Ecological Plasticity and the Future of the Argentine Giant Tegu (*Salvator merianae* Dumeril and Bibron, 1839) in the Southeastern US

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Abstract - *Salvator merianae* (Argentine Giant Tegu) is an invasive exotic species established in 2 as yet unconnected populations in central and southern Florida. Despite intense trapping, this mid-level carnivore remains well-established in a portion of extreme southern mainland Florida where it was first released 20 y ago. High fecundity, nest-guarding, rapid growth to large body size, and broad trophic width by which it negatively impacts wildlife contribute to its success as a colonizing species. Native to more temperate habitat, it experiences a defined winter and summer in South America unlike the wet–dry seasons of southern Florida. We conducted a qualitative comparison of key life-history traits from source areas to those of southern Florida that provided a measure of its ecological plasticity and formed the basis for expectations associated with northward expansion. Our examination of 1168 specimens collected during 2011–2017 revealed an overlap between the sexes in timing of fat storage prior to brumation and late-winter–early-spring peak in gonadal size. Females were ovigerous during March–May and possibly June, and clutch size averaged 28.6 eggs. Hatching was possible during May–August, and both sexes reached sexual maturity by 2 y of age. In this subtropical system, length of seasonal activity, gonadal cycles, and size and age at sexual maturity differed from those of source areas, indicative of the degree of plasticity among these traits over a short period of time. We found that the climate of the Southeast is amenable to the colonization of this vagile species. Our findings are suggestive that a return to the strongly selected seasonal activity and gonadal cycles of central Argentina will accompany the Argentine Giant Tegu in its northward dispersal into more temperate conditions even as it retains a somewhat relaxed cycle in southern Florida.

Introduction

The southeastern United States, exclusive of Florida, is home to 6 exotic species of amphibians and reptiles (Powell et al. 2016), nearly all of which were first reported from southern Florida, where most are statewide or nearly so in geographic distribution (Meshaka 2011). Among the larger-bodied members of the exotic Florida herpetofauna that prey on native vertebrate species, *Python bivittatus* Kuhl (Burmese Python), established in Florida since at least 2000 (Meshaka et al. 2000), is considered capable of dispersing northward into the Southeast (Rodda et al. 2008, but also see Pyron et al. 2008).

Salvator merianae (Dumeril and Bibron) (Argentine Giant Tegu) is the largest and geographically most widespread of the 4 exotic teiid lizards that are established

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in Florida (Meshaka 2011). Widely distributed in South America, where the southern terminus of its geographic range is central Argentina, the Argentine Giant Tegu is harvested for its hide and meat (Fitzgerald 1994, Norman 1987) and is commonly found in the US pet trade. As a result of the latter, 2 disjunct colonies have become well-established in Florida. One, in west-central Florida, has been in existence since the early 2000s (Enge 2007, Pernas et al. 2012). The epicenter of the second colony is in Florida City, Miami-Dade County, in extreme southern mainland Florida. This population has been in existence for almost 20 years. An active trapping program funded by the Florida Fish and Wildlife Commission (FFWC), the University of Florida, the National Park Service, US geological Survey, and colleagues in the Everglades Cooperative Invasive Species Management Area has removed more than 3300 Argentine Giant Tegus from the southern Florida site. These numbers do not include captures by private trappers.

Southern Florida tegus brumate entirely or intermittently for several months (McEachern et al. 2015), wander far when active (Klug et al. 2015), feed on a wide range of vertebrates that include eggs and adults of listed vertebrate species (Mazzotti et al. 2015), and can be highly fecund (Meshaka et al. 2018, Pernas et al 2012). The numbers of captures by FFWC et al. and increased distribution north and west towards Everglades National Park and east towards nests of *Crocodylus acutus* Cuvier (American Crocodile) at the Florida Power and Light Company Turkey Point Power Plant attest to its colonization success and highlight the increasing danger it poses to Florida biota. For the very reasons of its successful colonization abilities coupled with the negative impact on wildlife make imperative an understanding of its life-history traits in Florida relative to those of source areas with a more temperate climate. Quantifying plasticity in reproduction, seasonal activity, and growth would provide a better understanding of why the Argentine Giant Tegu is so successful in southern Florida and a way to evaluate the life-history response as the species disperses northward to regions of the southeastern United States with a more temperate climate, portions of which mirror the climate of its source areas.

Native populations of the Argentine Giant Tegu are subject to a distinct temperate climate, which enforces a highly seasonal gonadal cycle (Chamut et al. 2012, Manes et al. 2007, Noriega et al. 2002). Mating occurs soon after spring emergence, and a single large clutch is produced in early summer (Donadío and Gallardo 1984, Yanosky and Mercolli 1991). General activity is seasonally constrained, with brumation lasting up to 6 months (Donadío and Gallardo 1984). Although brumation in this species may be triggered by day length, more time for general and reproductive activity is afforded in southern Florida tegus where brumation is weakly enforced by climate. In light of its evolutionary history, colonization of portions of the Southeast are not unreasonable based upon similarities between the humid subtropical climate of that region and the species' native range, as per the Köppen climate classification and winter surface temperature isotherms (see images provided by the NOAA ESRL Physical Sciences Division, Boulder, CO, on their website at http://www.esrl.noaa.gov/psd/). To that end, outdoor captive breeding colonies were successful in northern Alabama (Langerwerf and Paris 1998).

Its presence in subtropical southern Florida in addition to its more temperate native habitat raise 2 questions examined in this study. First, has the Argentine Giant Tegu responded to the south Florida climate with changes in reproduction and growth as have many native amphibian and reptile species that dispersed southward from the North (Meshaka and Layne 2015)? Second, what could be expected in these life-history traits in northward dispersing tegus? To answer these questions, we examined gonadal conditions and body sizes of tegus trapped during 2011–2017 from a large and expanding southern Florida population. We qualitatively compared reproductive cycles, seasonal activity, and growth rate from southern Florida with data from source areas in South America. Differences therein quantify adaptive plasticity in these traits in southern Florida. Likewise, differences in southern Florida may reveal the extent to which aforementioned traits of northerly dispersing populations could be expected to shift as the species expands northward as predicted.

Materials and Methods

We collected Argentine Giant Tegus from a site in Florida City, Miami-Dade County, FL, located at SW 424th Street between US-1 and the C-111 and C-110 canals. Lizards were captured by hand, with Havahart raccoon traps, and using firearms. We received additional tegus from partnering agencies and individuals. Permits were granted and funding was provided by the Florida Fish and Wildlife Conservation Commission. Tegus were euthanized with a captive bolt gun, following American Veterinary Medical Association guidelines. IACUC protocol is UF IACUC No. 201708432. We performed necropsies of 1168 Argentine Giant Tegus collected from Miami-Dade County, FL, using a standardized method (Farris et al. 2013). We measured body mass using a Brecknell MS20 digital scale to the nearest g. We removed fat bodies, testes, and ovaries and weighed them with a VeriTas digital scale to the nearest 0.001 g. We measured testes length, vas deferens diameter at midpoint, oviduct diameter at midpoint, ovarian follicles, and corpora lutea using Mitutoyo Absolute P67 digital calipers to the nearest 0.01 mm. We measured snout–vent length (SVL) and total length (TL) using a flexible measuring tape. We determined sex by internal visual inspection of organs. For both sexes, we calculated gonadal:somatic index (GSI) by dividing the mass of the gonads by the mass of the entire body and estimated seasonal measures of fertility in males by the monthly distribution of left testis length and width at midpoint and vas deferens diameter divided by male SVL and multiplied by 100. We measured ovarian cycle by plotting the largest vitellogenic follicle of each female by month. Diameter of the left oviduct at midpoint was divided by female SVL and multiplied by 100 to provide a monthly distribution of their sizes associated with oviposition. We estimated clutch sizes using 3 methods: counts of (1) oviductal eggs, (2) enlarged ovarian follicles, and (3) corpora lutea. Evidence of multiple clutch production was ascertained by the presence of more than 1 set of luteal scars, simultaneous presence of shelled eggs and ovulatory follicles, or simultaneous presence of luteal scars and ovulatory follicles. Ovulatory follicles were similar in diameter to shelled

egg yolks. We generated sample statistics, 2-sample *t*-tests, and 1-way analyses of variance (ANOVA) that tested for monthly changes in gonadal size as a percentage of SVL using Excel 2016. Shapiro–Wilk normality test and Mann-Whitney rank sum test were calculated using SigmaPlot 11.0. We recognized significance as $P \leq 0.05$. Means presented are followed by 95% confidence intervals.

Results

Male fat and reproductive cycles

Fat cycle. Fat body mass, expressed as a percent of the total body mass of adult males varied significantly (ANOVA: $F = 24.981$, df = 8, $P < 0.001$) among months (Fig. 1). Active mate searching could explain the low fat mass in February and March. Fat mass was lowest during April–July and reached its peak mass in September, shortly before brumation (Fig. 1).

Gonadal cycle. GSI of adult males varied significantly (ANOVA: $F = 52.143$, df = 8, $P < 0.001$) among months (Fig. 2). The mean GSI was at its maximum in February and March, decreasing rapidly thereafter (Fig. 2) in association with mating. The monthly distribution of testis dimensions as a percent of male SVL varied significantly across months with respect to length (ANOVA: $F = 26.193$, df = 8, $P < 0.001$; Fig. 3a) and width (ANOVA: $F = 22.042$, df = 8, $P < 0.001$; Fig. 3b). Both measurements were largest during February–March. Testis size decreased thereafter, before recrudescence beginning in August (Fig. 3). The diameter of the vas deferens at
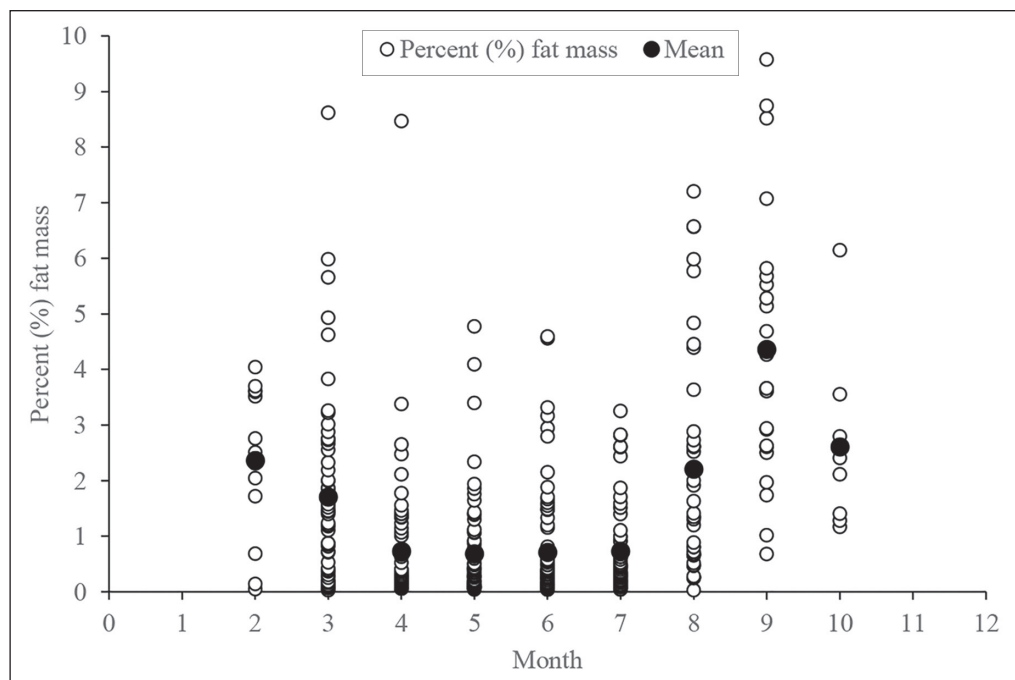

Figure 1. Monthly distribution of fat mass presented as a percent (%) of the total body mass of 416 male *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.

midpoint, expressed as a percent of the male's SVL, varied significantly across months (ANOVA: $F = 7.488$, df = 8, $P < 0.001$; Fig. 4). An accumulation of sperm was evident beginning in September, and mean diameter peaked in March. The largest diameters were found during March–May and there was an uptick in September (Fig. 4), suggestive of commencement of spermatogenesis in late summer followed by a pause until the following spring. Commensurate with drainage associated with mating, the vasa diameters decreased in size through August (Fig. 4).

Female fat and reproductive cycles

Fat cycle. Fat body mass, expressed as a percent of the total body mass of adult females varied significantly (ANOVA: $F = 15.963$, df = 7, $P < 0.001$) among months (Fig. 5). Mean fat mass was lowest during May–June. Subsequent increase in fat mass was evident during July–September and remained high through February after which time it decreased rapidly in association with clutch produci- ton (Fig. 5).

Gonadal cyle. The mean GSI was at its maximum in February; however, GSI values remained high through April (Fig. 6), after which time few gravid females were trapped. The diameter of the left oviduct at its midpoint, expressed as a percent of the female's SVL, varied significantly across months (ANOVA: $F = 10.819$, $df = 6$, $P < 0.001$; Fig. 7). The mean oviduct diameter decreased after March through the spring and then remained low throughout the rest of the year. Large oviduct diameters associated with oviposition were evident during March–June (Fig. 7).
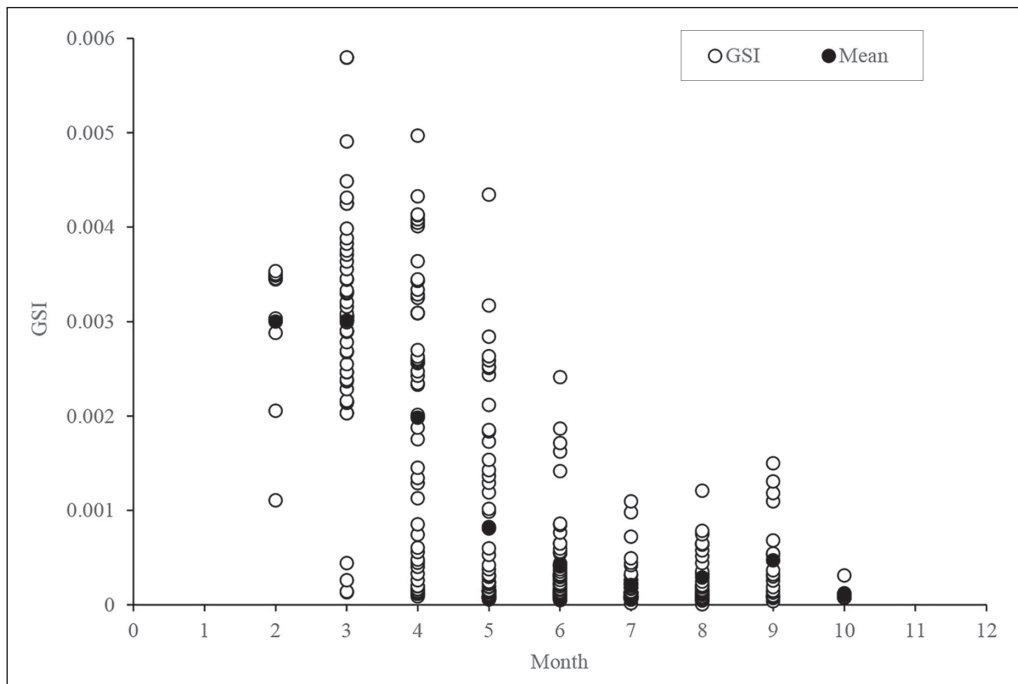

Figure 2. Monthly distribution of the Gonadal:Somatic Index (GSI) of 326 male *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.
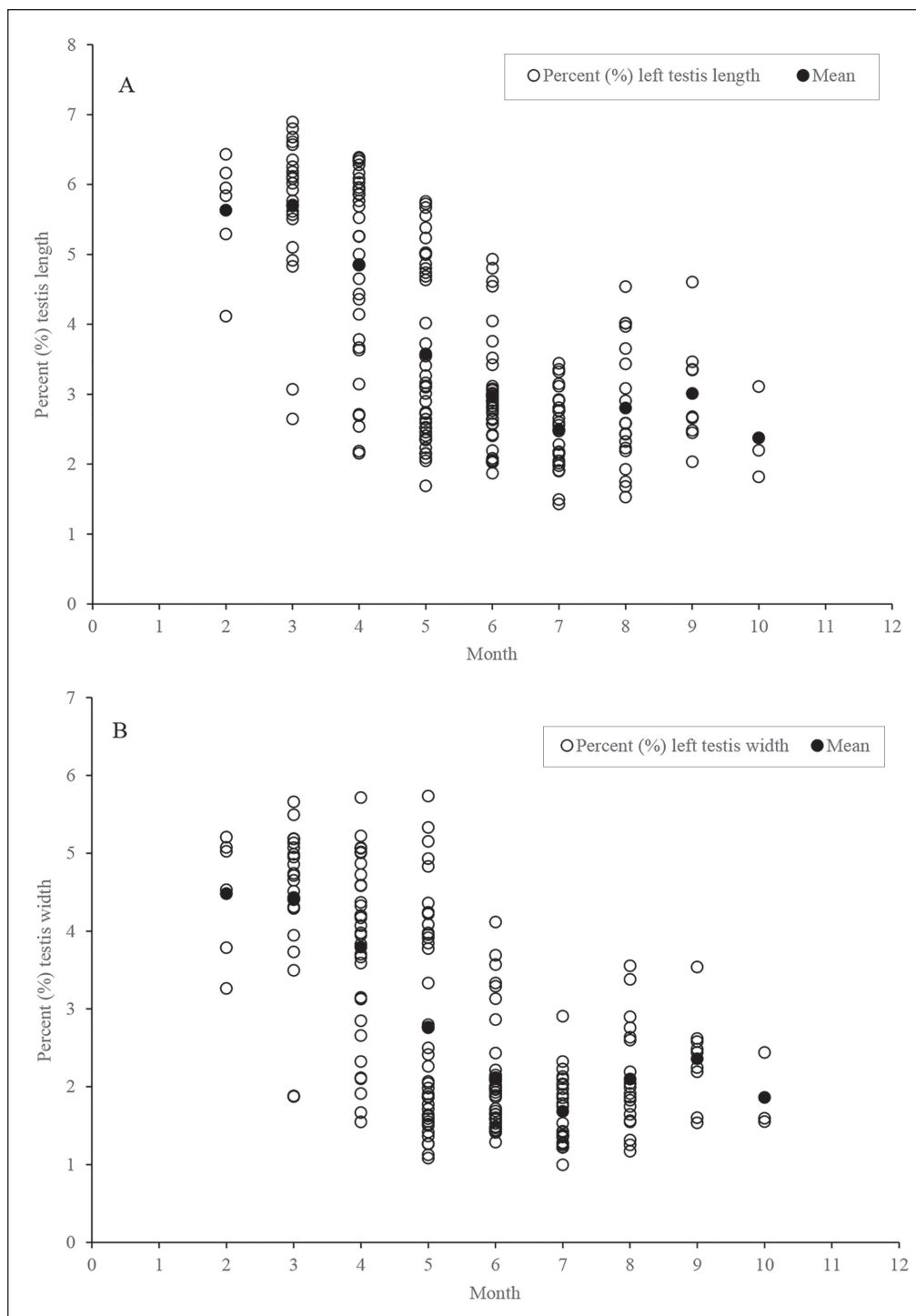
Figure 3. Monthly distribution of testis (A) length and (B) mid-width presented as a percent (%) of the snout–vent length (SVL) of 191 male *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.
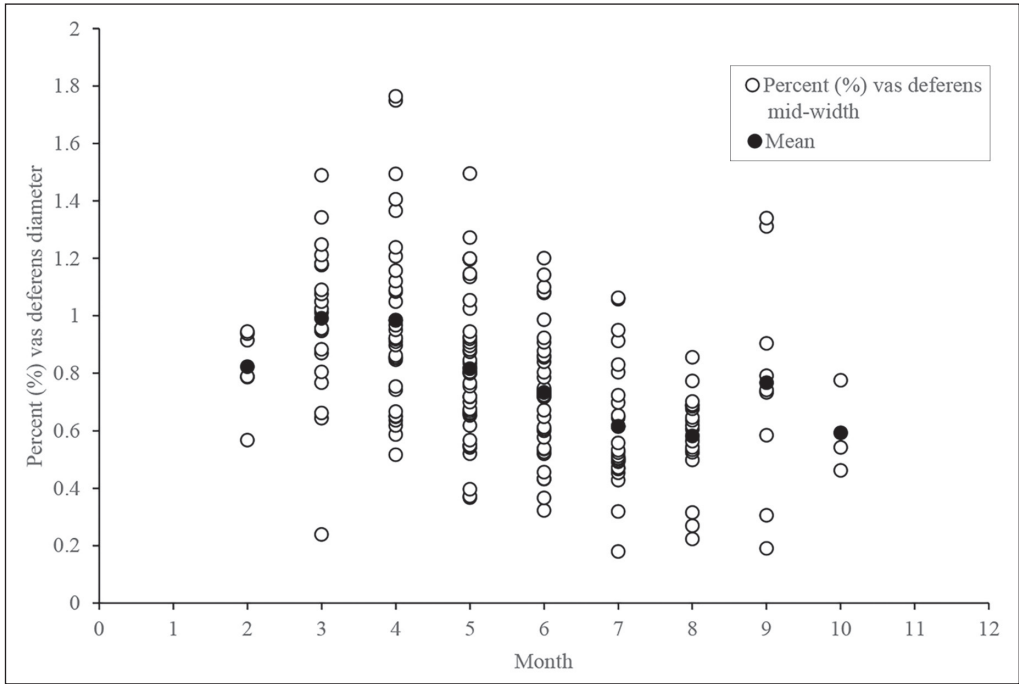
Figure 4. Monthly distribution of vas deferens diameter at center of length presented as a percent (%) of the snout–vent length (SVL) of 192 male *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.
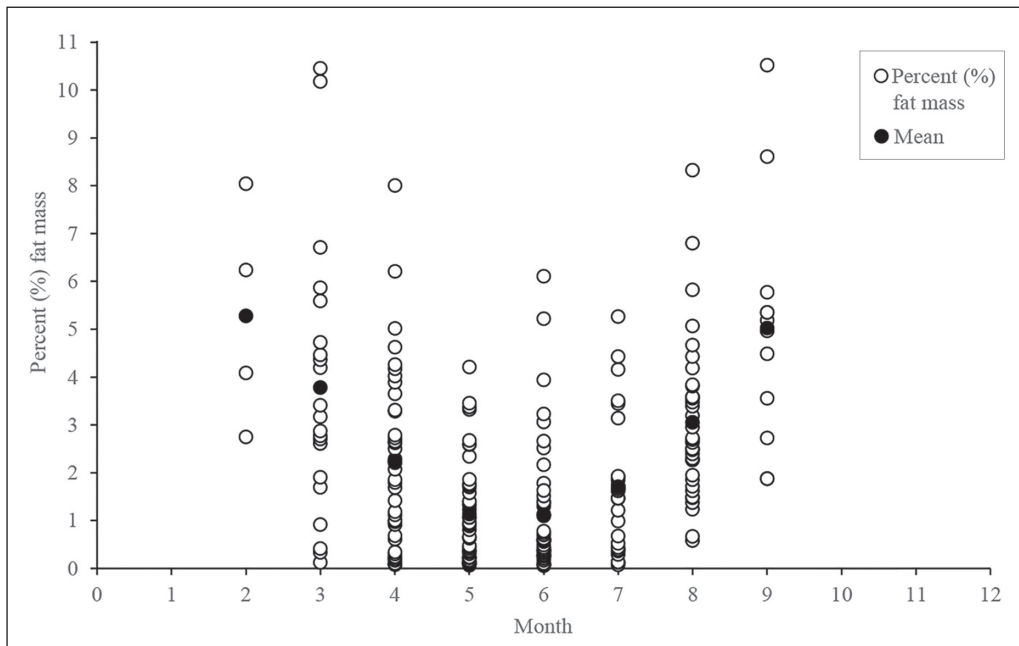

Figure 5. Monthly distribution of fat mass presented as a percent (%) of the total body mass of 236 female *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.
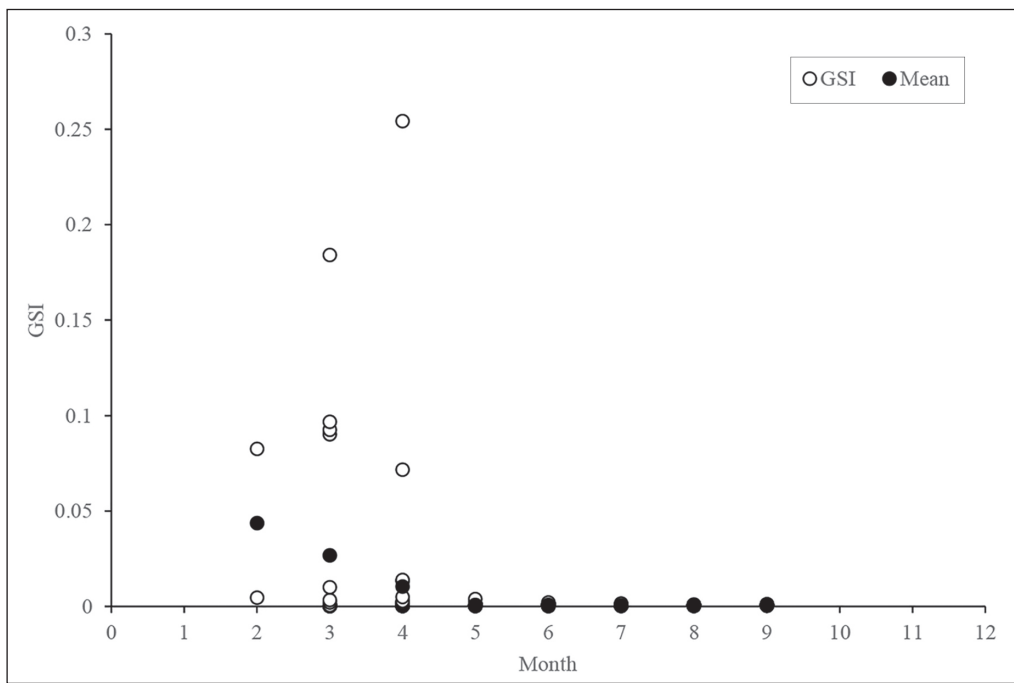
Figure 6. Monthly distribution of the Gonadal:Somatic Index (GSI) of 179 female *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.
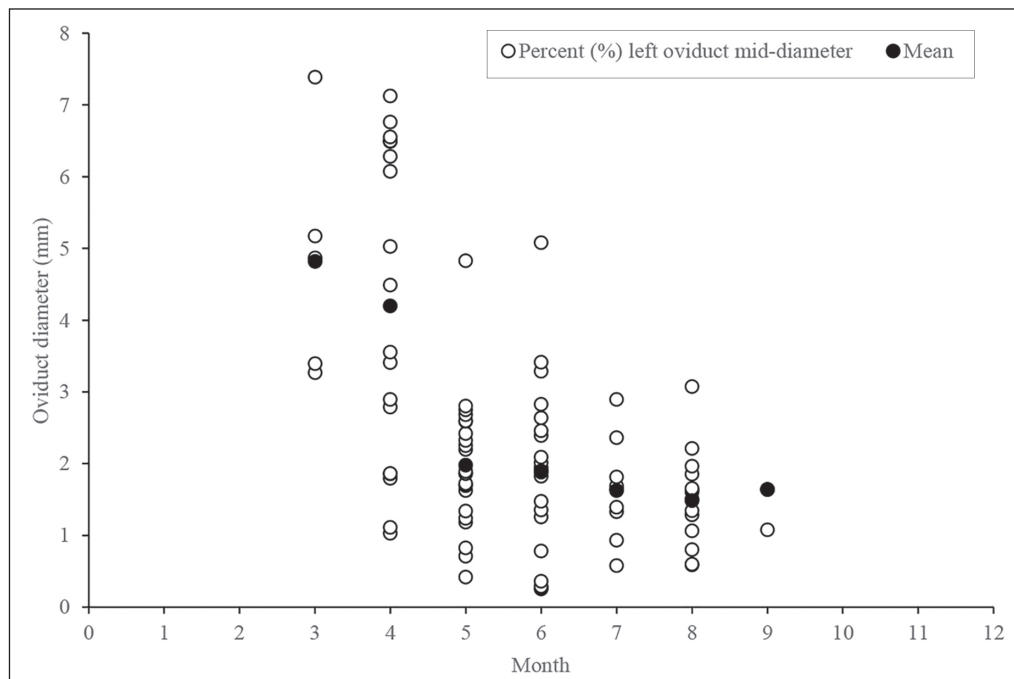

Figure 7. Monthly distribution of oviduct diameter at center of length presented as a percent (%) of the snout–vent length (SVL) of 91 female *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.

Ovarian cycle. Ovarian follicles >10.0 mm were present during most of March–August (Fig. 8). The monthly distribution of follicles indicated a rapid increase in their diameters as early as August and a resumption of follicular growth at least in March (Fig. 8). Shelled eggs (*n*, maximum luteal diameter) were present in March (34 eggs, maximum luteal scar not measured), April (30 eggs, 6.1 mm), and May (33 eggs, 6.9 mm). Corpora lutea associated with females without oviductal eggs (followed by largest diameters in parentheses) were detected in April (9.8 mm), May (3.2 mm), and June (6.7 mm). One female captured in April was found to contain 27 corpora lutea, the largest of which measured 6.1 mm. Shelled eggs were present but not counted. Therefore, this clutch size value is placed n the category of luteal count-derived estimation of clutch size. Oogenesis appears to have begun as early as August. From our data, no sign of multiple clutch production was evident in this sample, nor did all females produce a clutch annually.

Clutch characteristics. The number of eggs produced by a female each year was estimated using 3 techniques. Estimated clutch size based on counts of yolked ovarian follicles was normal in distribution ($W = 0.936$, $P = 0.40$) and varied between 17 and 43 eggs per clutch (mean = 29.2 ± 4.3 eggs, $n = 13$). Estimated clutch size based on numbers of oviductal eggs and luteal scars (27.4 ± 4.7 eggs, min–max = 21–34, $n = 7$) was normal in distribution ($W = 0.933$, $P = 0.60$) and did not differ significantly from those estimated by counts of yolked ovarian follicles ($t = 0.5454$, df = 18, $P = 0.59$). Combining the samples, we estimated an average of 28.6 eggs (± 3.1 eggs; min–max

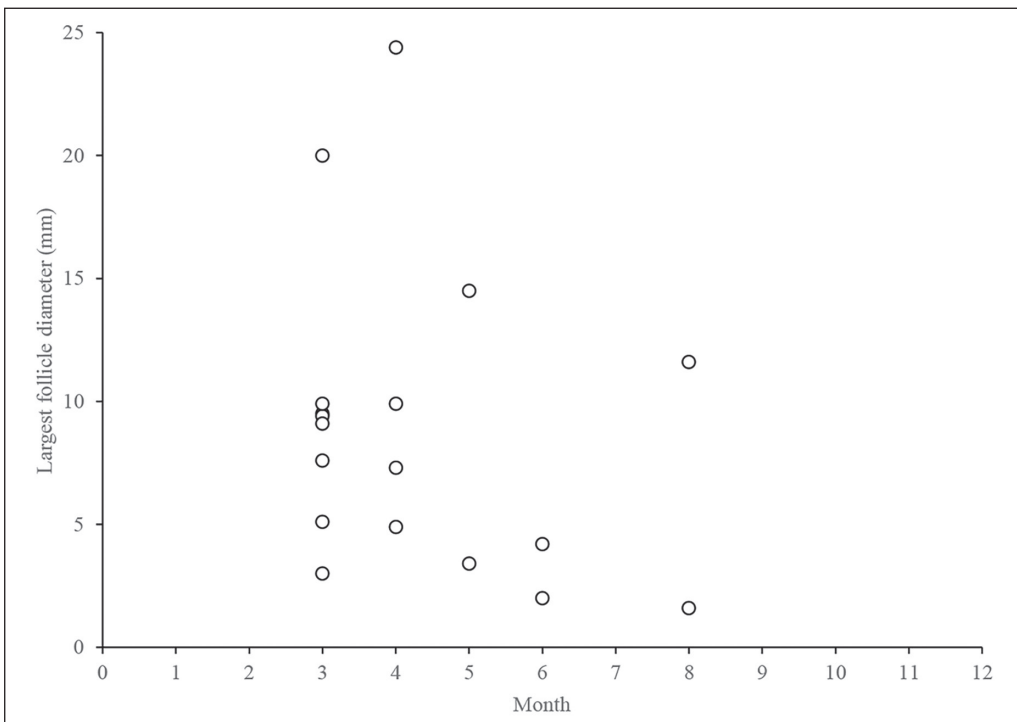

Figure 8. Monthly distribution of largest follicle diameter of 18 female *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017.

= 17–43) for 20 females (mean = 345.5 ± 11.9 mm SVL, min–max = 293–382). The relationship between clutch size (number of yolked ovarian follicles >10 mm, oviductal eggs, and corpora lutea) and female body size was positive and significant (Fig. 9). Highly fecund (Fig. 10), relative clutch mass (RCM) measured 18.4% for a 382-mm

$$y = 0.1152x - 11.259$$
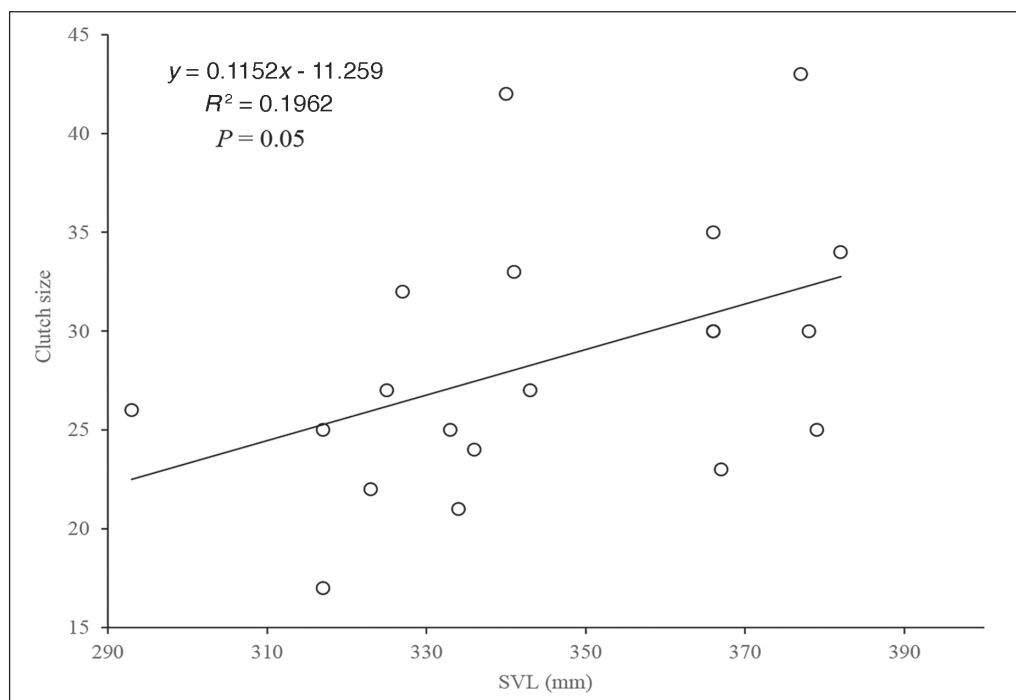$$R^2 = 0.1962$$
$$P = 0.05$$

Figure 9. Relationship of clutch size to female snout–vent length (SVL) in 20 female Argentine Giant Tegus (*Salvator merianae*) from southern Florida during 2011–2017.

Figure 10. An example of an ovigerous *Salvator merianae* (Argentine Giant Tegu) collected in southern Florida. Photograph © M.R. Rochford.

SVL female with 34 eggs in March and 25.4% for a 366-mm SVL female with 30 eggs in April. Hatching was possible during May–August (Fig. 11).
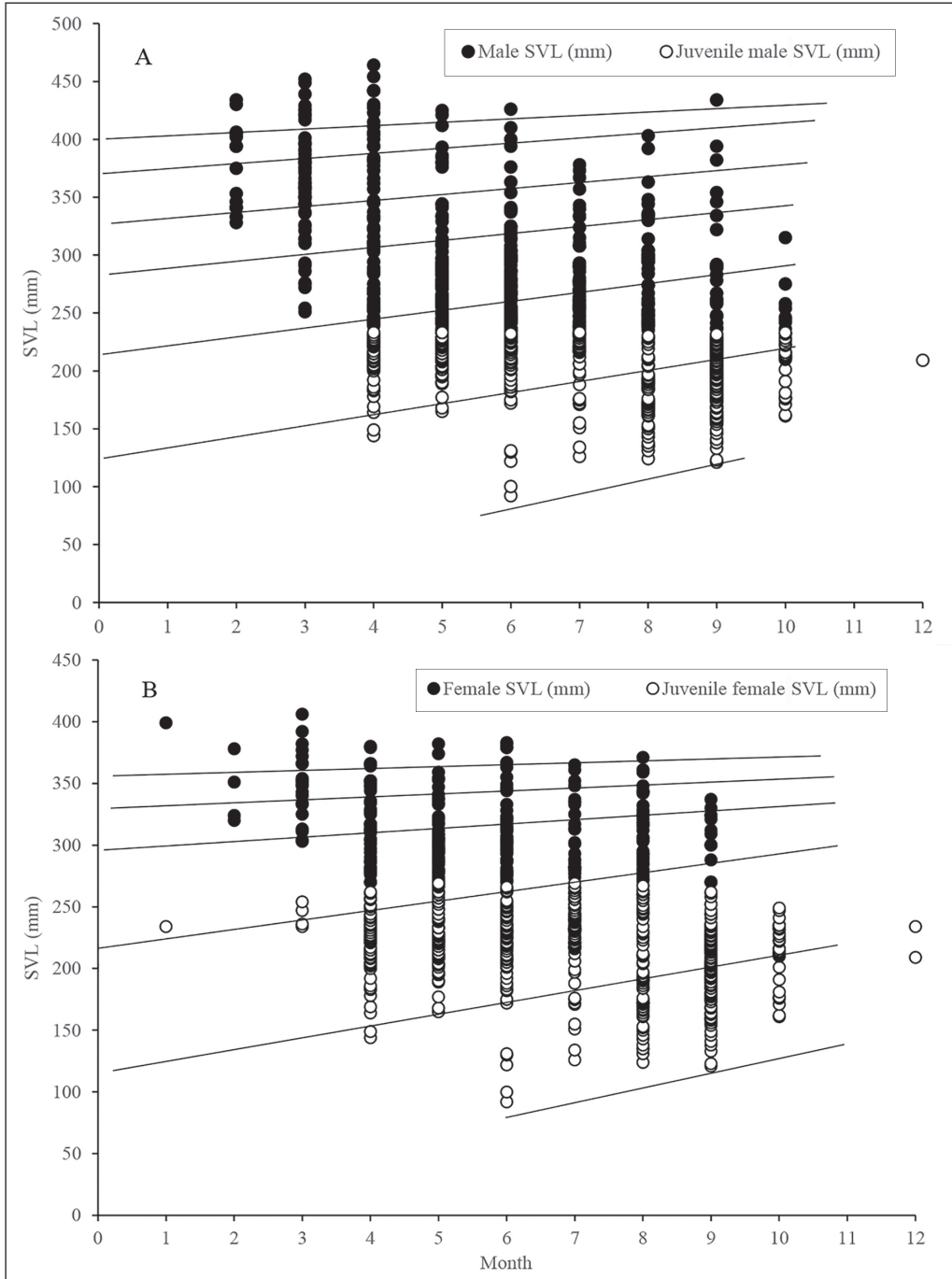

Figure 11. Monthly distribution of snout–vent length (SVL) of (A) 423 male and 344 juvenile and (B) 244 female and 491 juvenile *Salvator merianae* (Argentine Giant Tegu) from southern Florida during 2011–2017. Lines represent presumed age-body size cohorts.

Age and body size at sexual maturity

   In our sample, the minimum body size at sexual maturity was smaller in males (234 mm SVL) than in females (270 mm SVL). From presumed body/age class cohorts, a tegu hatched in July at 100 mm SVL could reach sexual maturity at ~21 months of age if male (Fig. 11a) and at 24 months if female (Fig. 11b). Overall, adult body size was not normally distributed in our samples of males (mean = 305.5 ± 5.4 mm SVL, min–max = 234–464, $n = 427$, $W = 0.914$, $P < 0.001$) and females (315.3 ± 4.0 mm SVL, min–max = 270–406, $n = 239$, $W = 0.952$, $P < 0.001$); however, adult body size differed significantly between the sexes (Mann-Whitney U statistic = 39537.00, $P < 0.001$). Among the largest 10% of each sample, adult body size was not normally distributed in our samples of males (mean = 418.4 ± 5.7 mm SVL, min–max = 394–464, $n = 43$, $W = 0.947$, $P = 0.05$) and females (376.6 ± 4.7 mm SVL, min–max = 363–406, $n = 24$, $W = 0.897$, $P < 0.02$); however, adult body size differed significantly between the sexes (Mann-Whitney U statistic = 22.00, $P < 0.001$).

Discussion

   Florida colonies of the Argentine Giant Tegu represent disjunct and the northernmost populations of the species (Enge 2007). Our study provided qualitative data for selected life-history traits of an exotic population that had established >20 years ago to compare with those farther south in the more temperate locales within its native range. Responses to a more subtropical ecossytem over 2 decades quantified the plasticity of these traits and indicated the extent to which these traits can be expected to revert in what we anticipate to be successful northward expansion of an invasive exotic species.

   Mating season varies geographically, with earliest and latest months found in southern Florida compared to other areas where this species is found (Table 1). Like Noriega et al. (2002) and Chamut et al. (2012), we detected an interrupted spermatogenic cycle whereby recrudescence occurs in autumn and remains suspended during the winter. Its sharp increase was apparent shortly after brumation and associated with mating. Not surprisingly, then, number of mating events peaked in March during February–May mating among tegus from our study area as well as those kept in outdoor enclosures in the same area (Table 1; R. Irwin, Tegus Only, Homestead, FL, pers. comm.). The greater duration of sperm production in our sample could be related to the shorter and intermittent brumation period in southern Florida compared to 6–8 months of activity in the species' more temperate native habitat (Table 1). Thus, while many South American counterparts were brumating in underground dens for 120–190 days (Table 1), 4 of 5 radio-tracked individuals near our study site remained in brumation 116–160 days (mean = 137 days), beginning 16 September–6 October and ending 29 January–22 February (McEachern et al. 2015). One male basked regularly during brumation (McEachern et al. 2015), a behavior possible in light of the climate of our site. Exceptionally, individuals from a site in southern Brazil, were active during February–October (Winck and Cechin 2008). However, brumation was uninterrupted in southern Brazil, and both emergence and dormancy initiation dates did not overlap between the sexes (Table 1; Winck and Cechin 2008).

Table 1. Comparison of life-history traits of *Salvator merianae* (Argentine Giant Tegu) having differed between source and target areas. Months of the Southern Hemisphere are adjusted to those of the Northern Hemisphere to reflect seasonal differences (e.g., for South America, the second month of winter has been converted to February, which is the second month of winter in the norther hemisphere, for ease of comparison.

Trait	This study	Southern Florida	Northern Alabama	South-central Pennsylvania	South America
Seasonal activity	Year-round	February–September or early October (Enge 2007); Late January–early October /intermittent/continuous (McEachern et al. 2015)	Mid-March–mid-September (Langerwerf 2006)	April–October (W.E. Meshaka, pers. observ.)	February–October: Males = February and March–August, Females = May–early-June–October in Brazil (Winck and Cechin 2008); Mid-March–October in Argentina (Duarte Varela and Cabrera 2000); March–October in Argentina (Chamut et al. 2012); 7–8 mo. (Andrade and Abe 1999)
Mating season	February–May or June	Late-Feburary–mid-May, Begins March (Enge 2007); March peak (R. Irwin, pers. comm.)	Begins mid-April (Langerwerf and Paris 1998)		March–May (Norman 1987); April in Argentina (Manes et al. 2007)
Commencement of follicular growth	March				April (Manes et al. 2007)
Ovigerous females /nesting	March–May, likely June	June (Enge 2007)			April–May in subtropical portion (Yanosky and Mercolli 1992); Mid-May in Paraguay (Norman 1987)
Hatching season	May–August				Late-June–early-July in Paraguay (Norman 1987)
Age at sexual maturity	By 24 months		Three years of age (Langerwerf 2006)		Third or fourth year of life in Paraguay (Fitzgerald 1994)
Female SVL (mm) at sexual maturity	270 mm				300 mm (Yanosky and Mercolli 1992)

Records from exotic outdoor colonies corroborate the latitudinal trend in length of activity season (Table 1). Tegus in Palm Beach County were active for 8 to 9 months, while those in northern Alabama (Langerwerf 2006 in Enge 2007) and south-central Pennsylvania were active 5 and 7 months, respectively (Table 1). In light of the shorter days and colder temperatures in locations north of our study as well as those farther south in the Southern Hemisphere, it should not be surprising, then, that individuals of our study population would respond to longer days and warmer temperatures of extreme southern Florida with longer active seasons. Trapping effort was not available for our study; however, the presence of trapped animals throughout the year, the earliness of gravid females, and the shorter and interrupted nature of brumation at our site (McEachern et al. 2015) suggest a much-weakened periodicity of seasonal activity in extreme southern Florida.

The ovarian cycle of the Argentine Giant Tegu at our southern Florida site was similar to that of conspecifics in the Santa Fe Province of Argentina (Manes et al. 2007) with respect to rapid follicular growth after emergence from torpor, followed by a mid-summer (August in Florida) pre-vitellogenic phase. However, the timing of follicular growth was a major difference between them in an otherwise synchronous gonadal cycle (Table 1). In the Santa Fe Province (Manes et al. 2007), a very rapid follicular growth commenced 15–20 days after mating in October (April in northern hemisphere). Between egg laying and mating-induced follicular growth, follicle size averages 1.28–4.52 mm. The monthly distribution of follicle size in our sample indicates a cycle that began at least as early as March, 1 month earlier than that of Santa Fe province (Manes et al. 2007). Follicles were still larger at our site during post-eclosion—February (August in northern hemisphere) at Santa Fe (Manes et al. 2007). Although southern Florida is cooler and drier during November–April, its dry-season climate is not as harsh with respect to temperatures that enforce brumation during winter months in its native range, increasingly so as one proceeds southward. As in the case of males at our site, we suggest that the ovarian cycle of females has within 20 y responded to the milder climate of southern Florida with an earlier start to and longer duration of reproductive activity. Manes et al. (2007) found that mating initiated follicular growth in Argentina. If this is so, then females at our site could be mating as early as February, whereas Argentine counterparts are still in brumation at that point in their seasonal cycle.

Nesting season also begins earlier and ends later in southern Florida than elsewhere in its native and introduced range (Table 1). We captured our few ovigerous females during March–May. We proffer that the high RCM (Meshaka et al. 2018, this study) precludes mobility and limits room for food, and the conversion of fat stores lessens the need to eat. Consequently, rapidly yolking females in all likelihood build and remain close to their nest. Incubation time of ~60 days is typical in Palm Beach County (Enge 2007) and Argentina (Yanosky and Mercolli 1995). Three months typifies the incubation period of eggs left in the ground in northern Alabama (Enge 2007, Langerwerf 2006). An ~2-month incubation period, the monthly distribution of body sizes (Fig. 11), and average hatchling sizes of 7.1 cm SVL (Yanosky and Mercolli 1992) to 8.9 cm SVL (Enge 2007, Langerwerf 2006), corroborate the determination of a longer nesting season than those of native populations (Table 1).

The distribution of juvenile body sizes at our site (Fig. 11) indicates a protracted hatchling emergence season of May to August in extreme southern Florida that, like the nesting season, is longer than that of South American native populations (Table 1). An important result of a protracted nesting and hatchling season is the colonizing advantage of mixed or staggered generations, which can buffer a population from density-independent catastrophes (Inger and Greenburg 1966), such as hurricanes and occasional severe frost in southern Florida.

Mixed generation times along with a shorter and incomplete brumation can lessen the accuracy of growth-rate estimations with the use of scattergrams of monthly body-size distributions (Fig. 11). Furthermore, intersite comparisons of age to sexual maturity must also take into account differences in minimum body sizes at maturity. Sexual maturity is reached sooner in southern Florida than at either latitudinal extremes (Table 1) with all females at our site breeding in late winter or spring, 8 or 9 months later, before the age of 3. Likewise, minimum body size at sexual maturity is 30 mm smaller at our southern Florida site than in Paraguay (Table 1). Interestingly, well-fed captive females can reproduce at less than 1 y of age, at which point they measure 610 mm TL (Enge 2007). Such early reproduction indicates that sufficient food and warmth results in faster growth to sexual maturity at our site, which can be duplicated under captive conditions elsewhere (Enge 2007). These comparisons indicate a relaxation in this aspect of female reproduction and growth at our subtropical site that differs from those of sites in its native range with a more temperate climate.

Unlike those of the gonadal cycle at our site, modifications were not evident in clutch production or characteristics. Females at our site produced one large clutch averaging 29 eggs. Clutches of 21 and 35 eggs were discovered within our study area (Pernas et al. 2012). In its native range, clutch sizes for Argentine Giant Tegus average 30 (Yanosky and Mercolli 1991) to 36 (max. = 54 eggs; Donadío and Gallardo 1984) eggs. Not all adult females produced clutches each year at our site or elsewhere; approximately one-half of the females in its native range produced clutches in a given year (Chamut et al. 2012). RCM can be very high (32–42% of total female mass) in this species (Lopes and Abe 1999, Meshaka et al. 2018), which could account for the inability of many females to produce eggs each year. The greater fat mass in females than in males during February at our site underscores the importance of those reserves in production of a large clutch. The similarity of clutch characteristics and fecundity between introduced and native populations seems counterintuitive in light of the differences in the length of respective activity seasons. Thus, the shorter duration and interruption of brumation in southern Florida compared to the uninterrupted 4- to 6-month brumation period in its native range has not equated with sufficient energy to produce more than 1 clutch each year or to produce eggs annually for all females.

Several of the life-history traits that we examined shifted latitudinally in this species, whereas others did not. Our findings provide confidence in our assessment of, and predictions for, the Argentine Giant Tegu in Florida. First and foremost, colonization of extreme southern Florida by this species was accompanied by

life-history traits that differed from those of source areas, evidenced plasticity in its biology, and conferred advantages in a novel environment. Climate of the southeastern United States does not appear to be a barrier to colonization of the Argentine Giant Tegu. The southeast shares a similar Köppen climatic zone with that of central portions of Argentina where southerly native population of the species experience shorter seasonal activity. Likewise, winter isotherms of surface air temperature for the Southeast US and areas surrounding Buenos Aires, during January and July, respectively, overlap (Images provided by the NOAA ESRL Physical Sciences Division, Boulder, Colorado, USA, from their website at http://www.esrl. noaa.gov/psd/). The area between Miami and the Florida panhandle is within 20–15 ºC. From the Florida panhandle northward to the latitude just below North Carolina and Tennessee, is within 15–10 ºC. The area south of Buenos Aires to Buenos Aires is within 5–10 ºC, and the next isotherm north of Buenos Aires is within 10–15 ºC. Thus, we are confident in our prediction that climate is amenable to the dispersal and colonization of this vagile species along the coasts and sandy uplands north into the Southeast US where climate is akin to that of more temperate source areas. To that end, northward dispersal will bring with the Argentine Giant Tegu the same life-history strategy of southern Florida until, at some latitude, the relaxed traits in southern Florida, having enhanced its colonization success, will presumably begin to shift back to those of its source areas. This being the case, delayed maturity and shorter active, nesting, and hatching seasons could render control efforts of northerly populations somewhat easier than in southern Florida, even if no less critical.

The Argentine Giant Tegu is a successful colonizing species in Florida. Its combination of life-history traits predisposes the species to a high likelihood of colonization success in portions of the Southeast. Its demonstrated ability to thrive in more temperate climes and its trophic position of mid-level predator are colonizing advantages that place large segments of the biotic community at risk to negative impacts by a novel predator well-suited to northern colonization.

Literature Cited

Andrade, D.V., and A.S. Abe. 1999. Gas exchange and ventilation during dormancy in the tegu lizard *Tupinambis merianae*. Journal of Experimental Biology 202:3677–3685.

Chamut, S., G.A. Jahn, O.E.A. Arce, and M.E. Manes. 2012. Testosterone and reproductive activity in the male tegu lizard, *Tupinambis merianae*. Herpetological Conservation and Biology 7:239–305.

Donadío, O.E., and J.M. Gallardo. 1984. Biología y conservación de las especies del género *Tupinambis* (Squamata, Sauria, Teiideae) en la República Argentina. Revista del Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" (Zoologia) 13:117–127.

Duarte Varela, C.F., and M.R. Cabrera. 2000. Testing skeletochronology in Black Tegu lizards (*Tupinambis merianae*) of known ages. Herpetological Review 31:224–226.

Enge, K.M. 2007. Bioprofile for the Argentine Black and White Tegu (*Tupinambis merianae*). Florida Fish and Wildlife Conservation Commission, Tallahassee, FL. 27 pp.

Farris S.C., M.A. Squires, F. Ridgely, E. Lavergne, M. Serota, R. Bijlani, and F.J Mazzotti. 2013. Necropsies of reptiles: Recommendations and techniques for examining invasive species. University of Florida IFAS Extension. Gainesville, FL. 26 pp.

Fitzgerald, L.A. 1994. The interplay between life history and environmental stochasticity: Implications for the management of exploited lizard populations. American Zoologist 34:371–381.

Inger, R.F., and B. Greenburg. 1966. Ecological and competitive relations among three species of frog (genus *Rana*). Ecology 47:746–759.

Klug, P.E., R.N. Reed, F.J. Mazzotti, M.A. McEachern, J.J. Vinci, K.K. Craven, and A.A. Yackel Adams. 2015. The influence of disturbed habitat on the spatial ecology of Argentine Black and White Tegu (*Tupinambis merianae*), a recent invader in the Everglades ecosystem. Biological Invasions 17:1785–1797. DOI:10.1007/s10530-014-0834-7.

Langerwerf, B., and M. Paris. 1998. Argentine Giant Tegus. Reptiles 6:40–41.

Lopes, H.R., and A.S. Abe. 1999. Biologia reprodutiva e comportamento do teiú, *Tupinambis merianae*, em cativero (Reptilia, Teiidae). Pp. 259–272, *In* T.G. Fang, O.L. Montenegro, R.E Bodmer, (Eds.) Manejo y Conservación de Fauna Silvestre en América Latina. Editorial Instituto e Ecología, La Paz, Bolivia. 496 pp.

Manes, M.E., T. Noriega, F. Campos Casal, and S. Apichela. 2007. Ovarian changes during the reproductive cycle of the *Tupinambis merianae* lizard raised in a temperate environment. Cuadernos de Herpetología 21:21–29.

Mazzotti, F.J., M. McEachern, M. Rochford, R.N. Reed, J. Ketterlin Eckles, J. Vinci, J. Edwards, and J. Wasilewski. 2015. *Tupinambis merianae* as nest predators of crocodilians and turtles in Florida, USA. Biological Invasions 17:47–50.

McEachern, M.E., A.A. Yackel Adams, P.E. Klug, L.A. Fitzgerald, and R.N. Reed. 2015. Brumation of introduced Black and White Tegus, *Tupinambis merianae* (Squamata:Teiidae), in southern Florida. Southeastern Naturalist 14:319–328.

Meshaka, W.E., Jr. 2011. A runaway train in the making: The exotic amphibians, reptiles, turtles, and crocodilians of Florida. Herpetological Conservation and Biology, 6(Monograph 1):1–101.

Meshaka, W.E., Jr., and J.N. Layne. 2015. The herpetology of southern Florida. Herpetological Conservation and Biology 10(Monograph 5):1–353.

Meshaka, W.E., Jr., W.B. Loftus, and T.M. Steiner 2000. The herpetofauna of Everglades National Park. Florida Scientist 63:84–103.

Meshaka, W.E., Jr., F.J. Mazzotti, and M.R. Rochford. 2018. Relative clutch mass in four exotic reptile species from southern Florida. The Herpetological Bulletin 143:23–25.

Noriega, T., M.A. Ibáñez, E. Bru, and M.E. Manes. 2002. The testicular cycle of captive *Tupinambis merianae* lizards in a temperate environment. Cuadernos de Herpetología 16:119–127.

Norman, D.R. 1987. Man and tegu lizards in eastern Paraguay. Biological Conservation 41:39–56.

Pernas, T., D.J. Giardina, A. McKinley, A. Parns, and F.J. Mazzotti. 2012. First observations of nesting by the Argentine Black and White Tegu, *Tupinambis merianae*, in south Florida. Southeastern Naturalist 11:765–770.

Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to the Reptiles and Amphibians of Eastern and Central North America. 4th Edition. Houghton Mifflin Harcourt. Boston, MA, 494 pp.

Pyron, R.A., F.T. Burbrink, and T.J. Guiher. 2008. Claims of potential expansion throughout the US by invasive *Python* species are contradicted by ecological niche models. PLoS ONE 3(8):e2931. DOI:10.1371/journal.pone.0002931.

Rodda, G.H., G.S. Jarnevich, and R.N. Reed. 2008. What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park? Biological Invasions 11:241–252. DOI:10.1007/s10530-008-9228-z.

Winck, G.R. and S.Z. Cechin. 2008. Hibernation and emergence pattern of *Tupinambis merianae* (Squamata: Teiidae) in the Taim Ecological Station, southern Brazil. Journal of Natural History 42:239–247.

Yanosky, A.A., and C. Mercolli. 1991. Preliminary observations on the reproductive cycle of female tegu lizards (*Tupinambis teguixin*). Cuadernos de Herpetología 6:27–30.

Yanosky, A.A., and C. Mercolli. 1992. Tegu lizard (*Tupinambis teguixin*) management in captivity at el Bagual Ecological Reserve, Argentina. Archivos de Zootecnica 41:265–278.

Yanosky, A.A., and C. Mercolli. 1995. Incubacion artificial de huevos de la iguana overa (*Tupinambis teguixin*). Archivos de Zootecnica 44:379–389.