Atoll, as part of a crocodile survey of the atoll (Platt and Thorbjarnarson, 1997). These remains consisted of a forefoot and pieces of shell with attached skin and were deposited in the Campbell Museum, Clemson University, Clemson, SC, USA (CUSC 1382).

It is believed this turtle originated on Turneffe Atoll as the nearest known mainland populations of *R. areolata* are approximately 45 km from the capture site. Given the rapid digestion of flesh and bone in the crocodilian stomach (Davenport et al., 1990), the undigested state of the remains indicates the turtle had been consumed very recently. In addition, the probable population of *R. areolata* reported from Blackbird Cay is only ca. 10 km from the capture site.

These observations constitute a significant range extension for the species, and we suggest that *R. areolata*, albeit rare on the island, should henceforth be considered a member of the atoll's terrestrial fauna. While nothing is known concerning the ecology of this insular population, *R. areolata* on the mainland feed extensively on various fruits. On Turneffe Atoll, the turtles are probably dependent on littoral forest as a source of fruit for both food and water. Significantly, the Turneffe Atoll population may be threatened if clearance of littoral forest for the construction of tourist facilities and fishing camps continues unabated.

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Size Differences in Hind Limbs and Carapaces of Hatchling Green Turtles (*Chelonia mydas*) from Hawaii and Florida, USA

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For decades biologists have commented on morphological differences in green turtles (*Chelonia mydas*) from the Atlantic and Pacific Ocean basins. A number of investigators have enlisted morphological differences in arguments to separate *C. mydas* (a polymorphic species) into several subspecies or races (e.g., *C. m. agassizii*, *C. m. carrinegra*, *C. m. japonica*). Deraniyagala (1939) felt that differences noted between Atlantic and Indo-Pacific forms were ontogenetic variations. Carr (1952, 1964, 1972) described two morphs of *C. mydas* in the Pacific. One morph was characterized by a deep body as well as dark pigmentation on the scales and plastron; the other had yellowish pigmentation and a flatter profile. He made brief mention that Pacific green turtles differed in form from Caribbean turtles. Caldwell (1962) listed a number of carapace, plastron, and scalation features that distinguished the different Pacific and Atlantic morphs. He felt that these differences were sufficient to justify their designation as subspecies. Kamezaki and Matsui (1995), using skull morphology, described 5 distinct geographic groups from the Atlantic, Pacific, and Indian Ocean basins. Pritchard and Trebbau (1984) noted that some populations of *C. mydas* had pigmentation along the ventral surface of the marginal scutes, while others lacked this pigmentation. Ontogenetic changes in the plastral pigmentation of young green turtles from Hawaii have been documented (Balazs, 1986). No similar changes have been described in Western Atlantic green turtles, however, we have noted that plastron color changes from white in hatchlings to pale yellow in juveniles and adults from Florida (unpubl. data). An anecdotal observation suggested that the hind limbs of Hawaiian green turtles in the Pacific are proportionately larger than those of Atlantic turtles (A. Carr and L. Ogren, *pers. comm.* to GHB).

These observations prompted us to compare and contrast hind limb size and body size in hatchling green turtles from a Central Pacific population (Hawaii) and an Atlantic Ocean population (Florida). Our study shows that hind limb size and body size differ significantly and consistently between these two populations. This population-specific morphological variation can be attributed to differences in embryonic development. We interpret the presence of this polymorphic characteristic to be a consequence of geographic isolation and speculate as to the adaptive significance of these two morphs.

Methods. — We collected and measured 200 hatchlings (10 hatchlings from 10 nests of 10 different females at each of the two sites). Data were collected during 1989–91 in Hawaii and during 1991–92 in Florida. Hawaiian hatchlings originated from French Frigate Shoals (23°08'N, 166°02'W; see Balazs, 1976, 1980) and Floridian hatchlings originated from Boca Raton (26°19'N, 80°04'W). We measured hatchlings within one day of emergence. Data collection was restricted to hatchlings to insure that we measured population-specific differences in limb morphology and did not include any feet whose fleshy margin or terminal bony components may have been truncated by posthatching injury.

We measured, using vernier calipers, the midsagittal straight-line carapace length of each hatchling (SCL: to the nearest 0.1 mm) from the anterior-most point of the nuchal (cervical) scute to the posterior-most point of the last marginal scute. A flexible fiberglass tape measure was used for curved lengths (CCL: to the nearest 0.5 mm). CCL was measured on all Hawaii hatchlings ($n = 100$) and a subset of the Florida hatchlings ($n = 30$; due to the tape measure being unavailable during all collection times). Body size was compared between the two populations by t-test for unequal variances (SAS et al., 1981). Each measure (SCL and CCL) was tested separately.

Using identical techniques, we held each himb limb flat with light finger pressure while we traced both hind limbs of live hatchlings from the anterior-most point on the knee, along the anterior and posterior crus and tarsus, and around the pes. The planar surface areas of these tracings (Fig. 1) were measured using a digital scanning program (Sigma-Scan Digitizer, Jandel Scientific). The precision of this method (assessed by measuring each hind limb tracing 3 times) was ± 0.012 cm^2 (SE). The 3 tracing measurements were averaged, then the mean area of each hatchling's hind limbs was calculated, giving an average area for the pair. For each turtle, mean hind limb area (cm^2) was tabulated, then converted to its square root (√) so that limb size and carapace size shared the same units. Hereafter the √ mean hind limb area is referred to as "limb size."

Data were analyzed using two protocols. First, each individual was treated as a single data point (ignoring that groups of 10 hatchlings were from the same clutch); this is referred to as the "individuals protocol." A second analysis was made to insure that our results were not biased due to pseudoreplication; this treated data for individual hatchlings from the same clutch as repeated measures and was desig-

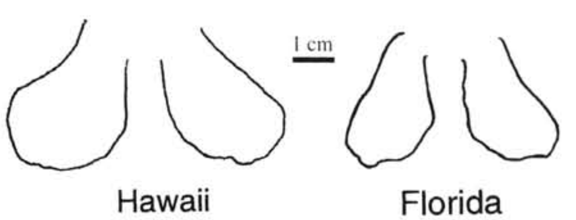

Figure 1. Sample tracings of the hind limbs of same-sized Hawaiian and Floridian hatchling green turtles. Bar = 1 cm.

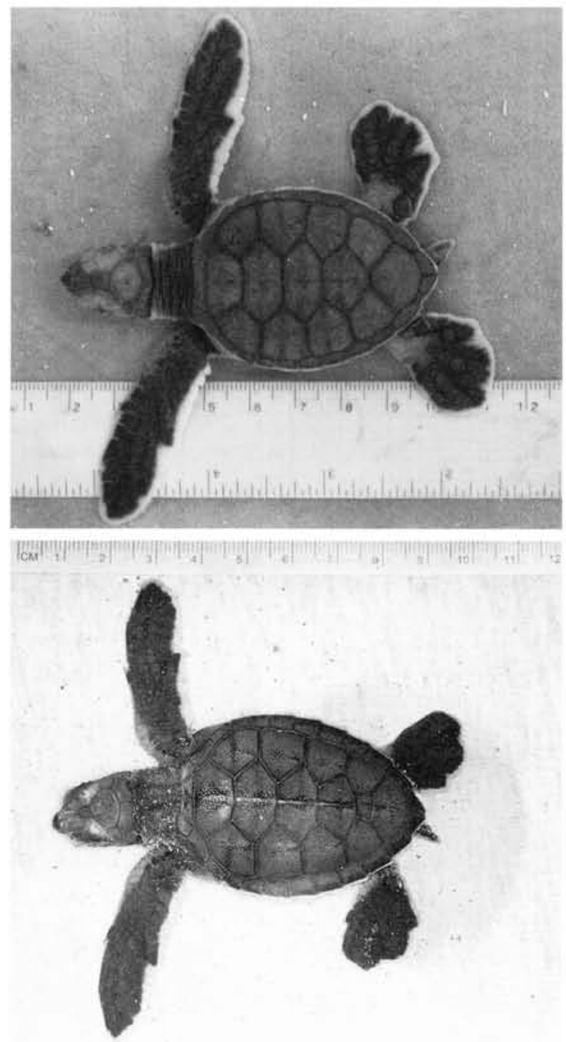

Figure 2. Photographs of Hawaiian (**top**) and Floridian (**bottom**) *C. mydas* hatchlings just after emergence from the nest. The two animals share the same straightline carapace length. Note the proportionately larger hind limbs of the Hawaiian hatchling.

nated the "nests protocol." The data for each clutch were pooled, described as a grand mean and SE then analyzed by repeated-measures models.

Using the "individuals protocol," hind limb areas were compared by t-tests (Sokal and Rohlf, 1981). The natural logarithm (ln) of limb size was plotted as a function of (ln) body size (SCL). The data for the two populations were then characterized as linear models through simple linear regression. We then investigated how limb size covaried with body size. The slopes and y-intercepts of the regressions were compared by ANCOVA, followed by *post hoc* (Tukey-Kraemer) tests to determine if those metrics were homogeneous (SAS et al., 1981; Bookstein et al., 1985; Abacus Concepts, 1992).

For the "nests protocol," mean hind limb areas of 10 clutches for each site were compared using Mann-Whitney tests. The mean (ln) limb size of each clutch was plotted as a function of its mean (ln) SCL. These data were then characterized as linear models. As above, we investigated how limb size covaried with body size by applying ANCOVA for repeated-measures to the data. We then determined if the slopes and y-intercepts were homogeneous (SAS et al., 1981; Sokal and Rohlf, 1981; Zar, 1984).

Results

Body size SCL measurements did not differ significantly between Hawaiian (51.97 ± 1.69 mm, n =100) and Floridian (51.69 ± 1.39 mm, n = 100) hatchlings (t = -1.29, df = 198). However, Hawaiian hatchlings had flatter carapaces (CCL = 54.63 ± 1.91 mm, n = 100) than Floridian turtles (56.92 ± 1.04 mm, n = 30). Because the CCL values differed (t' = 45.49, df = 99, 29; $p < 0.001$), we did not use this measure to investigate hind limb size as a function of body size. Turtles from Hawaii and Florida matched for similar SCL differed significantly in hind limb area (Figs. 2, 3).

Individuals Protocol. — Comparisons of hind limb size by "individuals protocol" showed that mean flipper area was 4.15 ± 0.42 cm^2 for Hawaiian hatchlings and 3.18 ± 0.25 cm^2 for Floridian hatchlings. The F_{max} test (Sokal and Rohlf, 1981) showed that the variances of the limb sizes (√mean hind limb area) were homogeneous. We transformed the data to its natural logarithm to insure uniform variance for both low and high values.

Least squares regression analysis was applied to (ln) SCL vs. limb size. We found no significant interaction between body size and population. Different regression lines (Model II - reduced major axis) described the relationship between (ln) SCL vs. limb size (Fig. 3). In the Hawaiian population this was: $y = 1.40 * (\ln)SCL - 4.82$, ($r = 0.62$, $p < 0.001$); and in the Floridian population it was: $y = 1.42 * (\ln)SCL - 5.01$, ($r = 0.50$, $p < 0.001$).

The ANCOVA of factors influencing limb size showed that body size was a significant factor. In this analysis, the interaction factor was not significant. Therefore, the slopes of the lines describing each population's limb size were statistically indistinguishable. Because the interaction term

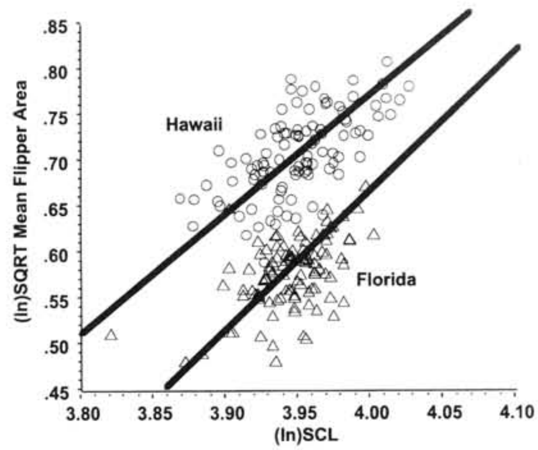

Figure 3. Linear regression of (ln)√mean hind limb area as a function of (ln)SCL. The slopes of the lines fitted to each population's data do not differ significantly, however, the y-intercepts do differ.

was not significant, it was removed from the model. The resulting ANCOVA (Table 1) showed that both population and body size factors affect (ln)√mean limb size. A comparison of the least squares means by t-test showed that they differ, hence, the y-intercepts differ.

Comparisons of limb size (√mean hind limb area) among individuals by t-test for unequal variances showed that the two populations differed (t' = 1800.00, df = 99, 99, $p < 0.0001$). Comparisons of least squares means matched for body size also showed that the Hawaiian turtles had significantly larger hind limbs than Floridian hatchlings (Figs. 2, 3).

Nests Protocol. — Least squares regression analysis was applied to (ln) mean SCL vs. (ln)√clutch mean hind limb area (hereafter referred to as "clutch limb size"). We found no significant interaction between body size and nest number. As in the analysis of individuals, different regression lines (Model II - reduced major axis) described the relationships (Fig. 4). In the Floridian population this was: $y = 1.84 * (\ln)SCL - 6.70$ ($r = 0.67$, $p < 0.03$); and in the Hawaiian population it was: $y = 1.17 * (\ln)SCL - 3.90$, ($r = 0.91$, $p < 0.001$).

The ANCOVA for repeated measures of factors influencing clutch limb size showed similar results to those

Table 1. ANCOVA of (ln)√mean hind limb area. The factors tested were body size (described by (ln) SCL) and population (Hawaiian vs. Floridian), and the interaction of these two was removed. Least squares means were compared by t-test to determine if the intercepts were similar. Post-hoc (Tukey-Kraemer) tests contrasted the two assemblages.

	df	SS	MS	F	Significance
Population	1	0.8139	0.8139	674.76	$p < 0.0001$
(ln)SCL	1	0.1155	0.1155	95.80	$p < 0.0001$
Residual	197	0.2376	0.0012		

Least Squares Means

	n	Mean	SE	Diff.	t-test
Florida	100	0.5773	0.0035	0.2212	39.6116
Hawaii	100	0.7090	0.0035		$p < 0.0001$

Tukey-Kraemer Comparisons

	Difference	Crit. Diff.	Significance
Hawaii vs. Florida	0.1320	0.0128	$p < 0.001$

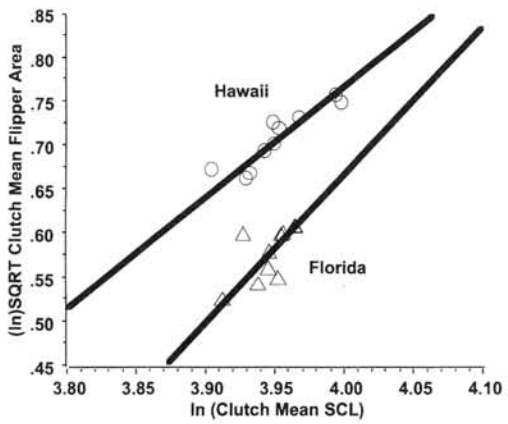

Figure 4. Linear regression of (ln)√clutch mean hind limb area as a function of (ln)clutch mean SCL. The slopes of the lines fitted to each population's measurements are not significantly different; the y-intercepts differ.

demonstrated in the individuals protocol; clutch limb size was significantly related to clutch mean body size. In this analysis, the interaction term was not significant and was removed from the model. The slopes of the lines describing each population's clutch limb size were statistically indistinguishable. The resulting ANCOVA (Table 2) showed that both population and body size factors affected (ln)clutch limb size. Comparison of the least squares means by t-test indicated that the y-intercepts differed.

Comparisons of clutch limb size between populations using the Mann-Whitney test showed that the two populations differed (U'=100.00, df = 10, 10; $p < 0.001$). Comparisons of least squares means matched for body size demonstrated that the Hawaiian turtles had significantly larger hind limbs.

Discussion

Green turtle hatchlings from Hawaii were similar in straight-line carapace length to hatchlings from Florida but were longer over the curve indicating that the Floridian hatchlings had flatter shells (when measured, all animals in this study had completely unfolded from their position in the egg). Hawaiian green turtle hatchlings had absolutely and proportionately larger hind limbs (Figs. 3–4). Hind limb size was related isometrically to carapace size in each population.

The linear regressions of the (ln) limb size as a function of carapace size resulted in different linear models for the two populations. Linear regression lines for the two populations had statistically similar slopes but different y-intercepts. Linear regressions models treating individual measures as independent samples gave similar overall results to those found using a grouped nests protocol, although specific details of the equations differed largely because of differences in the power of the tests. For each population the 95% confidence limits overlapped for the two methods of analysis so that, in this case, it was unbiased to rely upon sampling multiple hatchlings per clutch.

Different y-intercepts for the two populations implied that the hind limbs of Hawaiian turtles have grown more during prehatching embryonic development than those of Floridian turtles. However, the similar slopes indicated that the embryonic growth trajectories (relative growth rates of the carapace and flippers) sampled at emergence were the same in each population.

Several plausible (though not exclusive) hypotheses might explain the morphological patterns observed. (1) Differences in hind limb and carapace size may be due to heterochronic mutation (genetic changes that result in differences in the timing of developmental events) in one of the populations. (2) Developmental regulation of limb and carapace growth (cell proliferation and differentiation) might also account for the differences in limb size at hatching. (3) The carapace and hind limbs may be developmentally decoupled, as some experiments with snapping turtle (*Chelydra serpentina*) embryos suggest (Burke and Alberch, 1985; Burke, 1989), so that growth rates of limbs and carapace may vary independently but in a population-specific manner.

Genetic analyses (mtDNA) of matrilinages have shown that Hawaiian and Western North Atlantic green turtle populations diverged long ago (Bowen et al., 1992). Assuming the populations have been isolated since the formation of the Isthmus of Panama, they have had roughly 1.5–3 million years of divergence time. Hence, the populations have been free to follow separate evolutionary paths since their isolation from one another. As we noted earlier, studies of geographic variants can teach us not just what phenotypic variation is present, but also about variation in the underlying processes that are responsible for producing that phenotype. Although we hypothesize that heterochronic change may be responsible for the two morphs, we do not yet know how the mechanism varies. The mechanism(s) that are responsible for hind limb polymorphism in green turtles will remain unidentified until the developing embryos themselves have been compared.

Carr's and Ogren's initial observation that Hawaiian green turtles had larger hind limbs than Floridian turtles extended to both hatchlings and older animals. Preliminary measurements on juveniles and subadults suggest that the

Table 2. ANCOVA of ln√clutch mean hind limb areas. The factors tested were body size (described by (ln) clutch mean [= c.m.] SCL) and population (Hawaiian vs. Floridian). The interaction was not significant and was removed from the model. Least squares means were compared by t-test to determine if the intercepts were similar. Post-hoc (Tukey-Kraemer) tests contrasted the two assemblages.

	df	SS	MS	F	Significance
Population	1	0.0792	0.0792	209.88	$p < 0.0001$
(ln) c.m. SCL	1	0.0121	0.0121	32.15	$p < 0.0001$
Residual	17	0.0064	0.0012		

Least Squares Means

	n	Mean	SE	Diff.	t-test
Florida	10	0.5798	0.0062	0.1266	-13.9640
Hawaii	10	0.7064	0.0062		$p < 0.0001$

Tukey-Kraemer Comparisons

	Difference	Crit. Diff.	Significance
Hawaii vs. Florida	0.1320	0.0190	$p < 0.001$

differences we observed in hatchlngs are maintained through ontogeny. Hence, we plan to continue and expand the study to compare juveniles through adults from these populations.

At least one functional requirement may provide insight into the mechanical properties that must, in part, guide hind limb design. During swimming, sea turtles steer using a combination of hind limb rudder action and forelimb movements (Davenport et al. 1984; Lohmann, et al., 1995; Wyneken, 1997). During most swimming, the hind limbs typically contribute little to thrust production but are positioned to provide appropriate resistance for steering. Comparisons of green turtle hind limbs to traditional man-made paddles provide insights. We looked for mechanical examples in which paddles serve as rudders. Hawaiian canoe paddles used for steering are larger than standard thrusting paddles with a robust shaft (Buck, 1964; Holmes 1981). Generally paddles used for thrusting have a wide blade and a small diameter shaft. In comparison, rudders typically do not taper much where they join the hull lines of vessels they steer. Like canoe paddles, the hind limb morphology of green turtles more closely resembles a steering paddle with a large wide blade and stout shaft. However, sea turtle hind limb morphology is constrained by both their evolutionary history (modification of the basic turtle foot plan) and other essential limb functions, such as crawling, nest construction (for females), or grasping during mating (for males). Their design combines features of both paddles and rudders superimposed upon the blueprint of a turtle foot. While the larger size of Hawaiian green turtles' hind limb is consistent with this functional analogy of paddles, behavioral data supporting this hypothesis have not been recorded. We plan future studies to determine if Hawaiian and Floridian turtles differ in their steering behavior during swimming to determine if the Hawaiian turtles' hind limbs function more in steering (perhaps with less forelimb assistance) than in Floridian hatchlings.

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