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ORIGINAL PAPER

Geographic trend in sexual size dimorphism and body size of *Osteopilus septentrionalis* (Cuban treefrog): implications for invasion of the southeastern United States

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Abstract We collected *Osteopilus septentrionalis* from Central Florida for analysis of sexual size dimorphism and compared our data to published information from populations across the native and introduced range of the species. We found significant sexual size dimorphism (females larger), with the degree of dimorphism decreasing with increasing degrees north latitude, a trend largely driven by a pronounced decrease in female mean snout to vent length. Potential explanations for this trend include reduced growth rates, increased time to maturity, and reduced life expectancy, all of which may be tied to climatic variation. A trend of decreasing female mean size toward the northernmost extent of the current introduced range of this species may be indicative of diminished impacts and invasive success. Geographical variation in morphology and its associated implications should be evaluated when considering the potential impacts of invasive species.

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Introduction

Osteopilus septentrionalis (Cuban treefrog), native to Cuba, the Cayman Islands, and the Bahamas, has been introduced and become established in several sub-tropical and tropical locations (Duellman 2001; Lindsay and Cooper 2008; Meshaka 2001; Owen et al. 2005), including Florida (Barbour 1931). The range of *O. septentrionalis* in Florida (Fig. 1) is currently expanding, likely through human-mediated dispersal in ornamental plants, vehicles, boats, and cargo (Meshaka 1996a, 2001; Meshaka et al. 2004). Established breeding populations are now found throughout most of peninsular Florida (Johnson et al. 2003; Krysko et al. 2005) and localized introductions have been reported in the panhandle of Florida, coastal Georgia, South Carolina, Alabama, Texas, Maryland, Minnesota, and even Canada (Johnson 2004, Johnson unpubl. data).

Mounting evidence suggests that this frog negatively impacts native anurans (Meshaka 2001; Owen et al. 2005; Townsend 2000). Although once believed restricted to urban areas and unlikely to colonize natural areas (Butterfield et al. 1997), populations of *O. septentrionalis* have now been documented in a variety of natural habitats (both mesic and xeric) in

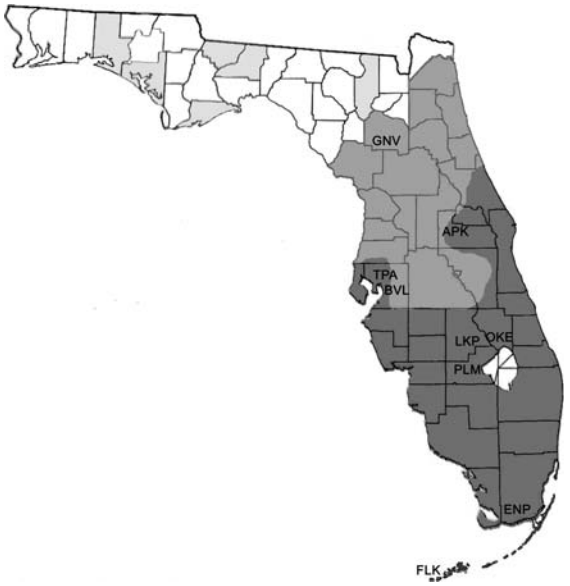

Fig. 1 Current known Florida distribution and recent range expansion of *Osteopilus septentrionalis*. Black indicates range reported by Meshaka in 2001, dark gray approximates current range, and light gray indicates areas where *O. septentrionalis* has been found but is not yet *reported* breeding. Some areas shown in white may represent lack of documentation, rather than absence of frogs. Florida field site locations are indicated by three-letter abbreviations corresponding to Table 2. (*Sources*: FWC; FLMNH herpetological specimen collection database; Johnson 2004; Johnson, unpubl. data; Johnston 2004; Krysko and King 1999; Krysko et al. 2005; Meshaka 1996a; Meshaka 2001; Townsend et al. 2002; Welker 2004)

Southern and Central Florida (Bartareau 2004; Johnson unpubl. data; Meshaka 2001; Meshaka et al. 2004; Wyatt and Forys 2004). In areas of Florida where *O. septentrionalis* is present in large numbers, native treefrog abundance and survival can be greatly reduced (Meshaka 2001; Rice et al. 2003). These large treefrogs prey on native anurans in urban and natural areas (Heflick 2001; Johnson unpubl. data; Meshaka 1996b; Meshaka 2001; Wyatt and Forys 2004), and their tadpoles have been experimentally shown to be superior competitors to tadpoles of some native anuran species (Smith 2005a, b). Reproductive interference by *O. septentrionalis* on other anurans has also been documented, although effects of such behavior may be minimal (Meshaka 1996c; Smith 2004).

Sexual size dimorphism (SSD) in *O. septentrionalis* is female-dominated (Meshaka 2001; Vargas-Salinas 2006a, b), a pattern seen in most anuran species that is related to sexual selection, breeding behavior, or sexual differences in growth, maturation, and population age structure (Howard 1981; Monnet and Cherry 2002; Shine 1979). In *O. septentrionalis*, female fecundity increases with increasing body size, but breeding is random (Vargas-Salinas 2006a, b) and sexual selection is not implicated as a cause of SSD (Vargas-Salinas 2006a, b). The explosive breeding behavior of *O. septentrionalis* likely favors small, agile males (Woolbright 1983), and males do not engage in territorial or competitive behaviors (Vargas-Salinas 2006a, b) that would favor large male size (Shine 1989). Growth estimates from capture data suggest that female *O. septentrionalis* may grow faster and mature later than males (Meshaka 2001), and that there are differences in age–sex structure among *O. septentrionalis* populations (Meshaka 2001). However, data from mark-recapture studies are needed in order to evaluate the role of growth, maturation, and age–sex structure in SSD of *O. septentrionalis*.

Previous information on SSD for *O. septentrionalis* in the introduced Florida range of this species has been limited to individuals from South Florida, with the exception of 128 specimens collected at three suburban sites in Central Florida (Meshaka 2001). However, as the range of *O. septentrionalis* continues to expand, collection of life history data near the forefront of range expansion is crucial in order to develop an understanding of the invasion ecology of this species. Here, we report on SSD in *O. septentrionalis* from natural and urbanized areas in Central and North-Central Florida, compare these data with previously published data from both native and introduced populations (Meshaka 2001; Owen 2005; Vargas-Salinas 2006a, b), and highlight a geographic trend in SSD with implications for invasion of the southeastern United States.

Materials and methods

Field collection

We collected *O. septentrionalis* ($n = 312$) from a variety of natural and disturbed habitats in Hillsborough, Polk, and Orange Counties in Central Florida (Table 1) using ground-based PVC pipe refuges (Boughton et al. 2000; Zacharow et al. 2003) to attract and capture frogs. We collected frogs from winter 2004 to fall 2005 at Wekiwa Springs State Park (WSSP, Apopka, Orange County),

Table 1 Field collected *Osteopilus septentrionalis* from Central Florida: site locality, habitat types, and number collected. All frogs were captured by deploying and monitoring ground-based PVC pipe refuges

Site (City, Co.)	Habitat type(s)	No. of frogs
Apopka, Orange	Mesic and scrubby flatwoods[a], sandhill[a], hydric hammock[a], upland mixed forest[a], wetland swamp[a]	158
Lakeland, Polk	Borrow area/shopping center[b]	3
Lakeland, Polk	Residential—med. density fixed single family dwellings[b]	2
Bealsville, Hillsborough	Bottomland forest[a], borrow area/residential—low density fixed single family dwellings[b]	120
Thonotosassa, Hillsborough	Potted plant/tree nursery[b]	9
Tampa, Hillsborough	Mesic flatwoods[a]	20

[a] Natural habitat types according to the classification proposed by the Florida Natural Areas Inventory (http://www.fnai.org/naturalcommguide.cfm)

[b] Disturbed habitat types according to the Florida Land Use, Cover and Forms Classification System—Florida Department of Transportation (http://www.dot.state.fl.us/surveyingandmapping/fluccmanual.pdf)

and from fall 2006 to summer 2007 at all sites (including WSSP). We transported frogs in a cooler to laboratory facilities and euthanized them by applying 20% benzocaine gel to the venter; we then transferred frogs to a −20°F freezer for at least 24 h. We later fixed specimens in 10% buffered formalin and transferred them to 70% EtOH for storage.

Museum specimens

In order to include populations at the northernmost extent of the current range of *O. septentrionalis*, we also collected data from specimens ($n = 73$) opportunistically collected and preserved in the herpetological collections of the Florida Museum of Natural History (FLMNH). These specimens were obtained at various locations in Gainesville (Alachua County), and represent one of the largest known breeding populations of *O. septentrionalis* in North-Central Florida.

Morphometrics and sex determination

We measured snout to vent length (SVL) of all *O. septentrionalis* specimens to the nearest 1.0 mm. Frogs were visually inspected for the presence of nuptial pads or externally visible eggs. We then dissected frogs by making a ‘T’ shaped incision on the ventral surface of each animal and determined sex by inspection of gonads under a dissecting microscope; we used Duellman and Trueb (1986) as a reference. We recorded measurements and sex of 385 individuals in order to evaluate SSD of *O. septentrionalis* in Central Florida. We measured frogs collected at WSSP for diet analysis ($n = 149$; Johnson unpubl. data) and FLMNH specimens ($n = 73$) after preservation; we measured all other frogs prior to preservation.

Analysis of SSD in Central Florida

We evaluated SSD of *O. septentrionalis* in Central Florida ($n = 385$) using specimens collected at our field sites and museum specimens. SVL data were not normally distributed (a strong negative skew was observed), and transformations failed to normalize data. We therefore used a non-parametric Mann–Whitney *U* test to analyze differences in body size (SVL) between sexes. We determined statistical significance at the level of $\alpha = 0.05$.

Analysis of geographic trends in SSD

We used scatter plots to qualitatively examine relationships between our data and published SSD data. Sample sizes at several of our sites were low, therefore we only included data from two of our field sites (WSSP/Apopka and Bealsville; $n = 269$) and from FLMNH specimens (Gainesville; $n = 73$). In order to ensure measurement consistency, we limited data from the WSSP/Apopka site to frogs preserved prior to measurement. We also included in our analyses published SSD data reported by Meshaka (2001; $n = 3{,}197$) from Central (1 site) and South Florida (5 sites) and the Caribbean (native range, 3 sites), by Vargas-Salinas (2006b; $n = 607$) from

Puerto Rico (1 site), and by Owen (2005; $n = 428$) from the British Virgin Islands (several sites). We rounded these published SVL values to the nearest 0.1 mm. Site-specific SSD data for *O. septentrionalis* collected at our field sites, along with published SSD data across the range of the species (Meshaka 2001; Vargas-Salinas 2006b), are shown in Table 2.

We used correlation analyses to evaluate the potential significance of trends by testing the relationship between female to male SVL ratio and mean female and male SVL and approximate degrees north latitude, expressed in decimal degree notation rounded to the nearest 0.1°. Where latitude was unknown, we closely approximated latitude using Google^{TM} Earth. All sites were located between approximately 65° to 85° west longitude (data were not available for introduced Hawaii populations), and a relationship with longitude was not found. Due to a lack of data from sites located between approximately 19° to 23° north latitude (e.g., central and southern Cuba, southern Bahamas), we were unable to determine the nature of the relationship between SSD and latitude (linear vs. curvilinear); hence, we report Spearman's correlation coefficients (nonparametric, linearity not assumed). We determined statistical significance at the level of $\alpha = 0.05$.

As a sampling 'control', we also separately analyzed SSD data reported by Meshaka (2001) from nine sites in Central and South Florida and the Caribbean. Meshaka (2001) captured frogs using a systematic visual search/hand capture technique, whereas data from other sites were collected using a variety of techniques (i.e., PVC pipe refuges, dip-netting, opportunistic hand capture). Thus, we excluded these data to control for potential variation due to differences in sampling techniques between researchers. Correcting for sampling biases provides a degree of confidence that observed differences in SSD across latitudes represent a biological phenomenon and are not simply an artifact of differences in collection methods between studies.

Results

SSD in Central Florida

Osteopilus septentrionalis in Central Florida have significant SSD ($U = 9246.5$, $P << 0.05$, $n = 385$), with females as the larger sex. Female mean SVL was 53.1 mm, and ranged from 25 to 79 mm ($n = 225$). Developing eggs were first observed in a female of 53 mm SVL. Male mean SVL was 43.1 mm, and ranged from 25 to 62 mm ($n = 160$). Nuptial pads, an external indication of sexual maturity, were first observed in a male of 26 mm SVL. Measurement data were not normally distributed (overall and sex-specific) and had a strong negative skew; there were few exceptionally large individuals of either sex.

Geographic trends in SSD

We observed a geographic trend in SSD of *O. septentrionalis*, with SSD becoming less pronounced toward the northern extent of the introduced range. Across the range of the species, SSD of *O. septentrionalis*, expressed as the ratio of female to male SVL, was significantly negatively correlated with degrees north latitude ($r_s = -0.679$, $P << 0.05$, Fig. 2a). Across all sites ($n = 14$) mean SVL also decreased significantly with increasing degrees north latitude (Fig. 2b) in females ($r_s = -0.858$, $P << 0.05$) and males ($r_s = -0.765$, $P << 0.05$). We observed similar trends in 'control' data from Meshaka's (2001) sites ($n = 9$) of decreasing female to male SVL ratio (Fig. 3a) and decreasing female and male mean SVL (Fig. 3b) with increasing degrees north latitude. However, this negative correlation was only significant for female mean SVL ($r_s = -0.700$, $P < 0.05$).

Discussion

Osteopilus septentrionalis in Central Florida has significant SSD, with females larger than males, consistent with published SSD data for populations in South Florida and the Caribbean. We identified a statistically significant trend of decreasing SSD and mean SVL of both sexes with increasing degrees north latitude across the Caribbean and Florida range of *O. septentrionalis*. Analysis of a subset of these data (from Meshaka 2001) to control for potential confounding effects of sampling differences between researchers revealed a similar trend, although the correlation was only statistically significant for mean female SVL. The lack of statistical significance of the geographical trend in SSD and male SVL in this

Table 2 Site-specific sexual size dimorphism of *Osteopilus septentrionalis*

	Latitude	Location	Male SVL	Female SVL	F:M	Source
Central FL	29.7°N	Gainesville (GNV)	45.8 ± 6.3; 26.0–58.0; 32	61.7 ± 11.0; 33.0–79.0; 41	1.3	FLMNH Specimens
	28.7°N	Apopka (APK)	39.1 ± 8.6; 25.0–54.0; 57	47.9 ± 13.5; 25.0–75.0; 92	1.2	Field Collection
	27.9°N	Bealsville (BVL)	47.1 ± 5.6; 35.0–62.0; 54	58.0 ± 6.9; 38.0–72.0; 66	1.3	Field Collection
	27.9°N	Tampa (TPA)	47.7 ± 5.2; 35.9–59.0; 41	63.3 ± 8.6; 45.0–86.0; 87	1.2	Meshaka 2001
South FL	27.3°N	Lake Placid (LKP)	47.9 ± 9.6; 34.4–85.0; 24	67.3 ± 12.5; 50.4–122.0; 36	1.4	Meshaka 2001
	27.2°N	Okeechobee (OKE)	46.6 ± 5.8; 34.4–58.8; 114	62.7 ± 9.3; 44.8–96.6; 180	1.3	Meshaka 2001
	26.9°N	Palmdale (PLM)	46.9 ± 5.1; 34.4–56.6; 51	57.3 ± 7.6; 45.0–81.0; 77	1.2	Meshaka 2001
	25.7°N	Everglades NP (ENP)	46.1 ± 5.1; 28.9–59.8; 814	64.2 – 10.6; 44.5–99.0; 987	1.4	Meshaka 2001
	24.6°N	Lower FL Keys (FLK)	52.9 ± 3.4; 47.0–58.8; 20	71.3 ± 5.1; 62.1–80.5; 33	1.5	Meshaka 2001
Caribbean	25.0°N	Bahamas (BI)	44.0 ± 6.3; 29.0–58.0; 102	65.8 ± 1.6; 44.6–83.8; 57	1.3	Meshaka 2001
	23.2°N	Cuba (CBA)	47.4 ± 7.8; 27.0–83.0; 180	71.8 ± 13.4; 44.1–122.0; 212	1.5	Meshaka 2001
	19.3°N	Cayman Is. (CI)	53.2 ± 7.0; 38.5–89.0; 64	75.6 ± 11.4; 47.1–119.0; 118	1.4	Meshaka 2001
	18.4°N	Puerto Rico (PR)	52.7 ± 4.5$^{a;}$ 41.5–67.0; 291	75.7 ± 7.8^{a}; 57–107; 316	1.4	Vargas-Salinas 2006b
	18.3°N	British Virgin Is. (BVI)	56.2 ± 6.1; 30.0–72.5; 214	77.3 ± 10.4; 41.3–99.1; 214	1.4	Owen 2005

SVL data rounded to the nearest 0.1 mm are given as mean followed by standard deviation (when known, ‘a’ indicates standard error), range, and sample size. Abbreviations in parentheses correspond to Figs. 2a, 3a

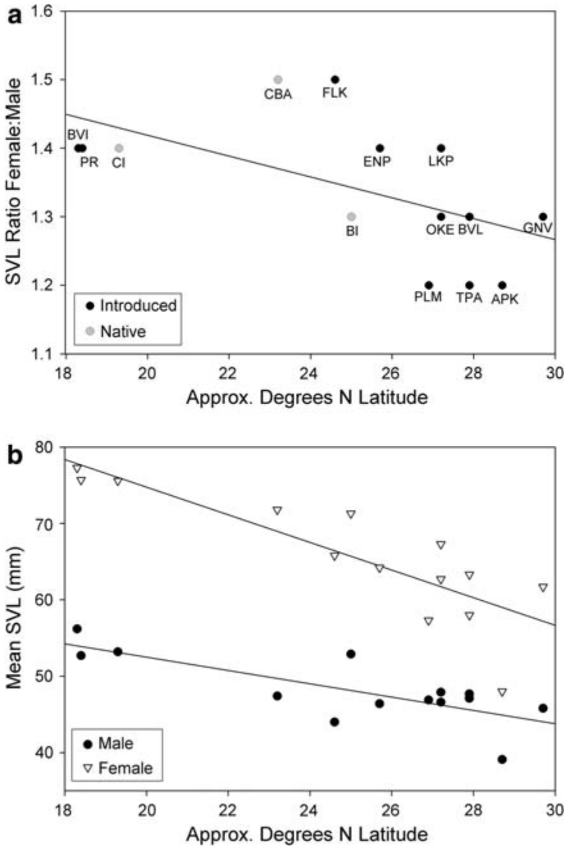

Fig. 2 Geographic trends in sexual size dimorphism of *Osteopilus septentrionalis* at sites across the native and introduced range—data from field collected specimens, Meshaka (2001), Owen (2005) and Vargas-Salinas (2006b). Abbreviations correspond to site abbreviations listed in Table 2. Female to male SVL ratio (**a**) and both mean male and female SVL (**b**) show significant negative correlation with degrees north latitude

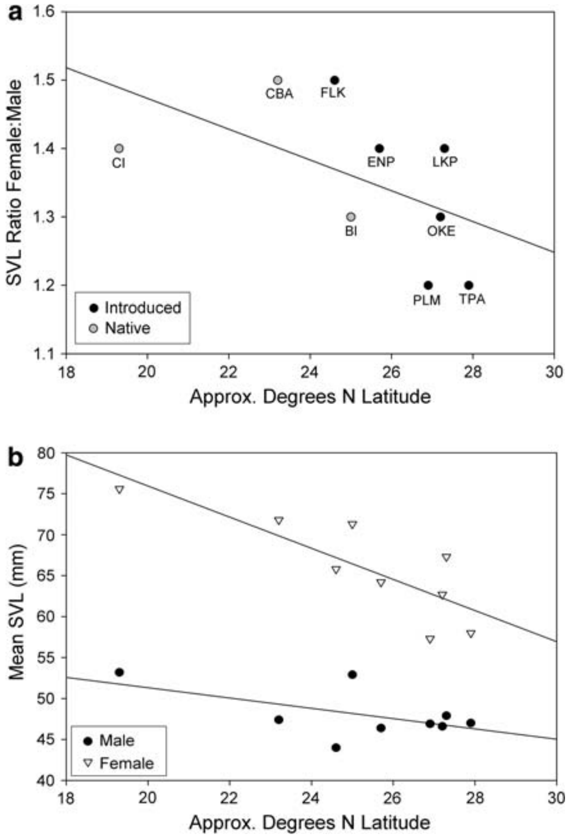

Fig. 3 Geographic trend in sexual size dimorphism of *Osteopilus septentrionalis* at 'control' sites across the native and introduced range—all data from Meshaka (2001). Abbreviations correspond to site abbreviations listed in Table 2. Female to male SVL ratio (**a**) and mean female SVL (**b**) decrease with increasing degrees north latitude, this correlation is significant only for mean female SVL

subset of data may be due to sampling differences between researchers, or may simply be an artifact of limiting the latitudinal range. Nonetheless, these results support our finding of a geographical trend in SSD and body size of *O. septentrionalis* and suggest that this trend is largely driven by a highly significant decrease in female mean size (SVL) with increasing degrees north latitude.

Geographical variation in body size trending toward an increase in size with increasing latitude (or elevation) is well known in endotherms, as described by Bergmann's Rule (also known as James's Rule). Some ectotherms follow this rule (including anurans, weakly) or the inverse, and the type and degree of concordance with this rule can vary within families (Ashton 2002). Geographical (latitudinal or altitudinal) variation in SSD and related life-history characteristics, such as fecundity, growth and development, and age at maturity has also been documented in anurans, although the nature of this variation is likely complex and highly variable (Ashton 2002; Morrison and Hero 2003; Rosso et al. 2004; Schäuble 2004). Schäuble (2004) found that, although latitude was a significant predictor of geographical variation in SSD of a pair of myobatrachid congeners with opposing patterns of dimorphism (*Limnodynastes tasmaniensis* – females larger, *Limnodynastes peronii* – males larger), climate was a more important predictor of variation for one species (*L. peronii*). Schäuble (2004) also found that, in both species, geographical variation in SSD is driven by variation in the mean body size of the larger sex. Ashton (2002) suggested that such geographic variation in anuran body size may be strongly tied to climatic variables, and Rosso et al. (2004) further suggested that geographic variation in body size of *Hyla intermedia* is the result of effects of climate on mortality of larvae and juveniles.

In the case of *O. septentrionalis*, decreasing female mean size in more northern climes may be the combined result of reductions in growth and life expectancy. Meshaka (2001) found that estimated post-metamorphic growth rate decreased from south to north, whereas estimated time to reach maturity and to reach mean size after maturation increased in both sexes, consistent with our finding of a geographical trend in body size and SSD of *O. septentrionalis*. In northern populations, lower temperatures result in shorter growing seasons, and shorter breeding seasons (Meshaka 2001) may result in shifts in energy allocation to breeding (rather than growth), particularly in females. This decrease in growth may be further compounded by a reduction in life expectancy. If SSD of *O. septentrionalis* is related to population age structure, as seen in *Rana catesbeiana* (Howard 1981), such a reduction in life expectancy would be expected to exert the greatest effects on mean size of the more long-lived, and thus larger, sex (i.e., females). Life expectancy may be reduced by an increase in the prevalence of cold-induced mortality as temperatures decrease along a south to north cline. Currently, the extent of *O. septentrionalis* establishment in Florida (Fig. 1) parallels frost occurrence zones (Chen and Gerber 1990; NOAA-NCDC 2005); uninvaded areas to the northwest experience lower extreme minimum temperatures and much higher incidence of frost (although the lack of established populations in these areas may be simply a function of time rather than climate). Life expectancy might also be reduced in northern populations as a result of depredation by an increasing diversity of snakes due to the peninsula effect (Means and Simberloff 1987). However, potential predators include not only snakes (Love 1995; Meshaka and Ferster 1995; Meshaka and Jansen 1997) but also birds, mammals, and alligators (Bartlett and Bartlett 1999; Meshaka 1996d). Certainly, investigation of the effects of such factors as climate and depredation on body size, SSD, and life expectancy of *O. septentrionalis* might provide valuable insights on the invasion ecology of this species.

This geographical trend of decreasing SSD driven by a pronounced decrease in female size toward the northernmost extent of the introduced range of *O. septentrionalis* undoubtedly has important implications for impacts of invasion of the southeastern United States. Most importantly, a decrease in mean female size toward the northernmost extent of the introduced range may be accompanied by a reduction in predation on native vertebrate fauna. Across its introduced range, *O. septentrionalis* is known to prey upon at least six families of native anurans and some small squamates (Campbell 2007; Heflick 2001; Johnson unpubl. data; Maskell et al. 2003; Meshaka 2001; Vargas-Salinas personal communication). Predation on native anurans by *O. septentrionalis* is predominantly attributed to the largest females; analyses of gut contents have found that anurans were consumed by up to 12.4% of females but only up to 3.5% of males (Heflick 2001; Meshaka 2001; Johnson unpubl. data). These studies suggest that native anurans feature prominently in the diet of large female *O. septentrionalis*. Thus, a decrease in female size in northern populations provides encouraging evidence for a possible reduction of the potentially deleterious impacts on native anurans toward the northern extent of the introduced range.

Smaller mean female size is also indicative of a decrease in mean female fecundity. Female *O. septentrionalis* are highly fecund, producing large clutches of eggs that increase in number with increasing female SVL (Meshaka 2001; Owen 2005; Vargas-Salinas 2006b). In contrast, mean clutch size of native hylids generally falls well below even the minimum clutch size of *O. septentrionalis* (Meshaka 2001). According to the regression of clutch size on SVL of Meshaka (2001), a reduction in mean female *O. septentrionalis* SVL of only 10 mm could reduce mean clutch size by more than 1,400 eggs. When compounded by shorter breeding seasons resulting from cooler temperatures (Meshaka 2001), a decrease in female size could significantly reduce fecundity of northern populations.

Such a decrease in fecundity might not only limit invasion success by reducing reproductive output, but also help to ameliorate competitive effects by reducing the density of *O. septentrionalis* tadpoles at breeding sites. Under laboratory conditions, the presence of *O. septentrionalis* larvae at equal densities with native tadpoles significantly reduced growth rates and delayed metamorphosis of two native species (*Hyla cinerea* and *Bufo terrestris*; Smith 2005). However, in the field, *O. septentrionalis* tadpoles are commonly found at much greater densities than native tadpoles (Guzy et al. 2006; McGarrity and Johnson, unpubl. data). In addition to perhaps reducing tadpole densities and thereby lessening competitive effects, a decrease in female fecundity also has the potential to constrain the invasive success of this species by reducing population size, growth, and ability to rapidly colonize new areas.

When evaluating the potential impacts of an invasive species in order to develop or prioritize management efforts, it is important to consider sources of variation in these impacts. For example, predictive models of habitat suitable for pythons (*Python molurus*) in the United States indicated that climate change over time could greatly increase the potential distribution (and thus potential impacts) of these invasive snakes (Rodda et al. 2008). Similarly, population matrix models used to guide efforts to control invasive bullfrog (*Rana catesbeiana*) populations have shown that demographics and life history vary among regions and sites, resulting in variation in impacts—inclusion of this variation is critical to maximizing the efficacy of control efforts (Adams and Pearl 2007; Govindarajulu et al. 2005). Evaluation of variability in the toxicity of an invasive toad (*Rhinella marina* [=*Bufo marinus*]) to native predators in Australia suggested the possibility of geographical and temporal (time since invasion) variation in impacts (Phillips and Shine 2006), information that may prove invaluable in guiding control efforts. Our results show a geographic trend of reduction in mean SVL of female *O. septentrionalis* with increasing latitude, and suggest that ecological impacts of invasion may lessen as the range of this invasive frog expands northward. A significant decrease in mean female size as the range of this invasive frog expands northward might reduce predation on native vertebrates, and an accompanying decrease in fecundity might help to ameliorate competitive effects of invasive tadpoles and even hinder the spread of this species, reducing its capacity to successfully colonize new areas. However, additional research on a variety of topics will be required in order to fully evaluate the implications of this geographical trend on the success of *O. septentrionalis* invasion of the southeastern United States.

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