REPTILES & AMPHIBIANS

Effects of Physical Disturbances on Egg Incubation in the Brown Anole (*Anolis sagrei*): Implications for Embryo Survival during Hurricanes

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Abstract.—Eggs of reptiles that inhabit hurricane-prone regions are often subjected to environmental stressors caused by these storms. Some studies have examined how stress resulting from submersion in water or exposure to salinity affects embryonic development and hatching success, but none have evaluated the effects of physical disturbances associated with strong winds. To demonstrate plausible effects of physical stressors associated with hurricane-force winds, we simulated two situations that are likely experienced by eggs of Brown Anoles (*Anolis sagrei*), which inhabit areas affected by frequent hurricanes. First, we simulated conditions during which eggs are blown or dropped from a standard 3-m height (e.g., like those in arboreal nests); second, we shook eggs to simulate physical disturbances associated with being vigorously blown by strong winds. We then compared hatching success, body size, and running performance of offspring from these treatments to control eggs/hatchings that were not disturbed during incubation. We demonstrated that eggs that were dropped had reduced hatching success compared to both the shaken and control groups, but those shaken did not differ from the control group. Additionally, we found no differences in hatchling body size or performance among treatments. Overall, our study demonstrated some resilience of Brown Anole eggs to major disturbances, which might contribute to the success of this species in highly disturbed habitats throughout its native and invasive ranges.

Reptilian populations that inhabit coastal regions regularly experience hurricanes and tropical storms (Maxwell et al. 2018). Such severe weather events can have detrimental effects at individual and population levels, as well as influence ecological processes (Dalsgaard and Temeles 2024). For example, hurricanes have been shown to reduce population sizes and abundance in the endangered Lesser Antillean Iguana (*Iguana delicatissima*) (van den Burg et al. 2022), and to generate strong selective pressures on morphology in populations of *Anolis* lizards across the Caribbean (Donihue et al. 2020). Impacts of hurricanes on reptilian populations have been attributed to the negative effects of strong winds or tidal surges associated with these storms (Schoener et al. 2001; Lance et al. 2010). Moreover, most research on the impacts of hurricanes has focused on individuals of older age classes (e.g., juveniles and adults), rather than on eggs and embryos that do not have the capacity to escape the effects of these storms. Indeed, effects of water inundation due to hurricanes on egg survival in sea turtle nests are a concern for many of these imperiled species (Dewald and Pike 2013).

Flooding is a primary consequence of tropical storms and has the potential to negatively impact organisms and ecological processes in coastal areas (Michener et al. 1997; Maxwell et al. 2018). Egg survival of coastal reptiles might be particularly vulnerable to the effects of water inundation. For instance, survival of sea turtle eggs is negatively affected by submersion in freshwater or seawater beyond a six-hour duration (Limpus et al. 2020). In contrast, eggs of Brown Anoles (*Anolis sagrei*) can survive submersion in sea water for at least six hours, which has implications for recolonization of island habitats after adults are swept away by hurricanes (Schoener et al. 2001; Losos et al. 2003). Eggs of Eastern Fence Lizards (*Sceloporus undulatus*) also can survive submersion in freshwater for about six hours. This tolerance to submersion could influence gene flow as eggs might be transported long distances by floods or rivers (Heger and Fox 1992). Collectively, these studies indicate that water inundation and physiological tolerances of embryos could have important effects on population demographics and persistence.

While flooding associated with tropical storms has clear implications for hatching success of eggs, comparatively little is known about how strong winds could impact embryonic survival. To address this knowledge gap, we studied Brown Anoles (*Anolis sagrei*), small lizards from Cuba and The Bahamas that

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have become invasive in the southeastern United States and other parts of the world (Goldberg et al. 2002; Kolbe et al. 2004; Norval et al. 2012). Brown Anoles lay single eggs every 7–14 days over a long breeding season that extends from April to October (Lee et al. 1989), with the latter half of the egg-laying season coinciding with the primary hurricane season in the species' native range and in its non-native range in the southeastern United States. Particularly relevant is that Brown Anoles often lay eggs in areas that offer little protection from these weather events. Indeed, eggs of *A. sagrei* often are laid under shallow leaf litter or in debris that accumulates on palm trees at the junction of the trunk with the fronds (Pruett et al. 2020). Several *Anolis* species also are known to occasionally nest in arboreal habitats, such as tree holes (Andrews 1988; Robinson et al. 2014; Delaney et al. 2023). Eggs that are laid in such microhabitats are vulnerable to the effects of strong winds associated with hurricanes, as they can be blown from tall trees or shaken vigorously. To the best of our knowledge, no studies have examined the possible effects of these physical disturbances. Using the Saffir-Simpson scale, tropical storms are categorized as hurricanes when winds exceed 119 kph and can range beyond 251 kph (National Weather Service 2024), and such winds could easily cause the small eggs of anoles (~0.15–0.18 g) to be thrown about regardless of their location in terrestrial or arboreal nest sites.

The primary aim of this study was to quantify the effects of physical stressors that could be induced by hurricane-force winds. We examined how vigorous shaking or sudden jolts associated with strong winds, being swept away by floods, or being dropped from an arboreal nest affect egg hatching success, hatchling body size, and hatchling running performance. We hypothesized that these stressors cause increased egg mortality and/or induce low-quality phenotypes of hatchlings (e.g., small size, reduced locomotor performance).

Methods

A breeding colony of Brown Anoles (N_{males} = 53, $N_{females}$ = 53) collected at Tomoka State Park, Florida, USA, on 3–5 April 2023 (Fig. 1) was transported to Auburn University and male/female pairs were housed in plastic bins (28 l; 46.7 x 31.8 x 29.2 cm). Bins included a mold-resistant carpet, two bamboo perches, artificial plants, and a small pot filled with potting soil as a nesting site for females. Lizards were fed crickets dusted with vitamin and calcium powder twice weekly and watered daily with a spray bottle. Nesting pots in cages were checked three times weekly for eggs between 30 July and 14 August 2023.

All eggs (N = 63) were weighed within 30 minutes of collection and then subjected to one of three treatments (dropped, shaken, or control) within ~48 hours of ovipositioning. Eggs in the drop treatment (N = 21) were placed in a 50-ml Falcon tube and dropped from a height of 3 m into a 22-liter plastic bucket; this treatment was meant to mimic the conditions under which eggs could be thrown around during hurricane conditions and could also simulate being blown from an arboreal nest site. Eggs in the shaken treatment (N = 21) were placed in a 100-ml beaker filled with dry vermiculite then placed on a Fisher Scientific vortex (model number 02215365) at 3,200 rpm over a 4.9-mm diameter and shaken for 30 seconds. This treatment was meant to mimic conditions during which eggs are swept away during floods or undergo conditions that would result in them being jostled for short periods of time. Eggs in the control group (N = 21) were not manipulated. After treatments, all eggs were individually placed in glass jars (59.15 ml) in which they were half-buried in moist vermiculite (water potential = -150 kPa) for incubation; jars were covered in plastic wrap (sealed with a rubber band) to prevent moisture loss. All jars were placed in an incubator set at a constant 28 °C. Eggs were checked daily for hatchlings. Any eggs that were clearly dead (completely deflated) were removed from the incubator and recorded.

Figure 1. Brown Anoles (*Anolis sagrei*) are small lizards native to Cuba and the Bahamas that are invasive in the southeastern United States and other areas around the world. Females like that pictured lay a single egg every 7–14 days over an extended breeding season lasting from April to October. Photograph by Daniel A. Warner.

After hatching, all lizards were measured to the nearest mm for SVL and tail length and to 0.0001 g for mass. All were inspected for deformities before and after measurement, but none were found. To measure running performance on the day of hatching, hatchlings were placed on a 1-m wooden track at a 45° incline with sand grains glued to the track to increase traction. Photo sensors (connected to a stopwatch on a computer) were located every 25 cm that recorded the time that the lizards took to run each 25-cm interval along the length of the track. Each hatchling was subjected to three running trials with a 5–10-minute break between trials. Hatchlings were encouraged to run by gently tapping them with a paint brush. If a hatchling refused to run or climbed out of the track, the trial was marked as a failure and redone after a break. If a lizard had three failed attempts, no further trials were performed for that lizard.

Effects of treatment on egg survival was analyzed using binomial generalized linear models, with egg mass as a covariate. All body-size and performance variables were analyzed with linear mixed models. Locomotor performance was measured as the fastest speed recorded over 25-cm and 100-cm distances; these two distances enabled us to quantify two ecologically meaningful measures of locomotor performance – maximum speed over a short distance (25 cm) and sustained speed over a longer distance (100 cm). Statistical analyses of body size included a covariate of egg mass, and those for locomotor performance included a covariate of SVL. Interactions between egg mass and treatment were initially included but were removed in all models when found to be non-significant. All models were originally fit with a random intercept of maternal identification, but this was excluded if a model without the random effect was a better fit. When assessing model fit using AIC if $\Delta AIC < 2$ we opted to use the simple model. All analyses were performed in R (R Core Team 2022); mixed models were created in the LMER package (Bates et al. 2015), and pairwise comparisons were performed in the emmeans package (Lenth et al. 2018).

Results

When modeling egg survival, the model without the random effect was the best fit model ($\Delta AIC = 1.917$). For hatchling mass, the mixed model with maternal identification as a random intercept was the best fit ($\Delta AIC = 6.2$). The models for SVL, TL, 25-cm sprint speed, and 100-cm sprint speed were best fit without random effects ($\Delta AIC = 0.23$ for SVL, $\Delta AIC = 0.20$ for tail length, $\Delta AIC = 0.0$ for 25-cm sprint, $\Delta AIC = 0.0$ for 100-cm sprint). Eggs that were dropped had substantially reduced survival (23.81%; Table 1; Fig. 2) compared to both the control (61.90%; $p = 0.0154$) and shaken treatments

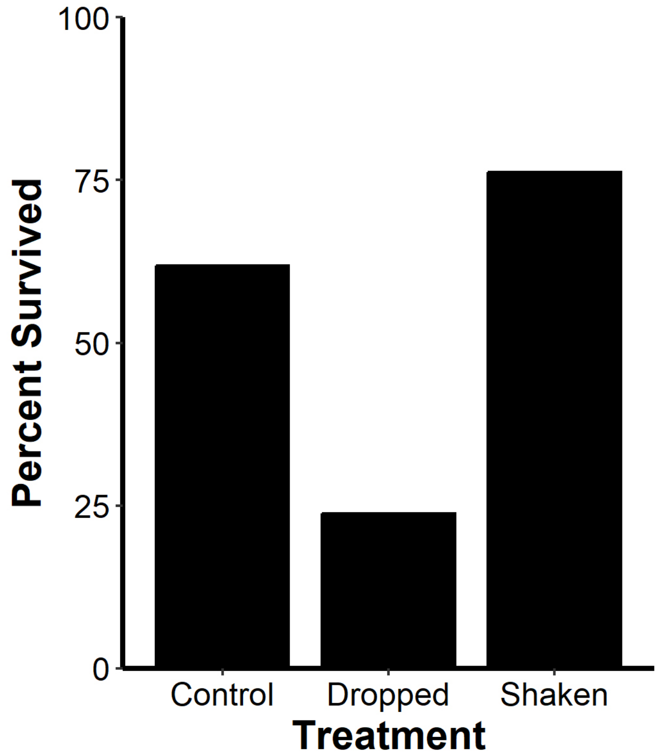

Figure 2. Percent of eggs of Brown Anoles (*Anolis sagrei*) that hatched during each treatment. Sample sizes (N = 21) were the same for each treatment.

Table 1. Effects of treatment and egg mass on egg survival in the Brown Anole (*Anolis sagrei*). All estimates in the model summary are compared to the control as a reference group. Values in bold face are statistically significant.

Independent Variables	Estimate	95% CI	Std. Error	Z-value	P-value
Dropped	-1.7068	1.3741	0.6929	-2.463	**0.0138**
Shaken	0.7016	1.3690	0.6884	1.019	0.3081
Egg Mass	-10.5015	20.2575	10.1345	-1.036	0.3001
Pairwise Probabilities	**Estimate**	**—**	**Std. Error**	**Z-ratio**	**P-value**
Control vs. Dropped	0.392	—	0.142	2.771	**0.0154**
Control vs. Shaken	-0.146	—	0.141	-1.039	0.5520
Dropped vs. Shaken	-0.539	—	0.131	-4.101	**0.0001**

(76.19%; p = 0.0001). Egg survival in the shaken treatment did not differ from the control treatment (p = 0.3081). Egg mass did not affect survival (p = 0.3001). Egg treatment had no effect on hatchling mass, SVL, or tail length (Table 2). Although egg mass predicted hatchling mass (p = 0.0001), it was only marginally related to hatchling SVL (p = 0.0887) and not related to tail length (p = 0.393). Sprint speed of hatchlings did not differ among treatments for the individuals that survived and were measured (Table 2).

Discussion

Hurricanes and tropical storms have sustained winds that often uproot trees and shift soil and ground debris. Consequently, eggs of reptiles that inhabit hurricane-impacted areas are likely affected by these events. Our results demonstrate that Brown Anole eggs and embryos are resilient. However, some types of wind-related disturbances (being dropped) appear to be more important than others (being shaken) in terms of their effect on egg-hatching success.

Dropping eggs negatively affected hatching success. Indeed, the impact of being dropped could cause the vitelline membrane to rupture or the extraembryonic membranes to detach from the eggshell, eventually leading to embryonic death (Rafferty and Reina 2012; Williamson et al. 2017). Although some eggs survived the impact of being dropped (~25%), such effects appear to be more extreme in other reptilian species. Eggs of some species of turtles, for instance, are more sensitive to movement or slight shifts in orientation (Limpus et al. 1979; Parmenter 1980), but this might depend on the developmental stage of the embryo (Limpus et al. 1979; Williamson et al. 2017). One caveat of our drop treatment is that most Brown Anole eggs are laid below the height that we tested (3 m), as many eggs are either on the ground or less than 1 m above the ground (Pruett et al. 2020; Delaney et al. 2023). If this is the case, the force experienced by an egg falling out of a tree is probably less than that of our treatment. However, given the light weight of anole eggs (~0.15 g), hurricane gusts could move eggs at high speeds that could induce similar, if not greater, impact forces than our treatment. Future studies should test this idea by dropping eggs at different heights or launching eggs horizontally at different velocities and measuring the force of impact (simulat-

Table 2. Effects of treatment on hatchling body size and sprint speed in the Brown Anole (*Anolis sagrei*). Models for body size used egg mass as a covariate, and those for sprint speed used snout-vent length (SVL) as a covariate. In all models, the control group is the reference for the estimates. The value in bold face is statistically significant.

	Estimates	95% CI	Std. Error	T-value	P-value
Hatchling Mass (mm)					
Dropped	-0.0101	0.0188	0.009	-1.028	0.3138
Shaken	-0.0086	0.0118	0.006	-1.404	0.1762
Egg mass	0.6173	0.2629	0.138	4.471	**0.0001**
SVL (cm)					
Dropped	0.2392	1.7981	0.880	0.272	0.7877
Shaken	-0.2735	1.2645	0.619	-0.442	0.6619
Egg mass	16.3963	35.4261	9.318	1.760	0.0887
Tail Length (mm)					
Dropped	-0.7306	-3.4640	1.693	-0.431	0.669
Shaken	0.4935	2.4649	1.205	0.410	0.685
Egg mass	16.4263	36.2708	17.734	0.926	0.362
25-cm Sprint (m/sec)					
Dropped	0.0537	0.2984	0.014	0.369	0.715
Shaken	-0.0020	-0.0215	0.011	-0.195	0.847
SVL	0.0024	0.0060	0.002	0.846	0.405
100-cm Sprint (m/sec)					
Dropped	-0.0025	0.0855	0.041	-0.627	0.536
Shaken	0.0072	0.0617	0.031	0.240	0.812
SVL	-0.0025	-0.0172	0.008	-0.305	0.726

ing those induced strong winds) to determine if egg survival varies under such different conditions.

Eggs in our shaken treatment had similar survival compared to those in our control treatment. While the shaken treatment involved vigorous vibrations, this treatment was of short duration and apparently did not result in rupture or detached extraembryonic membranes. Although we have never observed Brown Anole eggs being moved or vibrated by strong winds, this may occur when piles of debris or cover objects where females often lay eggs (Pruett et al. 2020) are disturbed during major storms. Other types of physical disturbances that vibrate or vigorously shake eggs might also occur. Eggs could be shaken when female Brown Anoles occasionally move eggs in their mouths (Delaney et al. 2021) or by ground vibrations associated with human activities (e.g., road traffic; Mhanna et al. 2012) or natural events (e.g., heavy rainfall). Indeed, soil vibrations caused by rainfall can induce emergence of toads from underground refugia (Márquez et al. 2016). While our treatment might not have exactly mimicked environmental vibrations that Brown Anole eggs experience naturally, disturbances similar to our shaken treatment likely occur frequently enough in nature that Brown Anole eggs and embryos have adapted to such conditions, possibly explaining the lack of an effect of vibration on egg survival and hatchling phenotypes. This possibility can be addressed by stimulating the frequency and intensity of natural disturbances to eggs and assessing their effects on development.

Future experiments also should consider the timing of disturbance in relation to embryonic stage. Because anole eggs are laid continuously throughout a long reproductive season (Hall et al. 2020), embryos will vary in stages of development at any given time when a natural disturbance arises. In our study, however, all eggs were subjected to treatments at about the same developmental stage (within 2 days of ovipositioning), and the effects that we observed (or lack thereof) could be very different if the treatments were applied at later stages of development. For instance, in many oviparous reptiles, the embryo is not fused to the inner membrane of the shell immediately after ovipositioning and it could take hours to days before embryonic membranes have attached, particularly in turtles (Ewert 1991; Rafferty et al. 2013). Thus, movement immediately after ovipositioning could have few developmental effects, whereas disturbance during or after attachment could be more detrimental to the embryo (Williamson et al. 2017; but see Aubret et al. 2015). Considering that most squamate embryos are typically attached to the eggshell at ovipositioning (Andrews 2004), the impact from being dropped at this developmental stage could have torn or detached the embryonic membranes of most eggs in our treatment, resulting in mortality. Nevertheless, the development of extraembryonic membranes can vary at different stages of development (Andrews 2004) in ways that could make different embryonic stages more or less sensitive to physical disturbances. Further studies that examine the effects of disturbance across different stages of development are warranted (e.g., Limpus 1979; Aubret et al. 2015; Williamson et al. 2017).

Hatchling morphology and performance was not affected by our treatments. Other studies also have shown few effects of moving or turning eggs in some other squamate taxa (Marcellini and Davis 1982; Aubret et al. 2015), but most have not evaluated potential long-term effects. Indeed, turning eggs of Viperine Watersnakes (*Natrix maura*) did not affect embryonic mortality or offspring morphology and performance, but post-hatch survival over the following three weeks was reduced for hatchlings from eggs that were inverted during incubation (Aubret et al. 2015).

Our treatments involved vigorous movements that might have had longer-term effects that we did not quantify. We could possibly see physiological or neurological effects similar to those of shaken-baby syndrome that can occur in neonatal humans (Lancon et al. 1998). Such effects often lead to development deficiencies, brain damage, or even death during neonatal or juvenile development. In our study, treatments were applied during a time when the brain is developing in *A. sagrei* (e.g., when the mesencephalon is expanding; Sanger et al. 2008); therefore, consequences on cognition, neuromuscular coordination, and behavior are worth examining in future studies.

Experimental work on the effects of tropical storms on *Anolis sagrei* has focused primarily on water inundation during egg incubation (Losos et al. 2003) or population-level consequences at later life stages (Donihue et al. 2020). To our knowledge, this is the first study that examined potential effects of wind-related disturbances on eggs. Although our experimental treatments approximated various effects of wind during a hurricane or tropical storm, more work is needed to quantify the physical impacts that eggs would actually experience during major storms. Our drop treatment negatively affected egg-hatching success; however, we suspect that this will have little effect on populations that inhabit large land areas (e.g., mainlands or large islands), but could lead to negative consequences for populations on small islands where abundances may be relatively low (e.g., Kolbe et al. 2012; Fargevieille et al. 2022). Overall, our findings provide some insights into factors that could affect population establishment and persistence, particularly in this invasive lizard. Many anoles live in small island systems (Kolbe et al. 2012; Reynolds et al. 2019) from which eggs can be transported to nearby islands during hurricanes, which allows for recolonization and gene flow between populations (Schoener et al. 2001; Kolbe et al 2004). Moreover, our field site in Florida consists of chains of small spoil islands that are near the mainland, and high winds from storms likely are responsible for transporting eggs (and juveniles and adults) from island to island. The resilience of eggs and embryos to these wind-related disturbances likely facilitate dispersal and geneflow, which almost certainly contributes to the success of *A. sagrei* in hurricane-impacted areas and to their expansion into non-native areas.

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Literature Cited

Andrews, R.M. 1988. Demographic correlates of variable egg survival for a tropical lizard. *Oecologia* 76: 376-382. https://doi.org/10.1007/BF00377032.

Andrews, R.M. 2004. Patterns of embryonic development, pp. 75–102. In: C.D. Deeming (ed.), *Reptilian Incubation: Environment, Evolution and Behaviour*. Nottingham University Press, Nottingham, UK.

Aubret, F., G. Blanvillain, and J.R. Kok. 2015. Myth busting? Effects of embryo positioning and egg turning on hatching success in the water snake *Natrix maura*. *Scientific Reports* 21: 13385. https://doi.org/10.1038/srep13385.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed effect models using lme4. *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Dalsgaard, B. and E.J. Temeles. 2024. Hurricanes threaten species and alter evolutionary trajectories on tropical islands. *Current Biology* 34: 1115–1120. https://doi.org/10.1016/j.cub.2024.10.011.

Delaney, D.M., R. Brandt, C.M. Beaumont, and D.A. Warner. 2021. *Anolis sagrei* (Brown Anole). Egg-carrying behavior. *Herpetological Review* 52: 643.

Delaney, D.M., S. Tiatragul, and D.A. Warner. 2023. *Anolis sagrei* (Brown Anole). Arboreal nesting. *Herpetological Review*. 54: 464–465.

Dewald, J.R. and D.A. Pike. 2013. Geographical variation in hurricane impacts among sea turtle populations. *Journal of Biogeography* 41: 307–316. https://doi.org/10.1111/jbi.12197.

Donihue, C.M., A.M. Kowaleski, J.B. Losos, A.C. Algar, S. Baeckens, R.W. Buchkowski, A.C. Fabre, H.K. Frank, A.J. Geneva, R.G. Reynolds, J.T. Stroud, J.A. Velasco, J.J. Kolbe, D.L. Mahler, and A. Herrel. 2020. Hurricane effects on Neotropical lizards span geographic and phylogenetic scales. *Proceedings of the National Academy of Sciences of the United States of America* 117: 10429–10434. https://doi.org/10.1073/pnas.2000801117.

Ewert, M.A. 1991. Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds, pp. 173–191. In: D.C. Deeming and M.W.J. Ferguson (eds.), *Egg Incubation. Its Effects on Embryonic Development in Birds and Reptiles.* Cambridge University Press, Cambridge, UK.

Fargevieille, A., A.M. Reed, A.F. Kahrl, T.S. Mitchell, A.M. Durso, D.M. Delaney, P.R. Pearson, R.M. Cox, and D.A. Warner. 2022. Propagule size and sex ratio influence colonisation dynamics after introduction of a non-native lizard. *Journal of Animal Ecology* 91: 845–857. https://doi.org/10.1111/1365-2656.13671.

Goldberg, S.R., F. Kraus, and C.R. Busey. 2002. Reproduction in an introduced population of Brown Anoles, *Anolis sagrei* from O'ahu, Hawai'i. *Pacific Science* 56: 163–168. https://doi.org/10.1353/psc.2002.0014.

Hall, J.M., T.S. Mitchell, C.J. Thawley, J.T. Stroud, and D.A. Warner. 2020. Adaptive seasonal shift towards investment in fewer, larger offspring: Evidence from field and laboratory studies. *Journal of Animal Ecology* 89: 1242–1253. https://doi.org/10.1111/1365-2656.13182.

Heger, N.A., and S.F. Fox. 1992. Viability of lizard (*Sceloporus undulatus*) eggs exposed to simulated flood conditions. *Journal of Herpetology* 26: 338–341. https://doi.org/10.2307/1564892.

Kolbe, J.J., R.E. Glor, L.R. Schettino, A.C. Lara, A. Larson, and J.B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431: 177–181. https://doi.org/10.1038/nature02807.

Kolbe J.J., M. Leal, T.W. Schoener, D.A. Spiller, and J.B. Losos. 2012. Founder effects persist despite adaptive differentiation: a field experiment with lizards. *Science* 335: 1086–1089. https://doi.org/10.1126/science.1209566.

Lance, V.A., R.M. Elsey, G. Butterstein, P.L. Trosclair III, and M. Merchant. 2010. The effects of Hurricane Rite and subsequent drought on alligators in southwest Louisiana. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 313A: 106–113. https://doi.org/10.1002/jez.577.

Lancon, A.J., D.E. Haines, and A.D. Parent. 1998. Anatomy of shaken baby syndrome. *The Anatomical Record* 253: 1–31. https://doi.org/10.1002/(SICI)1097-0185(199802)253:1<13::AID-AR8>3.0.CO;2-F.

Lee, J.C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989: 930–937. https://doi.org/10.2307/1445979.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2018. Package "Emmeans." R Package Version 4.0-3. <http://cran.r-project.org/package=emmeans>.

Limpus, C.J., V. Baker, and J.D. Miller. 1979. Movement induced mortality of loggerhead eggs. *Herpetologica* 35: 335–338.

Limpus, C.J., J.D. Miller, and J.B. Pfaller. 2020. Flooding-induced mortality of loggerhead sea turtle eggs. *Wildlife Research* 48: 142–151. https://doi.org/10.1071/WR20080.

Losos, J.B., T.W. Schoener, and D.A. Spiller. 2003. Effect of immersion in seawater on egg survival in the lizard *Anolis sagrei. Oecologia* 137: 360–362. https://doi.org/10.1007/s00442-003-1363-8.

Marcellini, D.L. and S.W. Davis.1982. Effects of handling on reptile egg hatching. *Herpetological Review* 13: 43–44.

Marquez, R. J.F. Beltran, D. Llusia, M. Penna, and P.M. Narins. 2016. Synthetic rainfall vibrations evoke toad emergences. *Current Biology* 26: R1247–R1271. https://doi.org/10.1016/j.cub.2016.11.005.

Maxwell, S.L., N. Butt, M. Maron, C.A. McAlpine, S. Chapman, A. Ullmann, D.B. Segan, and J.E.M. Watson. 2018. Conservation implications of ecological responses to extreme weather and climate events. *Diversity and Distributions* 25: 613–625. https://doi.org/10.1111/ddi.12878.

Mhanna, M., M. Sadek, and I. Shahrour. 2012. Numerical modeling of traffic-induced ground vibration. *Computers and Geotechnics* 39: 116–123. https://doi.org/10.1016/j.compgeo.2011.07.005.

Michener W.K., E.R. Blood, K.L. Bildstein, M.M. Brinson, and L.R. Gardner. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications* 7: 770–801. https://doi.org/10.2307/2269434.

National Weather Service. 2024. Saffir-Simpson Hurricane Wind Scale. <https://www.weather.gov/hgx/tropical_scale>.

Norval, G., S.R. Goldberg, and J.J. Mao. 2012. The reproductive cycle of the brown anole *Anolis sagrei*, an introduced lizard species in Taiwan. *The Journal of Russian Herpetology* 19: 75–81.

Parmenter, C.J. 1980. Incubation of the eggs of the green sea turtle, *Chelonia mydas*, in Torres Strait, Australia: the effect of movement on hatchability. *Australian Wildlife Research* 7: 487–491. https://doi.org/10.1071/WR9800487.

Pruett, J.E., A. Fargevieille, and D.A. Warner. 2020. Temporal variation in maternal nest choice and its consequences for lizard embryos. *Behavioral Ecology* 31: 902–910. https://doi.org/10.1093/beheco/araa032.

R Core Team. 2022. *R: A Language and Environment of Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.

Rafferty, A.R. and R.D. Reina. 2012. Arrested embryonic development: a review of strategies to delay hatching in egg-laying reptiles. *Proceedings of The Royal Society B* 279: 2299–2308. https://doi.org/10.1098/rspb.2012.0100.

Rafferty A.R., R.G. Evans, F.T. Scheelings, and R.D. Reina. 2013. Limited oxygen availability in utero may constrain the evolution of live birth in reptiles. *American Naturalist* 181: 245–253. https://doi.org/10.1086/668827.

Reynolds, R.G, J.J. Kolbe, R.E. Glor, M. Lopez-Darias, C.V. Pourroy, A.S. Harrison, K. de Queiroz, L.J. Revell, and J.B. Losos. 2019. Phylogeographic and phenotypic outcomes of brown anole colonization across the Caribbean provide insight into the beginning stages of an adaptive radiation. *Journal of Evolutionary Biology* 33: 468–494. https://doi.org/10.1111/jeb.13581.

Robinson, C.D., B.K. Kircher, and M.A. Johnson. 2014. Communal nesting in the Cuban Twig Anole (*Anolis angusticeps*) from South Bimini, Bahamas. *Reptiles & Amphibians* 21: 71–72. https://doi.org/10.17161/randa.v21i2.13993.

Sanger, T.J., J.B. Losos, and J.J. Gibson-Brown. 2008. A developmental staging series for the lizard genus *Anolis*: A new system for the integration of evolution, development, and ecology. *Journal of Morphology* 269: 129–137. https://doi.org/10.1002/jmor.10563.

Schoener, T.W., D.A. Spiller, and J.B. Losos. 2001. Natural restoration of the species-area relation for a lizard after a hurricane. *Science* 294: 1525–1528. https://doi.org/10.1126/science.1064396.

van den Burg, M.P., H. Madden, T.P. Wagensveld, and E. Boman. 2022. Hurricane-associated population decrease in a critically endangered long-lived reptile. *Biotropica* 54: 708–720. https://doi.org/10.1111/btp.13087.

Williamson, S.A., R.G. Evans, and R.D. Reina. 2017. When is embryonic arrest broken in turtle eggs? *Physiological and Biochemical Zoology* 90: 523–532. https://doi.org/10.1086/692630.