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GONADAL CYCLE AND GROWTH OF A WEST INDIAN LIZARD, THE NORTHERN CURLYTAIL LIZARD (*LEIOCEPHALUS CARINATUS ARMOURI*), IN SOUTHERN FLORIDA

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***Abstract.*—Reproduction and growth of the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*), a West Indian species, was studied in southern Florida, where it has been introduced. A single clutch of four large eggs was produced over a four-to-five month egg-laying season, although multiple clutch production by some females could not be ruled out. Sexual maturity was reached in less than one year of life. We suggest that this combination of life history traits places this species close to the center between the opposing life history strategies of early maturing, multiple-brooded species and later maturing, single-brooded species. Although its fecundity is not high, staggered generations as a result of a four-to-five month egg-laying season and rapid growth to sexual maturity contribute to its colonization success in an expanding geographic range in Florida.**

Key Words.—colonization, exotic species, Florida, Northern Curlytail Lizard, reproduction

INTRODUCTION

Florida has become home to a remarkable number of exotic species (Simberloff et al. 1997), including 46 established species of amphibians and reptiles (Meshaka et al. 2004; Meshaka 2006). Despite the ubiquity of many of these species, detailed ecological studies (e.g., in anoles [Lee et al. 1989; Meshaka and Rice 2005], geckos [Meshaka 1995; 2000; Punzo 2001], and anurans [Meshaka 2001; Punzo and Lindstrom 2001; Meshaka and Layne 2005]) are few, and comprehensive life history studies (e.g., Goin 1946; Meshaka 2001) are fewer still. Yet, data from those types of studies provide exactly the type of information necessary to understand why a species succeeds or fails such as, the Cuban Treefrog (*Osteopilus septentrionalis*) in Florida (Meshaka 2001) and the Mediterranean Gecko (*Hemidactylus turcicus*) in the Southeastern United States (Meshaka et al. 2006a) and subsequently to make sound management decisions regarding that species (Bury 2006; McCallum and McCallum 2006). Moreover, breeding populations of exotic species offer the opportunity to examine responses (ecological, reproductive) of those species to the new environment (biotic and abiotic) they experience following introduction. These responses (if any) can provide clues about the underlying evolutionary process producing them (Mayr 1963; Greene 1986).

In this study, we examined reproduction and growth in a population of the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*). This lizard was introduced to Florida from the West Indies in about 1945 (Weigl et al. 1969) and is currently widespread along the coast of southern half of the Florida peninsula and has several inland populations (Meshaka et al. 2004, 2005). We place our results in the context of life history theory, which identifies a potential continuum between two opposing sets of traits. At one end of this continuum are those species that mature early in life, produce multiple clutches per season, experience low annual survivorship, and are generally short-lived (Tinkle et al. 1970; Dunham and Miles 1985). At the other end of this continuum are species that mature late in life, produce single clutches (or broods) per season, experience high annual survivorship, and are generally long-lived. In this connection, we relate our findings as they apply to successful colonization in an exotic species whose introduced range in Florida continues to expand (Meshaka et al. 2005).

MATERIALS AND METHODS

Multiple daytime visits were made in most months during August 2003-July 2004 to sites located along roads within coastal Palm Beach and Martin counties, where the species is very abundant. Lizards were captured by hand or noose. Specimens were preserved in 70% ethyl alcohol and deposited in the section of Zoology and Botany of the State Museum of Pennsylvania, Harrisburg, Pennsylvania, USA. For all lizards, body length in mm snout-vent length (SVL) was measured to 0.1 mm, and tails were examined for signs of regeneration. Examination of the gonads determined sexual maturity. Lengths of the right testes were measured and plotted as a percent of the SVL to determine the seasonal testicular cycle. In females, ovarian follicles and oviductal eggs were counted and measured to determine the ovarian cycle and clutch characteristics. In both sexes, abdominal fat bodies were staged at one of three levels: 0 = no evidence of fat, 1 = fat present in the lowest regions of the body cavity, 2 = fat extending throughout much of the body cavity.

RESULTS

***Testicular cycle.*—**Testicular recrudescence, the renewal of germinal epithelium of the next period of spermiogenesis, began in January, and the testes reached their maximum length during spring-summer (Fig. 1). Consequently, mean right testis length

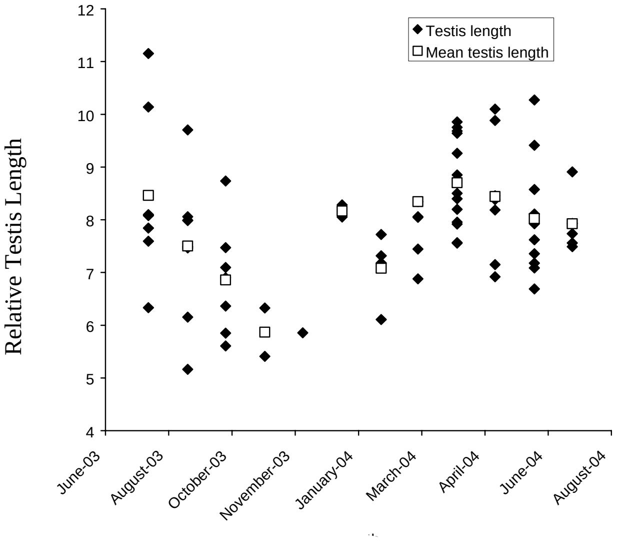

FIGURE 1. Testicular cycle of the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.The X and Y labels are too small on all graphs

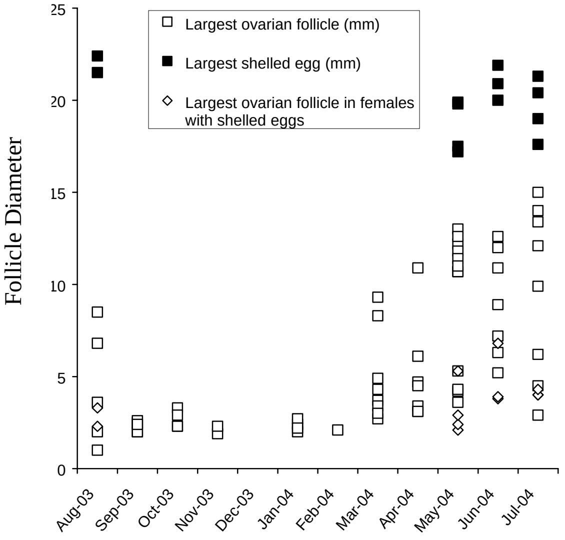

FIGURE 3. Ovarian cycle of the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.

as a percentage of male mm SVL co-varied positively ($r^2 = 0.40$; $P = 0.04$; Testis Length = 0.569 SVL + 5.308) with end of the month day-length for 11 months. Male fertility, as measured by testis length, peaked during April-August, and courtship occurred through August and perhaps early September.

Male abdominal fat development.—The highest seasonal incidence of extensive abdominal fat development in males occurred during fall-winter (Fig. 2) when days were cool and short, and no breeding activity was apparent.

Ovarian cycle.—Vitellogenesis began in March with the first females producing shelled eggs two months later (Fig. 3). Production of shelled eggs continued through August; however, two observations indicated that egg deposition could extend in to early September. First, the last female was captured containing shelled eggs on 22 August 2003. The size distribution of ovarian follicles in July was in accordance with the seasonal increase in ovarian follicle size, such that shelled eggs would have been produced by September. The 6.8 mm and 8.5 mm ovarian follicles in August would not be shelled by September, and September females in turn contained ovarian follicles that were less than 3.3 mm in diameter, which signified the end of egg production until the following spring (Fig. 3). This seasonal distribution of ovarian follicle size was predictable in that it co-varied positively with end of the month day-length ($r^2 = 0.80$; $P < 0.001$; Follicle Size = 0.0216 Day-length – 20.733).

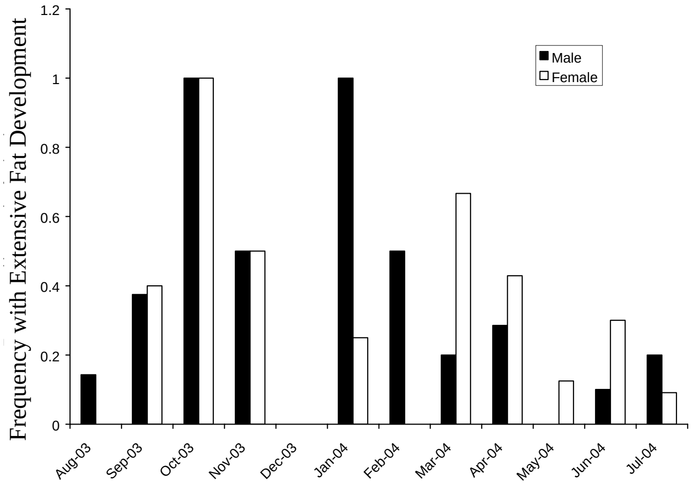

FIGURE 2. Seasonal frequency of extensive fat body development in male and female Northern Curlytail Lizards (*Leiocephalus carinatus armouri*) in southern Florida.

Clutch size.—Mean clutch size did not differ significantly ($t = -1.22$; $P > 0.05$) whether estimated by enlarged ovarian follicles (mean = 4.3; $S = 1.0$; range = 2-6; $N = 35$) or shelled eggs (mean = 3.9, $S = 1.1$; range = 2-6; $N = 12$). Clutch size co-varied positively with female body size as estimated by counts of shelled eggs ($r^2 = 0.38$; $P = 0.03$) and ovarian follicles ($r^2 = 0.18$; $P = 0.01$) (Fig. 4).

Egg dimensions.—The shelled eggs were large in both mean length (19.1, $S = 1.7$ mm; range = 15.8-22.4; $N = 47$) and mean width (10.8, $S = 0.9$ mm; range = 9.0-12.9; $N = 47$). However, no significant relationship ($P > 0.05$) was found between maximum or mean shelled egg length and female body size (Fig. 5). Neither maximum nor mean shelled egg length, likewise, did not co-vary significantly ($P > 0.05$) with clutch size (Fig. 6).

Number of clutches.—Based on the number of females captured containing shelled eggs and enlarged follicles, it appears that only one clutch was produced annually by most but not necessarily all females. In this regard, we noted two females containing shelled eggs

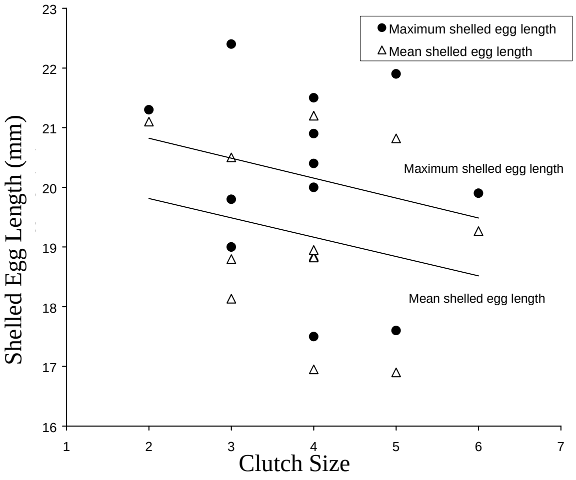

FIGURE 6. Relationship between shelled egg length and clutch size in the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.

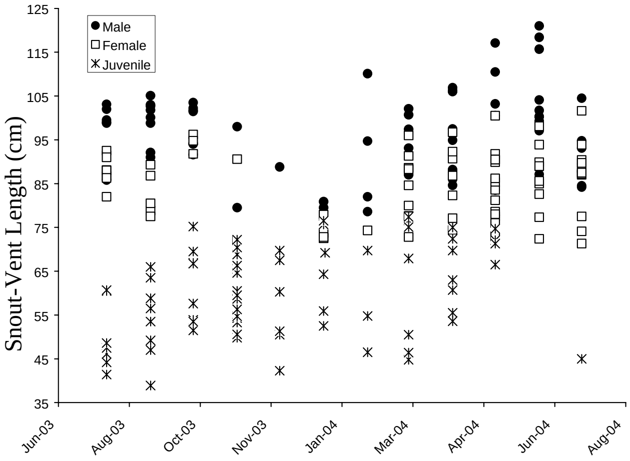

FIGURE 7. Seasonal distribution of body size in the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.

and the largest enlarged secondary ovarian follicles (Fig. 3). The first female, 90.5 mm SVL and captured on 8 May 2004, contained four ovarian follicles (the largest of which was 5.3 mm) and contained six shelled eggs.

The second female, 89.0 mm SVL and captured on 29 June 2004, contained four ovarian follicles (the largest of which was 6.5 mm) and contained five shelled eggs. We are unsure if those ovarian follicles accompanying the shelled eggs represented the beginning of a second clutch that would have been laid in July and August, respectively, or if they represented accessory follicles that were abandoned in the development of the females' first and only clutch. Likewise, the pattern of ovarian follicles accompanying all shelled egg-bearing females could offer the possibility of multiple clutch production that began in June and ended in August as well as representing atresia, the spontaneous degeneration of the ovarian follicle. Thus, although single clutch production was apparent in most females, multiple clutch production by some segment of the population could not be ruled out.

Female abdominal fat development.—The highest seasonal incidence of extensive abdominal fat development in females occurred during fall-spring (Fig. 2). The absence of females during December and small numbers of females in the winter might obscure the specifics of the winter pattern; however, the overall pattern appeared to be one of rapid fat deposition beginning in September after egg-laying only to deplete in spring in advance of clutch production. In this connection, of the 12 shelled egg-bearing females, nine lacked fat and three contained partial body fat. Thus, the seasonal depletion of fat could be related to both its use for energy during the winter months and in clutch production.

Hatching season.—Because of an extended egg-laying season, juveniles of various size-classes were present throughout much of the year (Fig. 7). The smallest individuals were collected on 14

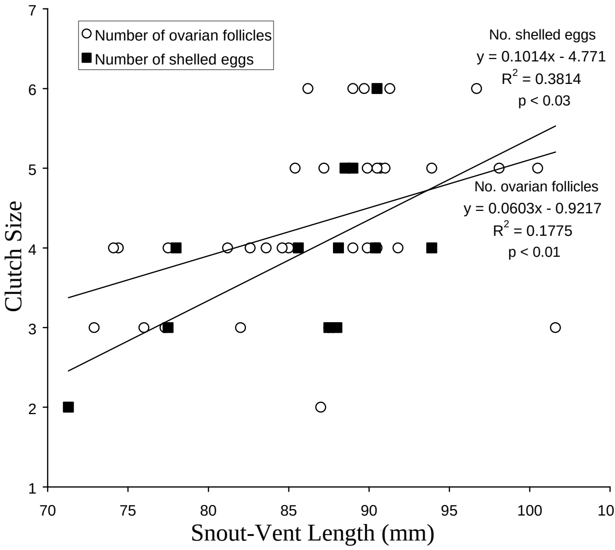

FIGURE 4. Relationship between clutch size and female body size in the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.

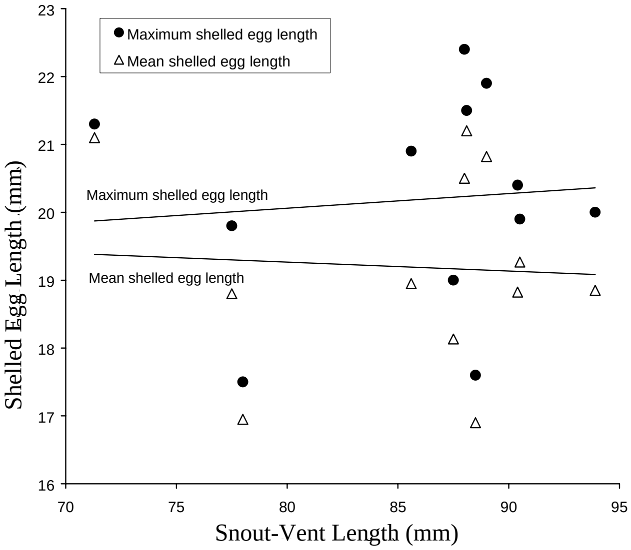

FIGURE 5. Relationship between shelled egg length and female body size in the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*) in southern Florida.

September (SVL = 38.9 mm) and 16 August (SVL = 41.1 mm) (Fig. 7), and these sizes were near the 38.1 mm SVL that approximates hatchling body size in this species (Richard D. Bartlett, pers. comm.). A 45.0 mm SVL juvenile captured on 23 July probably represented an early July or late June hatchling; therefore, it was from an egg laid somewhere between one and two months after the first shelled egg-bearing females were captured (Fig. 3). The smallest individuals captured in December, January, and March probably hatched one to two months prior to capture, which could be the result of a combination of eggs deposited in August combined with slightly cooler temperatures during development.

***Growth and Maturity.*—**From growth trajectories beginning in August (Fig. 7), it appeared that six months since hatching were needed to reach the minimum sexually mature body size in males (SVL = 78.6 mm) and five months to reach that size in females (SVL = 71.3 mm). In turn, nine months since hatching were needed to reach mean adult body size of males (mean SVL = 96.9, S = 9.4 mm; range = 78.6-121.0; N = 72) and about seven months to reach mean adult body size of females (SVL = 84.6, S = 7.8 mm; range = 71.3-101.6; N = 75). These trajectories translate to approximately 6.5 mm/mo of growth for both sexes until reaching mean body size. Males were larger than females in minimum, maximum, and significantly so in mean adult body size (t = -8.62; df = 145; P < 0.001).

***Regenerated Tails.*—**Frequency of tail regeneration varied among different segments of the south Florida population. Evidence of regenerated tails was high in males (63.4%) and females (45.3%), but detected in only 14.1% of juveniles.

DISCUSSION

Most of our findings were similar to those of two other studies of *L. c. armouri* in Florida (Callahan 1982; Meshaka et al. 2004), the exceptions of which seem best explained by differences in sample size. Like Meshaka et al. (2004), we found that testes were larger in May and July than in September and November. The relationship between testicular cycle and day length in southern Florida *L. c. armouri* will presumably play a role as the species disperses northward and with this dispersal face reproductive constraints. From examination of 15 females and inferences from the seasonal appearance of hatchlings, Callahan (1982) thought oviposition occurred during June-July, although enlarged ovarian follicles were found in July. From a sample of 24 females in July, Meshaka et al. (2004) found oviductal eggs in females during May and July but none thereafter. However, like Callahan (1982), Meshaka et al. (2004) found July females that contained yolked follicles. The differences among the three seasons appears best explained by sample sizes of Callahan (1982) and Meshaka et al. (2004) that were less than one third that of our sample size. Nonetheless, these aforementioned studies accurately identified the peak months of the egg-laying season. As in the findings of Callahan (1982), we found a positive relationship between clutch size and body size. Neither Callahan (1982) nor Meshaka et al. (2004) detected evidence of multiple clutch production. It is conceivable that with a four-to-five month egg-laying season, multiple clutches could be produced far enough apart from one another that the simultaneous presence of shelled eggs and enlarged ovarian follicles would be rare. However, our findings point to generally but not exclusively single clutch production in southern Florida. The strong relationship between ovarian cycle and day length in southern Florida *L. c. armouri* will presumably even more so than in males affect the length of the breeding season in northern populations, perhaps limiting clutch frequency if the egg-laying season is sufficiently curtailed.

The 30-60 day incubation period suspected by Callahan (1982) seemed likely at our sites as well, with the possible exception for end-of-the-season clutches. Minimum and mean adult body sizes of males (80 mm SVL and 92.0 mm SVL, respectively) and females (73.0 mm SVL and 87.0 mm SVL, respectively) of Callahan (1982) as well as those of males (81.2 mm SVL and 94.7 mm SVL, respectively) and females (70.2 mm SVL and 82.9 mm SVL, respectively) measured by Meshaka et al. (2004) are similar to our respective findings. Thus, our findings were probably typical for southern Florida *L. c. armouri*.

Our findings place *L. c. armouri* closer to the center between the opposing life history strategies of early maturing, multiple-brooded species and later maturing single-brooded species (Tinkle et al. 1970; Dunham and Miles 1985), whereby it matures quickly but generally produces single large clutches annually. Although comparative reproductive studies of this species in its native range are nonexistent, some comparisons are possible with a few congeneric species.

Leiocephalus psammodromus is an early maturing, multiple-brooded species (Smith and Iverson 1993). Southern Florida *L. c. armouri* (this study) and *L. psammodromus* (Smith and Iverson 1993) are similar with respect to fat body cycles, testicular cycle, egg-laying season, egg dimensions, hatching season, minimum body size at maturity, and adult body sizes. However, *L. c. armouri* differed from *L. psammodromus* in producing a larger clutch size (2 eggs/clutch in *L. psammodromus*) and a single annual clutch (multiple clutch production in *L. psammodromus*), a positive relationship between body size and clutch size (not evident in *L. psammodromus*), and faster age to maturity (1.5-2 yrs in *L. psammodromus*).

Leiocephalus schreibersii in Hispaniola is apparently asynchronous in its egg-laying and lays three-egg clutches (Tom A. Jenssen, pers. comm.). *Leiocephalus semilineatus*, the smallest *Leiocephalus* species, lays smaller clutches (1-2 eggs) of smaller eggs (mean length = 11.0 mm) than *L. c. armouri*, and no relationship exists between female body size and clutch size in *L. semilineatus* (Nelson et al. 2001).

That congeners may not share all reproductive patterns does not conflict with Dunham and Miles' (1985) findings of a strong effect of family and body size to fecundity and age to maturity in lizards. In this regard, they found that within-family patterns are also shaped by such factors as local adaptation and physiological constraints to reproductive characteristics such as clutch size and frequency. Consequently, phylogenetic constraints are apparent in reproductive patterns at the family level and below but not to the exclusion of what can sometimes be difficult-to-separate environmental effects.

We suggest that the life history strategy of *L. c. armouri* in southern Florida, which differs in some respects from its congeners, is a response to a seasonally rich nutrient base in southern Florida that allows for *L. c. armouri* to produce a generally single but larger clutch size than its congeners. In this scenario, the large eggs of *L. c. armouri* are a response by this species whose young are subjected to a wide range of predators. The seasonal abundance of prey for *L. c. armouri* in southern Florida may be all the greater in light of the fact that the species inhabits areas developed to the degree that potential saurian competitors are rare if even present (Smith and Engeman 2004a; Meshaka et al. 2005). In this connection, predation by *L. c. armouri* results in severe negative impacts on population sizes of the exotic Brown Anole (*Anolis sagrei*) in southern Florida (Callahan 1982), a phenomenon that occurs quickly elsewhere following the introduction of *L. carinatus* to small islands inhabited by *A. sagrei* (Schoener et al. 2002). Perhaps, an inflated seasonal abundance of prey during a relatively fixed four or five month egg-laying season may provide the opportunity to produce a larger clutch but generally within too short a time to accommodate a second clutch for the season.

Selection for large eggs as a response to high juvenile predation rates also seems likely in light of the wide range of predators with which it comes in contact in southern Florida. Confirmed predators of *L. c. armouri* in southern Florida include the feral Domestic Cat (*Felis cattus*) (Smith and Engeman 2004a), Little Blue Heron (*Egretta caerulea*) (Smith and Engeman 2004b), Northern Mockingbird (*Mimus polyglottus*) (Smith et al. 2006a), Loggerhead Shrike (*Lanius ludovicianus*) (Smith et al., 2006b), and conspecifics (Dean et al. 2005). Additional southern Florida predators known to eat lizards include the Red-shouldered Hawk (*Buteo lineata*), Broad-winged Hawk (*B. platypterus*), Cattle Egret (*Bubulcis ibis*), Blue Jay (*Cyanocitta cristata*), Racer (*Coluber constrictor*), and Corn Snake (*Elaphe guttata*), (Callahan 1982; Meshaka et al. 2004; this study). Other herons and egrets stalk *L. c. armouri* in southern Florida (Smith and Engeman 2004a) including Yellow-crowned Night-heron (*Nycticorax violaceus*), Great Egret (*Casmerodius albus*), and Cattle Egret (*Bubulcus ibis*) (HTS, pers. obs.). Differential predation rates that focused on juveniles could very well have maintained selection for the single large clutch of large eggs and subsequent rapid growth of young to maturity that we found at our study area (Laurie Vitt, pers. comm.). Underscoring the degree of predation at our site, evidence of regenerated tails was apparent least among juveniles, which suggested to us that juveniles fared poorest in surviving a predation attempt.

What remains to be seen is the degree to which reproductive flexibility, such as multiple clutch production, in *L. c. armouri* is realized among years at our sites and also in extreme southerly locations in its native range with different prey bases and climates. To date, however, general ecological studies of West Indian lizards are rare (Schwartz and Henderson 1991; Rodriguez Schettino 1999) and do not appear to be evident in *L. carinatus*, but the questions surrounding the potential range in reproductive responses in *L. c. armouri* is no less intriguing.

In Florida, this species continues to expand rapidly its geographic range along the coast on its own and through human-mediated dispersal (Meshaka et al. 2005, 2006). Early maturity in southern Florida *L. c. armouri* provides short generation times, which is an advantage to colonizing species (Ehrlich 1989), and occurs in most of the successful exotic species of amphibians and reptiles in Florida (Meshaka et al. 2004; Meshaka 2006). As measured by annual clutch production and compared to other exotic reptiles in Florida, southern Florida *L. c. armouri* was not a highly fecund species, and high fecundity is also a correlate of successful colonization (Baker 1965) that is common to much of Florida's successful exotic herpetofauna (Meshaka et al. 2004). However, a four-to-five month egg-laying season was long enough to provide this species with staggered generations that can buffer the population from disturbances that otherwise negatively impact species with limited seasonal reproduction (Inger and Greenberg 1966). As in the case of the Cuban Treefrog, *Osteopilus septentrionalis*, in Florida (Meshaka 2001), the combination of rapid maturity, a mix of size and age-classes in any given month, and an extended egg-laying season has contributed to the successful colonization of southern Florida *L. c. armouri* by providing founders of new populations or survivors of a catastrophe a short wait until the breeding season. This combination of traits will be an advantage to *L. c. armouri*, as it has to *O. septentrionalis* (Meshaka 2001), in persisting in peripheral areas, which are often subject to density-independent catastrophes (Mayr 1963). In light of the relationship between day length and reproductive cycle, especially in females, notwithstanding its colonizing advantages, *L. c. armouri* would be expected to experience some degree of reproductive constraint as it disperses northward.

This species coexists well with humans, is vagile, and occupies habitat that is similar to that of its native range (Callahan 1982; Meshaka et al. 2004, Smith and Engeman 2004a; Meshaka et al. 2005, 2006b), all of which are positive colonizing traits (Brown 1989; Ehrlich 1989). The traits outlined above, despite relatively low fecundity, contribute to its success in its introduced Florida range and corroborate the increased likelihood of success among species in which these traits are met.

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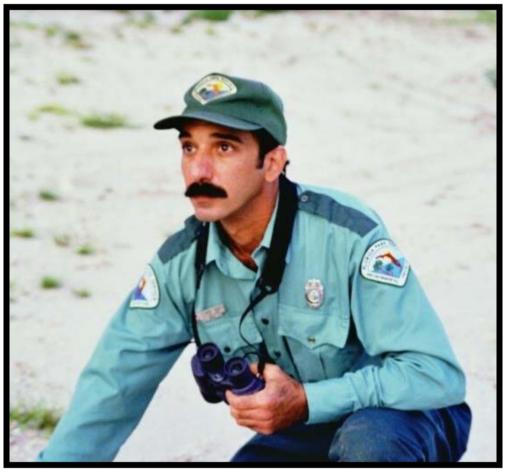

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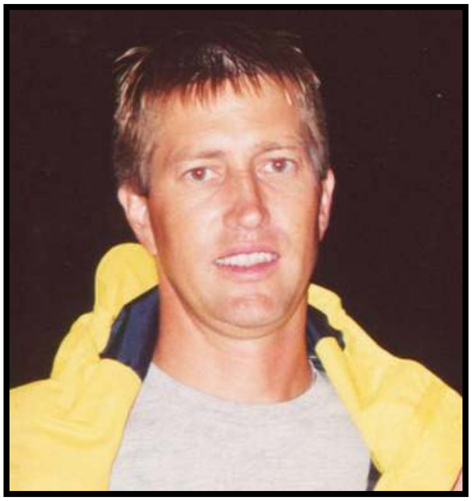

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