile and larval salamanders of its habitat associates listed above were available. Likewise, absent were small fish that we did not identify but did observe in flowing water on top of muck beds or adjacent to them. Among these were guppies (probably Mosquito Fish, *Gambusia affinis*), eastern shiners in the genus *Notropis*, and darters in the family Percidae. The small amount of vegetation we found in the gut contents samples probably was accidentally ingested detritus.

The aquatic snake and turtle associates we found while raking muck likely represent only a small number of predators of *Amphiuma pholeter*. That we occasionally found small juvenile *A. means* in *A. pholeter* muck sites indicates it is likely that adult *A. means* move through saprist mucks, possibly to find incubating sites for their own egg clutches, and therefore may prey upon *A. pholeter*. Many other vertebrate predators, such as Raccoons (*Procyon lotor*) and wading birds, probably prey on *A. pholeter*, but feral Pigs (*Sus scrofa*) may be the worst (Wood and Roark 1980).

Amphiuma pholeter differs markedly from its more-distantly related relatives *A. means* and *A. tridactylum* in terms of morphology, diet, and habitat preference. Surveys for this species must take this into account. *Amphiuma pholeter* is unlikely to be caught in the large mesh, open-water traps used for the other species of amphiuma. Window-screen wire funnel traps set along drift fences in shallow, first-order creeks and seepage bogs have been successful (Enge 1998, 2002, 2005; Enge and Wood 1998, 2000), however, and are probably the best way to survey for this species where saprist soils are uncommon or experience frequent drying.

Amphiuma pholeter is considered a rare species (Florida Natural Areas Inventory [FNAI]. 2019. FNAI–Element Tracking Summary. 2019–04–19. Available from https://www.fnai.org/trackinglist.cfm. [Accessed 27 April 2020]) and is listed on the International Union for Conservation Biology (IUCN) Red List as Near Threatened (IUCN 2020) in part because its geographic range is limited, and within that range it is mostly found in muck habitats. Because of this habitat specificity, threats to *A. pholeter* populations occur through alteration and degradation of their aquatic habitats by drainage, impoundment, runoff of agricultural pollution, sedimentation, and land development.

Acknowledgments.—All procedures were approved under Florida State University Animal Care and Use Committee protocols 1015 and 1624 and collecting permissions were obtained from landowners. Permits from states were not needed in Florida for the work we did, and was not needed in Georgia in the 1970s and 1980s. We thank Guy H. Means and Ryan C. Means for invaluable assistance in the field. Dale Jackson (Florida Natural Areas Inventory), Paul Moler, Kevin Enge, Kristen Wood (Florida Fish and Wildlife Conservation Commission), and Kenneth L. Krysko (Florida Museum of Natural History) provided locality data. We thank Song Chow, Chris Black, John Epler, and William Heard for assistance with dissections and identification of gut contents. We thank Chace R. Holzheuser for preparing the distribution map. This study was supported by Tall Timbers Research Station and Coastal Plains Institute and Land Conservancy.

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