Oecologia (2003) 137:360–362
DOI 10.1007/s00442-003-1363-8

POPULATION ECOLOGY

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Effect of immersion in seawater on egg survival in the lizard *Anolis sagrei*

Received: 22 April 2003 / Accepted: 11 July 2003 / Published online: 9 August 2003

Abstract Studies on the lizard, *Anolis sagrei*, revealed that after Hurricane Floyd devastated the Bahamas in 1999, some populations consisted only of hatchlings. Because the storm surge of the hurricane completely inundated these islands, apparently for up to 6 h, survival of anole eggs in salt water for such periods is implied. To test this hypothesis directly, we placed *A. sagrei* eggs in saltwater for 3 or 6 h with unimmersed eggs serving as the control. Hatching success and incubation time did not differ among the three treatments. These findings help explain the persistence of anole populations on small islands vulnerable to hurricanes.

Keywords *Anolis* · Catastrophe · Egg · Extinction · Hurricane

Introduction

Although most studies of island biogeography focus on the attributes of free-living individuals, the adaptations of eggs may play an important role in determining the geographic distribution of a species. The colonization of isolated oceanic islands has long been of interest to biologists (e.g. Darlington 1957; Carlquist 1974). Most attention has been focused on the mechanisms, both active and passive, that permit adults and juveniles to survive long voyages across hostile seas, but colonization may also occur by means of eggs that survive an oceanic crossing and hatch, either en route or after arrival, to produce the founders of new populations. In a similar vein, populations on small and low-lying oceanic islands may periodically endure flooding during catastrophic hurricanes and other natural events. One factor that may affect the ability of a population to withstand such events is the extent to which eggs survive immersion in saltwater.

These issues were highlighted by studies on the effects of a recent catastrophic hurricane in the Bahamas. Hurricane Floyd, a class IV hurricane with sustained winds up to 250 km/h, passed over a set of small study islands near Abaco, Bahamas, in September 1999. The storm surge was approximately 3 m and many islands were completely submerged for periods estimated by locals as up to 6 h (Schoener et al. 2001a, 2001b). Lizards became completely extinct on some islands, but a substantial number of other islands whose maximum altitude was below the height of the storm surge had lizards present ~2 months after the hurricane (when we were first able to resurvey the islands). Intriguingly, all lizards found on the islands were of an age implying that they hatched after the hurricane. Thus, the hurricane apparently drowned or otherwise removed all lizards not in the egg stage, leaving behind a cohort of very young individuals as the islands' only inhabitants. While post-hurricane immigration of lizards was also involved, the ability of these populations to avoid extinction—and, for many of the islands for which abundance was measured, to return to pre-hurricane population levels—seems to have been partly the result of eggs that managed to survive the hurricane.

This suggests that *Anolis* eggs can survive immersion in saltwater for a substantial period of time. Despite three decades of research on the ecology of anoles, including a fairly extensive literature on anole egg biology (e.g., Sexton et al. 1979; Andrews and Sexton 1981; Andrews 1988), this hypothesis has never previously been tested.

Materials and methods

Gravid females of *A. sagrei* were obtained from Fort Myers, Fla. Eggs were placed in vermiculite mixed with water (1:1 ratio by mass) and incubated in Petri dishes placed in an incubator at 30°C.

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Eggs were immersed in saltwater early in development (within 10 days of being laid, which is approximately the first trimester of development). Saltwater was made using a saltwater aquarium mixture (Coralife Salt) that produced water with a specific gravity of 1.020. On the day of treatment, eggs of similar age were divided into groups of three. Within each group, eggs were randomly assigned to one of three treatments: control, 3 h immersion, or 6 h immersion. In some cases, only two eggs of similar age were available, in which case one treatment was randomly eliminated. In the immersion treatments, the vermiculite in the petri dish was saturated with saltwater such that the eggs were completely immersed. At the end of the treatment period, the eggs were moved to a new dish with fresh vermiculite. Control eggs were not immersed in saltwater but were also moved to new dishes.

Results

No difference existed in hatching success among the three treatments (Fig. 1; χ^2=0.99, 2 *df*, *P*=0.61; hatching success was: control 13/16; 3 h treatment 12/14; 6 h treatment14/15). Time to hatching was not significantly different among treatments (Fig. 2; analysis of variance on ln-transformed number of days: $F_{2,35}$=0.79, *P*=0.46; control: 25.8±1.1 (SD) days; 3 h treatment: 25.8±0.9 days; 6 h treatment: 26.2±0.7 days).

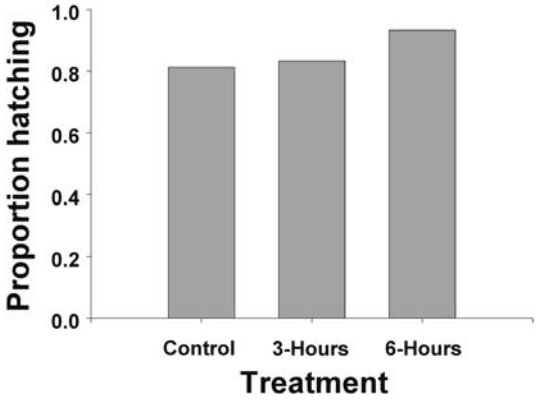

Fig. 1 Hatching success (proportion of eggs hatching) in the three saltwater immersion treatments: control (no immersion), 3 h immersion, and 6 h immersion

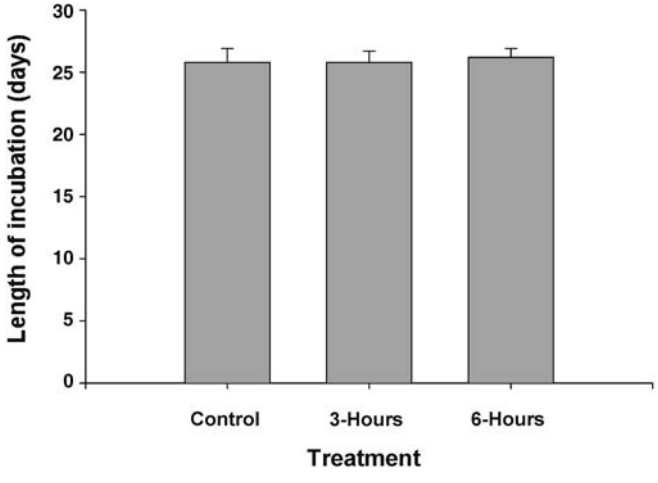

Fig. 2 Incubation time for eggs that hatched from the three saltwater immersion treatments: control, 3 h, and 6 h immersion. Error bars are one SD

Discussion

Our results indicate that immersion in saltwater for up to 6 h has no effect on young eggs. These results may explain how populations survived extinction after Hurricane Floyd, even though all lizards living on the islands were drowned or washed away. High water levels in this hurricane probably lasted no more than 6 h; hence, the hatchling lizards observed on the islands ~2 months later were probably the result of eggs laid on the islands that survived the hurricane (Schoener et al. 2001a, 2001b).

An alternative explanation for the post-hurricane presence of hatchling lizards on islands is that eggs were deposited on the islands by the hurricanes. However, this possibility is discounted by the findings that, 2 months after the hurricane, hatchling lizards were found only on islands that had had lizards before the hurricane, and that all surveyed islands with no lizards before the hurricane had none 2 months afterward (Schoener et al. 2001b). Hence, survival of eggs in situ is the most likely explanation for the presence of hatchling lizards on these islands.

Our results are in general agreement with several previous studies on other species of lizards. Gardner (1985) examined the effect of immersion in saltwater on eggs of the gecko *Phelsuma sundbergi* and found no effect. Brown and Alcala (1957) also found little effect on eggs of several other gecko species. Geckoes, however, have hard, calcareous eggshells, in contrast to the thinner and more flexible parchment-like eggs of anoles and most other squamates. Brown and Alcala also looked at the eggs of a skink, *Dasia smaragdina*, and found that their leathery eggs were greatly affected by immersion in saltwater. Finally, Heger and Fox (1992) examined the effect of immersion in freshwater on the parchment-like eggs of the iguanid lizard *Sceloporus undulatus* and found no effect.

Our finding that eggs can survive immersion in seawater raises questions about why population survival was higher after Hurricane Floyd than after Hurricane Lili 3 years earlier. In October 1996, Hurricane Lili, a class III hurricane with sustained wind speeds of about 185 km/h, passed directly over the island of Great Exuma, where a study of the population and food-web biology of two species of *Anolis* lizards had been ongoing for 3 years (Spiller et al. 1998). All nine populations on small, low-lying islands to the west of Great Exuma were exterminated. By contrast, none of the six populations on comparable islands east of Great Exuma went extinct, although the average reduction in population size there immediately after the hurricane was 34% (these islands were surveyed within days of the hurricane and populations were composed primarily of adult lizards, thus

indicating that egg survival was not responsible for population survival). The key difference between the two sets of islands was exposure to the storm surge: islands to the west bore the full brunt of the surge, which was ~5 m high, completely inundating the study islands. By contrast, eastern islands to the lee of Great Exuma were sheltered from the surge and were only peripherally flooded.

Why did eggs survive in Abaco after Hurricane Floyd, but not on the islands on the west side of Exuma after Hurricane Lili? We propose two possibilities. First, the study islands at Abaco were in a sheltered "creek" area, whereas the islands to the west of Great Exuma were in open ocean. Consequently, although both sets of islands were inundated by the storm surge, the manner in which the storm surge hit the islands was probably quite different. At the exposed Exuma site, the surge hit with great force, whereas at Abaco, the high water covered the island more gently. The fact that the vegetation on the Exumas was largely obliterated, whereas vegetation at Abaco lost many fewer branches, supports this scenario. As a result, it is possible that the force of the surge in the Exumas stripped all eggs from the island, along with the vegetation and free-living lizards. By contrast, eggs in Abaco may not have been dislodged, and thus remained to hatch, while the already-hatched lizards inexorably drowned as they were floated away.

Alternatively, it is possible that there were many fewer, or even no, eggs present in the Exuma islands when the hurricane hit. Hurricane Lili was 5 weeks later in the year than Hurricane Floyd. Extensive studies in Florida and the few Bahamian data suggest that the reproductive cycle is winding down by October (Licht and Gorman 1970; Lee et al. 1989). Consequently, the reproductive season had probably already ended in the Exumas by the time Lili struck, so that there were no eggs remaining to found a new cohort.

Furthermore, even if a few eggs remained, it is possible that they would be further along in the incubation period and thus more vulnerable to immersion in saltwater. Eggs early in incubation require little oxygen (reviewed in Packard and Packard 1988; Heger and Fox 1992), but older eggs have higher oxygen demands and thus would be more vulnerable to asphyxiation. Indeed, Gardner (1985) found that older gecko eggs were greatly affected by immersion, even when younger eggs survived unscathed. We did not have enough eggs to test this hypothesis, but preliminary results suggested that the same result may occur in *A. sagrei*: of six old eggs (16–22 days post-laying) immersed in saltwater for 6 h, three eggs failed to hatch, and two others (the oldest two eggs) hatched while immersed in saltwater [cf. Warkentin et al. (2001) on the phenomenon of premature hatching in response to stress in frog eggs]; only one egg, the youngest (16 days), produced a hatchling post-submergence. Thus, it is possible that even if a few eggs were still present in the Exumas at the time Lili hit, they may have been further along in development and thus not survived inundation. Further work is needed to examine whether the effect of immersion in saltwater varies with age in *Anolis* eggs.

Our results thus confirm that anole eggs, at least early in the incubation period, can withstand immersion in saltwater, thus providing a mechanism by which populations may survive catastrophic hurricanes even when all free-living individuals are exterminated. An interesting hypothesis suggested by this finding is that the effect of a catastrophic disturbance may be critically dependent upon when it occurs. The hurricane season in the Caribbean generally runs from June through November. Our observations suggest that storms late in the season may have more catastrophic effects on anole populations because there may be no bank of eggs available to reseed populations.

Acknowledgements J. Diani, C. Deggendorf, D. Piatchek, T. Witsberg and M. Leal for assistance in caring for lizards; R. Andrews, S. Echternacht, K. Warkentin and two anonymous reviewers for advice and discussion; and NSF (DEB-9903587 and DEB-9904121) for support.

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