



# Relationship between Predation and Maternal Investment in Curly-tailed Lizards

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**Abstract.**—The Northern Curly-tailed Lizard (*Leiocephalus carinatus armouri*) is invasive in Florida, where it has established multiple populations. Like most animals, the species faces various environmental pressures, including predation, which influences reproductive strategies. To test the hypothesis that a correlation exists between predation rates on females and offspring-resource allocation, we examined specimens from 11 populations in Florida, assuming that those with broken tails had encountered a potential predator. To quantify offspring-resource allocation, we used the number of ovarian follicles in each female and the ratio of number to average size of the largest follicles. We predicted that those traits would differ between lizards with and without broken tails. We did not detect the expected correlation, suggesting that predation pressure did not affect the number or size of follicles. Consistent with other lizard species, we did find that larger body size was correlated with a greater number of follicles.

In nearly all animals, environmental pressures like food availability, competition, predation, climate, and disease drive resource-allocation trade-offs, which influence reproduction and survival, especially in females (Caracalas et al. 2021). The environmental conditions a female experiences can result in maternal effects that influence the phenotypes of offspring (Marks et al. 2023). These can manifest as changes in offspring sex ratios, brood size, or hatchling size that can affect the offsprings’ survival or fitness (Marks et al. 2023; Caracalas et al. 2021).

Lizards employ varying reproductive strategies determined by their environments. When fewer resources are available, females might prioritize extending their lifespan and at least temporarily forego reproduction (Marks et al. 2023; Griesser et al. 2017; Caracalas et al. 2021). Alternatively, when fewer food resources are available, females might invest more energy into the size of a few individual eggs to maximize the success of each offspring (Cruz-Elizalde et al. 2023; Marks et al. 2023; Caracalas et al. 2021).

Predation also is a driving force behind reproductive trade-offs. It can force an animal to invest energy into mechanisms that support locomotor capacities, like sprinting (Marks et al. 2023). Energetic investments into foraging and sprinting can force a trade-off in females between optimal anti-predator strategies or allocating more resources to offspring (Marks et al. 2023). Increasing muscle size is especially costly, and it can limit the resources a female can allocate to production of eggs.

Also, the physical burden of a clutch reduces running speed and endurance (Cox et al. 2022).

Caudal autotomy is a predator-evasion tactic that involves self-amputation of the tail and, in some species, subsequent regeneration (Clause and Capaldi 2006; Barr et al. 2021). It allows a lizard to shed its tail when grasped by a predator and diverts the predator’s attention from the more vulnerable body because the amputated tail often is capable of rapid movements, giving the lizard an opportunity to escape (Brown et al. 1995; Clause and Capaldi 2006). However, tail loss can be physically, socially, and energetically costly. Varying among species, lizards’ tails play valuable roles in survival, fighting, locomotion, mate acquisition, and signaling. Additionally, the loss of a tail may result in decreased growth rates, loss of lipid energy reserves, and decreased reproductive capacity (Brown et al. 1995).

The Northern Curly-tailed Lizard (*Leiocephalus carinatus armouri*) employs caudal autotomy and exhibits vertical tail-curling behavior for reasons that include interactions with potential predators. Tail-curling can be used as a pursuit-deterrent to signal to a predator that it has been spotted, or to deflect attention to the tail, which can be autotomized (Cooper 2001; Kircher and Johnson 2017). Because the tail plays a larger role in predator evasion than in many lizards and because female curly-tailed lizards are much less likely to engage in intraspecific aggression than males (Knapp 2001), using broken tails as an indicator of predation pressure in females can be justified.

Native to the Bahamas, *L. carinatus armouri* was first reported in 1940 in Palm Beach County, Florida, and has since expanded its range across the state (Weigl 1969; Thomason et al. 2020). We have a poor understanding of the species' effects on native ecosystems; however, decreased numbers and shifts in microhabitats in Cuban Brown Anoles (*Anolis sagrei*) are evident wherever *L. carinatus armouri* is active (Smith and Engeman 2004), leading to speculation that native lizard populations might also be affected by *L. carinatus armouri*.

In one study, predation of juvenile *L. carinatus armouri* in South Florida was greater than that of adults (Meshaka et al. 2006), causing the authors to suggest that this selects for single clutches of large eggs and rapid growth of hatchlings to maturity. However, juvenile-focused predation also could select for greater numbers of offspring or clutches to increase chances of at least some juveniles surviving.

In this study we asked if maternal investment is related to predation pressure in South Florida populations of Northern Curly-tailed Lizards (*Leiocephalus carinatus armouri*) and sought to identify a trade-off between the energy spent on predator evasion and maternal investment.

### Methods

We collected female *L. carinatus armouri* from 11 populations in South Florida in June and July of 2018–2019. Sites were selected based on previous sightings and from reported locations on EDDmapS (2024), a web-based mapping system for documenting invasive species and pest distribution. We captured lizards using a noose tied to an extendable pole or glue board placed on the ground for about an hour at a time and constantly monitored. Lizards caught on glue boards were removed immediately. Lizards were euthanized and dissected under regulations outlined by the University of Florida Institutional Animal Care and Use Committee (#201709774) and permits issued by the Florida Fish and Wildlife Conservation Commission (EXOT-18-30) and Everglades National Park (EVER-2018-SCI-0036).

For broken tails, which are easily discernable even on regenerated tails, we measured the distance from the cloacal aperture to the break. To measure offspring investment, we examined clutch or brood size, the main variables used to assess reproductive trade-offs in egg-laying species (Griesser et al. 2017). Due to individual variation in ovarian cycles, only a few females had shelled eggs. Instead, as maturing follicles are present in all sexually mature females, we used the size and number of ovarian follicles to estimate potential maternal investment. Because follicles increase in size throughout the ovarian cycle (Meshaka et al. 2006; Silva et al. 2018), we counted and measured the largest size class of follicles in each ovary. For each female, we counted the total number of largest-size follicles and measured their diameters.

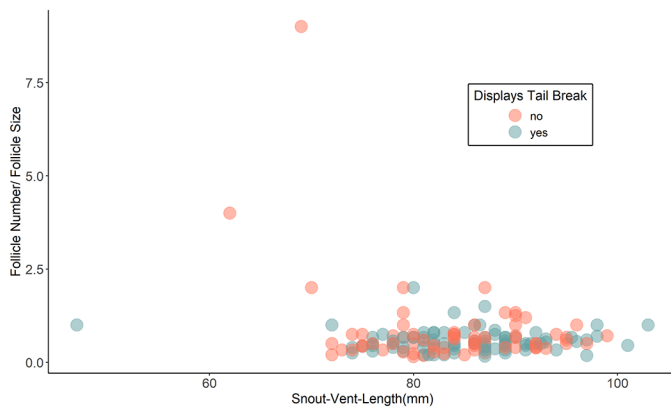
We created a compound variable that was a ratio of follicle number to follicle size to represent relative within-clutch investment. For example, five large follicles averaging 2 mm in diameter would result in a value of 2.5. Considering both numbers and sizes in one variable reduced the bias from the natural changes in the ovarian cycle and is the most informative way of determining whether selection favors numerous small offspring or fewer large offspring. We used Analysis of Variance (ANOVA) to determine if a correlation existed between broken tails and the number and size of follicles to test the predictions that the number and the ratio of number to size of follicles would differ between individuals with and without broken tails. Additionally, because body size could affect the trade-off between survival and reproduction, thus becoming a confounding variable in this study since females with greater body mass could invest in larger follicles, larger clutches, or suffer higher predation rates (Caracalas et al. 2021), we used SVL as a covariate in our ANOVA tests.

### Results

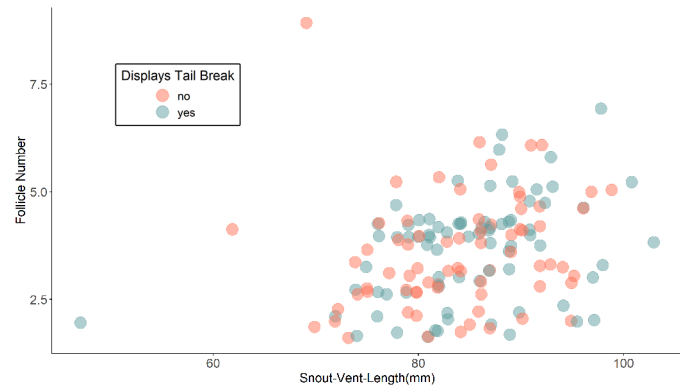
We found no statistically significant interactions between the ratio of follicle number to size and lizards with broken tails ( $F_{1,141} = 0.4198$ ,  $p = 0.5181$ ), between female SVL and number of broken tails ( $F_{1,141} = 0.6500$ ,  $p = 0.4215$ ), or between SVL and the ratio of follicle number to size ( $F_{1,141} = 1.1737$ ,  $p = 0.2805$ ). We did find a positive correlation between the number of largest follicles and SVL ( $F_{1,141} = 16.3670$ ,  $p = 8.56e-05$ ). However, this relationship did not differ between lizards with and without broken tails ( $F_{1,141} = 0.0934$ ,  $p = 0.7604$ ).

### Discussion

Numbers and sizes of follicles did not differ significantly between female lizards that had encountered predators and those that had not (Fig. 1), causing us to reject our hypothesis that predation rate was correlated with maternal investment. However, our methods considered only those lizards that survived encounters with broken tails, which created a survivorship bias. Also, because our data were obtained from preserved specimens (albeit wild-caught), we were unable to evaluate environmental variables (e.g., availability and quality of cover) across collection sites. In addition, because Northern Curly-tailed Lizards can undergo autotomy and regeneration several times in a lifetime (N. Claunch, pers. obs.), we could not determine when and how frequently autotomy occurred in each individual and, consequently, our metric could have underestimated predation pressure. Finally, accidents and intraspecific aggression, although less common among females, also could result in broken tails, which skews our data on predation pressure. Future studies on this subject might benefit by manipulating environmental conditions prior to reproduction and examining eggs and offspring phenotypes



**Figure 1.** In South Florida populations of Northern Curly-tailed Lizards (*Leiocephalus carinatus armouri*), the ratio of follicle number to follicle size in females was constant across individuals of different sizes, and no difference was evident between lizards with and without broken tails.



**Figure 2.** In South Florida populations of Northern Curly-tailed Lizards (*Leiocephalus carinatus armouri*), a positive relationship existed between SVL (mm) and the number of follicles in females, and this was consistent among individuals with and without broken tails.

from different maternal environments under controlled conditions (e.g., Griesser et al. 2017).

In several families of lizards and even in species that range across climactic zones and employ different reproductive strategies, body sizes of mature females and clutch sizes exhibit a linear relationship (Tinkle et al. 1970). Our results indicated that this also is the case for *L. carinatus armouri* in South Florida, in which the number of largest follicles increased with SVL (Fig. 2).

We did not detect a significant correlation between SVL and broken tails, indicating that body size in surviving females did not affect apparent predation pressure. Although Meshaka et al. (2006) observed a high rate of predation on juvenile *L. carinatus armouri* in South Florida, few studies address size-selective predation. Some predators appear to selectively prey on smaller individuals; for instance, Kookaburras (*Dacelo novaeguineae*) feed mainly on subadult Highland Water Skinks (*Eulamprus tympanum*) (Blomberg and Shine 2000). Others, like Small-Eyed Snakes (*Cryptophis nigrescens*), consume large and small skinks in approximately equal numbers (Downes 2002). Selective predation could be attributable to active choice by the predator, differential prey vulnerability, or both (Downes 2002). Assuming that the presence of broken tails is an accurate measure of predation pressure, the lack of a significant correlation between SVL and broken tails suggests that mature females of different sizes are equally vulnerable to predators, at least in South Florida.

Our findings indicated that energy invested by female *L. carinatus armouri* in predator evasion did not result in a decrease in offspring resource allocation. This might be one reason for this invasive species' success in South Florida and could imply that these populations might be resilient to removal tactics should eradication or removal efforts occur. Also, because Northern Curly-tailed Lizard habitat in South Florida has been dramatically altered by human activities,

studies in more natural habitats in their native island range could yield different results.

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### Literature Cited

- Barr, J.I., C.A. Boisvert, and P.W. Bateman. 2021. At what cost? Trade-offs and influences on energetic investment in tail regeneration in lizards following autotomy. *Journal of Developmental Biology* 9: 53. <https://doi.org/10.3390/jdb9040053>.
- Blomberg, S. and R. Shine. 2000. Size-based predation by kookaburras (*Dacelo novaeguineae*) on lizards (*Eulamprus tympanum*: Scincidae): what determines prey vulnerability? *Behavioral Ecology and Sociobiology* 48: 484–489. <https://doi.org/10.1007/s002650000260>.
- Brown, R.M., D.H. Taylor, and D.H. Gist. 1995. Effect of caudal autotomy on locomotor performance of wall lizards (*Podarcis muralis*). *Journal of Herpetology* 29: 98–105. <https://doi.org/10.2307/1565091>.
- Caracalas, H.E., S.S. French, S.B. Hudson, B.M. Kluever, A.C. Webb, D. Eifler, A.J. Lehmicke, and L.M. Aubry. 2021. Reproductive trade-offs in the Colorado checkered whiptail lizard (*Aspidoscelis neotesselatus*): an examination of the relationship between clutch and follicle size. *Evolutionary Ecology* 35: 779–794. <https://doi.org/10.1007/s10682-021-10131-y>.

- Clause, A.R. and E.A. Capaldi. 2006. Caudal autotomy and regeneration in lizards. *Journal of Experimental Zoology Part A: Comparative Experimental Biology* 305: 965–973. <https://doi.org/10.1002/JEZ.A.346>.
- Cooper, W.E. 2001. Multiple roles of tail display by the curly-tailed lizard *Leiocephalus carinatus*: Pursuit deterrent and deflective roles of a social signal. *Ethology* 107: 1137–1149. <https://doi.org/10.1046/j.1439-0310.2001.00754.x>.
- Cox, R.M., T.N. Wittman, and R. Calsbeek. 2022. Reproductive trade-offs and phenotypic selection change with body condition, but not with predation regime, across island lizard populations. *Journal of Evolutionary Biology* 35: 365–378. <https://doi.org/10.1111/JEB.13926>.
- Cruz-Elizalde, R., A. Ramírez-Bautista, A. Lozano, R. Luría-Manzano, X. Hernández-Ibarra, O. Ramos-Flores, A. García-Rosales, and C. Berriozabal-Isas. 2023. Reproductive strategies of a lizard community from an arid environment of Mexico. *Journal of Arid Environments* 208: 104875. <https://doi.org/10.1016/j.jaridenv.2022.104875>.
- Downes, J.S. 2002. Size-dependent predation by snakes: selective foraging or differential prey vulnerability? *Behavioral Ecology* 13: 551–560. <https://doi.org/10.1093/beheco/13.4.551>.
- EDDMapS (Early Detection & Distribution Mapping System). 2024. Northern curly-tailed lizard (*Leiocephalus carinatus armouri*). The University of Georgia Center for Invasive Species and Ecosystem Health, Athens, Georgia, USA. <<https://www.eddmaps.org/distribution/viewmap.cfm?sub=18354>>.
- Griesser, M., G.F. Wagner, S.M. Drobniak, and J. Ekman. 2017. Reproductive trade-offs in a long-lived bird species: condition-dependent reproductive allocation maintains female survival and offspring quality. *Journal of Evolutionary Biology* 30: 782–795. <https://doi.org/10.1111/jeb.13046>.
- Kircher, B.K. and M.A. Johnson. 2017. Why do curly tail lizards (genus *Leiocephalus*) curl their tails? An assessment of displays toward conspecifics and predators. *Ethology* 123: 342–347. <https://doi.org/10.1111/eth.12603>.
- Knapp, C.R. 2001. *Leiocephalus carinatus virescens* (Exuma Islands Curlytail Lizard). Interspecific aggression. *Herpetological Review* 32: 104–105.
- Marks, J.R., M. Sorlin, and S.P. Lailvaux. 2023. The maternal energetic environment affects both egg and offspring phenotypes in green anole lizards (*Anolis carolinensis*). *Ecology and Evolution* 13: e9656. <https://doi.org/10.1002/ECE3.9656>.
- Meshaka, W.E. Jr., H.T. Smith, and C.L. Dean. 2006. Gonadal cycle and growth of a West Indian lizard, the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*), in southern Florida. *Herpetological Conservation and Biology* 1: 109–115.
- Silva, D.D., M. Cassel, M. Mehanna, A. Ferreira, and M.A.H. Dolder. 2018. Follicular development and reproductive characteristics in four species of Brazilian *Tropidurus* lizards. *Zoological Science* 35: 553–563. <https://doi.org/10.2108/zs180030>.
- Smith, H.T. and R.M. Engeman. 2004. A review of the colonization dynamics of the Northern Curly-Tailed Lizard (*Leiocephalus carinatus armouri*) in Florida. *Florida Field Naturalist* 32: 107–113.
- Thomason, S.D., J.M. Broxton, C.M. Romagosa, and N.M. Claunch. 2020. Geographic distribution. *Leiocephalus carinatus* (Northern Curly-tailed Lizard). *Herpetological Review* 51: 272.
- Tinkle, D.W., H.M. Wilbur, and S.G. Tilley. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24: 55–74. <https://doi.org/10.2307/2406714>.
- Weigl, G.L., R.G. Dorney, and W.R. Courtenay. 1969. Survival and range expansion of the Curly-tailed Lizard, *Leiocephalus carinatus armouri*, in Florida. *Copeia* 1969: 841–842. <https://doi.org/10.2307/1441809>.