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Experiments on dispersal: Short-term floatation of insular anoles, with a review of similar abilities in other terrestrial animals

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Summary. The floatation ability of a common Carribean insular lizard, *Anolis sagrei*, was tested under controlled conditions in a laboratory seawater wave tank. Short-term passive floatation abilities are extensive: all 39 animals survived 1 h, and 30% of those tested were still afloat by 24 h.

The survival times for anoles in seawater are much greater than those reported in the literature for the 19 species of small mammals tested in freshwater; only medium-sized mammals have comparable abilities. Floatation, unaided by rafts, is a likely means of dispersal for anoles and perhaps other lizards between nearby islands such as in the Bahamas. The literature on observed overwater dispersal distances in non-volant animals is tabulated; data are rather scarce.

Introduction

"Lizards are disproportionately numerous on islands and this is proof that they have unusual powers of crossing salt water, but other factors are probably involved too" (Darlington 1957). Although pointing out that data concerning tolerances of many taxa to seawater are noticeably lacking and certainly worth investigating, Darlington asserted that "simple experiments to this end will not be final." Whether or not taxa have crossed seawater is "more likely to be shown by their distributions than by anything that can be learned in the laboratory."

As these quotations from Darlington exemplify, mechanisms of over-water transport for non-volant terrestrial animals have continually aroused curiosity. Transport by wind for arthropods is well-established (e.g., Gressitt and Nakata 1958; Carlquist 1974) and is even occasionally observed for frogs and earthworms (McAtee 1917). That organisms disperse by logs, floating debris or island fragments has many proponents (e.g., Darlington 1938; Gibbons and Coker 1978; Myers 1953; Visher 1925; Williams 1969) but few field records (Table 1; see also Ball and Glucksman 1975; King 1962). Some actively swimming lizards and mammals have been observed in both fresh and salt water (Table 1). But as Table 1 summarizes, dispersal records for rafting or floating animals are quite rare.

Passive floatation in seawater, while well-studied in plants, (Carlquist 1974; Darwin 1859; Edmondson 1941; Fridriksson 1975; Mason 1961; Rabinowitz 1978; Stephens 1958; Whitaker and Carter 1954), has seldom been investigated experimentally as a dispersal mechanism for animals. Brown and Alcala (1957) showed that eggs from 3 of the 4 species of gekkonid lizards tested survived at least 11 days' exposure to seawater. Darwin (1859) reported that *Helix* land snails possessing an intact operculum could withstand 3 weeks in seawater; 25% of 100 land snails belonging to 10 species survived 2 weeks submergence at sea. Simberloff and Wilson (1969) recorded floatation observations on several arthropod species (Table 1), as well as mentioning that many of the mangrove-island colonists remained afloat almost indefinitely in seawater. No other experiments are known to us which investigate passive transport in seawater among terrestrial animals. A large number of experiments on swimming ability in mammals have been performed in freshwater, however (see below).

This paper reports experiments on the passive floatation abilities of a widespread insular lizard, *Anolis sagrei*, from the Bahamas Islands. The experiments were performed in a laboratory wave tank. While they may not provide final answers *sensu* Darlington, they do at least offer documentation of a possible means of dispersal not adequately considered before.

Materials and methods

A rectangular plastic wave tank (2 m × 0.6 m × 0.6 m) was partially filled with continuously filtered seawater (29.5‰) maintained at *c* 25° C by a submersion heater. Water temperatures in this range ($\bar{x}=24.7$, $s=0.36$ (°C), $N=13$) were recorded day and night during Spring 1979 in shallow water on the Great Bahama Bank near Staniel Cay, Exumas, roughly the geometric center of the range of Bahamian *A. sagrei*. These temperatures are intermediate between winter and summer extremes for these shallow waters. Sea temperatures slightly lower are given by Storr (1964) and Turekian (1957) for deeper Bahamian waters.

Wave amplitude and frequency were adjusted to generate gentle waves of 1.5 cm in height and 49 cm in length at the middle of the tank and waves smaller and more frequent at either end. These waves represent moderately choppy conditions on banks near (10^2–10^3 m) Bahamian islands – conditions during hurricanes could of course be more extreme. The side of the wave tank acts as a reflector, bouncing waves back to their origin, a phenomenon which would not occur in open-ocean conditions and which made

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Table 1. Recorded natural dispersal of terrestrial animals via fresh or salt water

Taxon	Species	Distance	Transport mechanism	Source
Mammals				
Mice, voles and lemmings:				
	Microtus pennsylvanicus	up to 1 km	swimming	Crowell (1973)
	M. pennsylvanicus	18.4 m	swimming	Murie (1960)
	M. californicus	up to 12.2 m	swimming	Fisler (1961)
	Peromyscus leucopus	8–233 m	swimming	Sheppe (1965); Teeters (1945)
	P. maniculatus	3.1 m	swimming	Orr (1933)
	Lemmus lemmus	450–*c*1000 m	swimming	Myllymäki et al. (1962)
Squirrels:	*Tamiasciurus hudsonicus*	6 km	swimming-floating	Hatt et al. (1948); see also Schorger (1949)
	Spermophilus richardsonii	31.7 m	swimming	Fredrickson (1972)
	Sciurus niger	15.3 m	swimming	Applegate and McCord (1974)
Deer:	*Odocoileus virginianus*	1.2–4 km	swimming	R. Huey (personal communication)
Pigs		8–96 km	swimming	Wallace (1881)
Rabbits:	*Lepus californicus*	62–144 km	kelp raft	Prescott (1959)
Weasels:	*Mustela frenata*	12.2 m	swimming	Davis (1942)
Elephants		*c*9.6–48 km	swimming	Johnson (1980)
Reptiles				
Lizards:	*Sauromalus obesus*	16.7 m	floating-swimming	R. Huey (personal communication)
	Ameiva quadrilineata	3 m	swimming	Hirth (1963)
	Iguana iguana	20–200 m	swimming-floating	Fitch et al. (1971)
	Basiliscus vittatus	3 m	swimming	Hirth (1963)
Snakes:	*Crotalus adamanteus*	3.2–43.2 km	hyacinth raft	Clench (1925)
Amphibians				
Frogs:	*Bufo boreas*	1.6 km	swimming	J. Quinn (personal communication)
Insects				
Ants:	*Solenopsis invicta*	*c*1.6 km	floating	Morrill (1974 and personal communication)
	Pheidole peregrina	a few kms	driftwood raft	Wheeler (1916)
Grasshoppers		3–4 m	treading water	personal observation
Crickets:	*Cyrtoxipha*	2 m	floating	Simberloff and Wilson (1969)
Caterpillars:	*Automeris io*	8 m	floating	Simberloff and Wilson (1969)
Earwigs:	*Labidura riparia*	–	swimming	Simberloff and Wilson (1969)

the tank water choppier on one side. Subjects spent most time in the less choppy areas.

Adult *A. sagrei* collected on May 6, 1979 (and two individuals collected several years earlier), from Marsh Harbour, Great Abaco, Bahamas, were kept alive in large cages in a warm-temperature control room, where they were exposed to natural day-night cycles and fed small insects. Subjects were randomly selected for tests, except that no individual was tested more than 3 times, and all tests for the same individual were spaced at least a month apart. For identification, individuals were permanently marked by toe-clipping. Tests were mostly conducted spring and summer of 1979. A few animals were collected in 1980 from the same locality and tested in summer, 1980. After removal from cages, each animal was measured and allowed to adjust to test-room conditions for *c* one-half hour, then placed on a floating petri dish from which it was induced to enter the water. Before an individual lizard was selected, we designated a period of time during which the animal was to be floated. Four period lengths were used: Group 1 was tested for 1 h, Group 2 for 6 h, Group 3 for 12 h and Group 4 for 24 h. Subjects could not voluntarily emerge from the water since convex plexiglass framed the waterline; if this was kept moist it could not be scaled. After initial attempts to escape, subjects generally gave up and, even if the tank water was stilled, did not make further attempts to climb out. Animals were initially observed at relatively long intervals, but after noting 2 deaths whose timing could not be precisely ascertained, continuous monitoring of subjects for up to 6 h, and sometimes longer, was instituted. If animals completed the prescribed floatation period, they were recorded as "successful;" if subjects showed signs of stress, wave conditions were reduced to zero, and if they survived the duration of the test time in stilled seawater, their abilities were listed as "questionable;" observations of near drowning, or drowning, were recorded as "failures."

Results

Table 2 gives the duration of lizard floating times. These data are combined to produce a summary graph (Fig. 1), as follows. Each animal successfully completing a given period (1, 6, 12 and 24 h) was counted, and this total was divided by the total number of animals tested for at least that period of time (we arbitrarily counted the 4 "questionable" cases as successes [asterisks in Table 1]). Of the 39 test animals, all completed the 1 h test period, and the rate of success decreased linearly for increasing times of floatation. Eighty-four percent were able to float successfully for 6 h, while only 63% could complete a 12 h floatation. Still fewer, 30%, managed to complete a 24 h floatation successfully. Females were slightly less successful than males, but the difference was not significant (in separate χ^2-tests) for any test period. For a given test period, no relation of body size to duration of floating was apparent; size, however, varied little among the test animals (Table 2).

Table 2. Floatation observations on *Anolis sagrei*

Males						Females					
Snout-vent length (mm)	Subject number	Water temp C (°)	Test time (h)	Float time (h)	Date	Snout-vent length (mm)	Subject number	Water temp C (°)	Test time (h)	Float time (h)	Date
47.0	1	23.5	1	1	5-16-79	39.5	1	24.0	1	1	5-17-79
49.0	2	23.8	1	1	7-05-79	40.0	2	24.0	1	1	5-18-79
47.0	3	24.0	1	1	5-17-79	37.0	3	24.0	1	1	5-21-79
47.0	4	24.0	1	1	5-21-79	39.5	1	24.5	6	6	8-06-79
51.5	5	24.0	1	1	5-23-79	37.0	3	25.0	6	6	7-03-79
47.0	1	25.5	6	3[b]	7-05-79	35.0	4	24.0	6	6[a]	5-30-79
46.0	6	24.5	6	6[a]	5-29-79	42.0	5	24.0	6	6	6-01-79
49.0	7	24.0	6	6	5-31-79	39.5	7	24.0	6	6	6-08-79
adult	12	20.5	6	6	1-24-78	36.0	8	24.0	6	6	8-14-79
49.0	7	23.8–26.0	12	12[a]	8-07-79	36.0[c]	10	25.0	6	1[a, b]	8-20-79
46.0	9	23.2–25.0	12	12	8-10-79	38.0	9	25.8	12	12	8-15-79
43.0	11	25.0	12	12	8-16-79	37.0[d]	12	25.0	12	6[b]	9-05-79
47.5	14	24.5	12	6[b]	10-31-79	38.5	13	25.0	12	4[b]	9-06-79
47.0	15	25.5	12	12	11-19-79	37.0	14	23.8	12	12	10-22-79
51.0	8	25.0	24	24[a]	6-27-79	36.0	15	25.0	12	12	11-26-79
49.5	10	25.0	24	6[b]	8-13-79	37.0	3	25.0	24	$2\frac{1}{2}$[b]	2-07-80
50.0	13	24.5	24	9[b]	10-23-79	34.0	6	25.0	24	1[b]	7-02-79
45.0	16	24.3	24	24	8-18-80	36.5	11	25.0	24	$10\frac{1}{2}$[b]	8-21-79
						42.0	16	25.0	24	6[b]	8-25-80
						adult	17	25.0	24	6[b]	8-25-80
						36.0	18	25.0	24	24	8-26-80

[a] Indicates that wave conditions were changed to still from original setting
[b] Indicates that the test animal subsequently drowned or was close to drowning
[c] Indicates female with 2 eggs
[d] Indicates animal with broken jaw

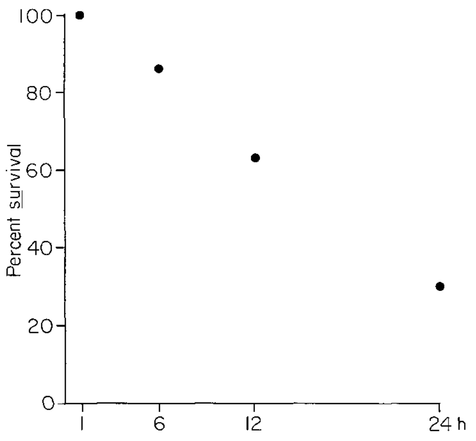

Fig. 1. Floatation success of *Anolis sagrei* exposed to seawater for various lengths of time. $N=39$ (1 h), $N=31$ (6 h), $N=16$ (12 h), $N=10$ (24 h). $R^2=0.997$

Lizards generally floated with forelegs vertical but with the remainder of the body floating horizontally on the water surface. The head was held well out of water. A female with twice the normal complement of eggs temporarily floated on one side (1 h) with her hindleg held up like a sail: later she floated on her back with all legs in the air and nearly drowned.

Discussion

The question of dispersal of terrestrial lizards between islands has never been addressed experimentally. The paradigmatic view of such dispersal is that it occurs via rafting, with the consensus being that "any colonizer making one of the long raft voyages across an ocean will arrive in a very unfavorable physiological condition on an inhospitable shore" (Williams 1969). Because seawater, along with exposure to sun, is viewed as a major desiccating factor, this opinion is understandable, although some species of Puerto Rican anoles have a high tolerance of salt water (Heatwole and Levins 1973). If seawater is the transport medium directly, the possibilities of desiccation on such a voyage could be greatly reduced, especially if the body is impermeable to water. The same might apply were the voyage made during heavy rains associated with hurricanes, a factor which might also lessen potential predation (Visher 1925). We feel the evidence provided here strongly supports the possibility of free-floating transport in seawater as an alternative to rafting for a common insular lizard.

For certain taxa, species successfully invading islands appear to belong to marginal mainland habitats; e.g., open forest or savanna for anoles (Williams 1969), and lowland forest, grassland and littoral environments for ants (Wilson 1959). Suggesting the importance of proximity to dispersal sites for plants, Carlquist (1966) notes that "although dispersal by seawater floatation has contributed little to montane floras of islands, one must remember that some plants for which seawater dispersal may seem unlikely are, in fact, capable of it." Comparison of characteristics of successfully colonizing ant species shows that they do not possess peculiar modes of dispersal or nest-site preferences that could account for their current expansions. Wilson (1961) suggests that their vagility may just be a result of proximity to launching sites. Similarly, among anoles expanding spe-

Table 3. Experiments on swimming and floating ability in terrestrial vertebrates

Taxon		Minimum (s)	Maximum (s)	Mean (s)	*N*	Reference
1. Kangaroo mice	*Microdipodops megacephalus*	14	$>7{,}200$	337[a]	18	Hafner and Hafner (1975)
	M. pallidus	20	435	88.1	10	
2. Rodents	*Peromyscus leucopus*	102	210	144	10	Getz (1967)
	Clethrionomys gapperi	66	380	207	10	
	Microtus ochrogaster	162	275	226	10	
	M. pennsylvanicus	86	277	172	10	
3. Lemmings	*Lemmus lemmus*[b]	900	1,410	1,095	4	Myllymäki et al. (1962)
4. Pocket mice	*Perognathus apache*	38	116	79.1	21	Schmidly and Packard (1967)
	P. merriami	56	158	94.0	22	
	P. flavescens	50	165	115	17	
	P. flavus	90	182	127	18	
5. Pocket gophers	*Geomys bursarius* (shallow)	?	885	362	24	Best and Hart (1976)
	Geomys bursarius (deep)	?	?	106	4	
	G. pinetis (shallow)	530	735	633	2	
	Pappogeomys castanops (shallow)	–	–	130	1	
6. Pocket gophers	*Geomys bursarius*	*c*160	*c*160	160	2	Kennerly (1963)
7. Pocket gophers	*Geomys bursarius*	50	219	133	55	Hickman (1977)
		8	190	51	58	
		18	903	241	64	
8. Mole rats	*Cryptomys hottentotus*	45	845	364	8[c]	Hickman (1978)
9. Mole rats	*Spalax ehrenbergi*	*c*0	>100	28	251	Hickman et al. (1983)
10. Mole rats	*Tachyoryctes splendens*	115	550	321	15	Hickman (1983)
11. Moles	*Scapanus latimanus*	–	–	360	1	Reed and Riney (1943)
12. Larger mammals	*Marmota monax*	4,320	1.47×10^5	4.23×10^4	5	Wilber and Weidenbacher (1961)
	Tamias striatus	360	480	420	2	
	Mephitis mephitis	2.60×10^4	2.78×10^4	2.67×10^4	2	
	Didelphis marsupialis	1.26×10^4	2.88×10^4	2.24×10^4	3	
13. Lizards	*Anolis sagrei*[d]	3,600	8.78×10^4	2.57×10^4	39	This study

[a] Geometric mean
[b] Field study, water slightly saline
[c] First trial only
[d] Salt water; mean is minimal, as many trials were not taken to failure

cies never include deep-shade, rain-forest or montane forms, places on mainlands from which rafts are rarely launched (Williams 1969). *A. sagrei* prefers low vegetation (Schoener and Schoener 1983a) so is especially common along shorelines; indeed we have occasionally noticed it foraging in the intertidal. Elsewhere (Schoener and Schoener 1983b) we have postulated that nearly all short-distance dispersal occurs during and in the immediate aftermath of hurricanes, when lizards are especially likely to be washed into the water – a fate to which littoral anoles would be particularly vulnerable.

Anolis sagrei has achieved notable success as a long-distance colonizer in the Caribbean. Williams (1969), who posits its ancestral island as Cuba, lists the over-water distances it has travelled successfully; omitting questionable importation, these range from 61 to 592 km, and extend even to the Central American coast. While the use of "stepping-stone" islands must account for some of these long-distance dispersals, such data give an indication of this species' potential for crossing water. No doubt some such dispersals were on rafts, but our experiments suggest that in addition, free floatation may well contribute to *sagrei*'s great vagility.

How do lizards float? McCann (1953) concluded that some Pacific gekkonids are capable of floating for prolonged periods; he attributes this ability to float "almost indefinitely without exerting any effort" to the structure of their tubercular or granular scales. When immersed in seawater "the spaces between the scales retain pockets of air between them and together form a cushion of air around the body," essentially providing a natural "life jacket." Unfortunately the species involved were not mentioned, and it seems that many geckos and anoles do not have such overlapping scales (P.F.A. Maderson, E.E. Williams, personal communication), so that this explanation may not generally hold.

Although air bubbles are indeed trapped by scales on the anoles' tail, limbs and body, this in itself is not sufficient to keep heavier animals afloat; dead adult males generally sink. Several other mechanisms may be involved in keeping live lizards afloat. One of these is surface tension, which is noticeable around the central regions of the body (although the forelimbs are generally below the water level and the head held high). Indeed, when we added detergent to the seawater in the wave tank to reduce surface tension, the 6 lizards so tested (2 males and 4 females) began sinking immediately. We conclude that floatation is dependent on surface phenomena, although gulping of air may additionally aid floatation.

Whatever the physiology of floatation, the linear function relating percent success to floating duration implies that the probability of failure is not constant during each small interval of time – otherwise the curve would exponentially decrease (e.g., Schoener and Schoener 1983c). Rather, this probability is low at first, then increases, though no sharp threshold is apparent.

A large number of experiments on mammals have been performed on maximum survival time in water. These were done in freshwater, and the mammals typically swam actively rather than floated. As Table 3 shows, most species fell far short of the abilities of *Anolis sagrei* in seawater – only the largest mammals tested (e.g., woodchucks, skunks) have comparable ability.

Finally, although lizards may typically not choose to float, on occasion they may leave especially poor islands in search of better ones, and we have shown them to do so experimentally (Schoener and Schoener 1983c). On the other hand, the disadvantages of floatation in seawater may be serious enough to rule out most such voluntary departures. One disadvantage, perhaps a major one, is predation. We know this is at least some danger to the lizards from our initial floatation experiments, which were done in a natural lagoon. Shortly after their inception, a 0.3-m fish pulled one of our test subjects underwater; although the lizard was immediately released by the fish and continued to float for 1 $^1/_2$ h more, its tail had been broken. When it was retrieved it seemed listless (probably it had experienced blood loss); subsequently it died. Floatation experiments were thereafter conducted in the laboratory.

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