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Carapacial Scute Variation in Kemp's Ridley Sea Turtle (*Lepidochelys kempi*) Hatchlings and Juveniles

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The carapacial scutes of 5,919 specimens of hatchling and juvenile Kemp's ridley sea turtles (Lepidochelys kempi), representing five different incubation-handling categories, were examined.

Scutes were examined with regard to variation within carapacial scute series and variation in carapacial scute pattern. The vertebral and marginal series were the most variable, the costal series showed less variability, and the nuchal scute was extremely stable. The most common scute pattern, observed in 44.7 percent of the specimens, was 13 pairs of marginals, 5 pairs of costals, 5 vertebrals and a single nuchal.

Comparisons among the five incubation-handling categories indicated that the least handled eggs produced turtles with lowest levels of variability in scute series and patterns, while the most roughly handled eggs produced hatchlings with highest levels of variability in scute series and patterns.

Comparisons between dead (unhatched embryos or hatchlings found dead in the nest) and live hatchlings suggested that selection may act to remove the extremes of carapacial scutation phenotypes from the population. Though there was evidence suggesting that dead turtles had more variable scute series than live turtles from the same incubation-handling categories, this evidence was not uniform among the categories.

Transplantation, translocation and artificial incubation of sea turtle eggs should be re-examined with greater scrutiny concerning their possible effects on viability of turtle populations. When the mechanisms causing scute abnormalities are better understood, scute patterns may be useful external indicators of normal or abnormal hatchlings as related to their future viability.

The large scales that cover the shell in nearly all turtles are called scutes. Deraniyagala (1939) referred to the number and arrangement of these scutes as scutation. There has been a great deal of stability in scutation of the carapace during chelonian evolution (Zangerl and Johnson, 1957). Despite this phylogenetic stability, individual variations in scutation have been observed for nearly all species of turtles that possess scutes. Previous workers have examined this variation in numerous studies and have suggested various genetic and environmental factors as causative agents.

While investigating scutation in the loggerhead sea turtle (*Caretta caretta*), Gadow (1899) noted that adults appear to have far less variation than do hatchlings of the same species. He proposed the idea of "orthogenetic variation," theorizing that young turtles that possess more than the normal complement of scutes undergo fusion of scutes during ontogeny such that the adult stage exhibits the normal reduced scute pattern. Newman (1906) opposed this view, and suggested that supernumerary scutes were an atavistic reappearance of scutes that had been lost during phylogeny. Brongersma (1968) questioned the validity of Gadow's (1899) study, pointing out that Gadow's specimens did not consist solely of loggerheads, but rather of a mixture of loggerhead and olive ridley (*Lepidochelys olivacea*) specimens, thus explaining the disparity in scute number between hatchling and adult turtles. Atavism (Newman, 1906) is also an unlikely explanation for the multiscutate condition, as additional scutes appear to arise by subdivision of those typically present (Coker, 1905a, b and c, 1910; Pritchard, 1969b; Hill, 1971), and because of the aforementioned phylogenetic stability in numbers of carapacial scutes.

Other authors have suggested that abnormalities of scutation arise from accidents or disturbances during ontogenetic development (Parker, 1901; Wandolleck, 1904; Hildebrand, 1930; Zangerl, 1969). Pressure within the nest as a result of crowding has been cited as a possible source of scute abnormalities (Coker, 1910). Hildebrand (1938) suggested that scute anomalies in diamondback terrapins (*Malaclemys terrapin*) resulted from changes in available oxygen supply during incubation. Abnormal scutation and other shell deformities were induced by Lynn and Ullrich (1950) in hatchling painted turtles (*Chrysemys picta picta*) and snapping turtles (*Chelydra serpentina*) through partial dessication of the eggs at certain stages of development. Temperature variation during incubation may also account for scute abnormalities. Scutellation patterns of garter snakes have been influenced by lowering the ambient temperature during gestation (Fox, 1948; Fox, Gordon and Fox, 1961). The work of Yntema (1976), Bull and Vogt (1979), Yntema and Mrosovsky (1980), and others concerning temperature-dependent sex determination indicates that morphogenetic effects can occur in turtles as a result of varied incubation temperature. Also, handling of eggs

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at certain stages of development has been cited as a source of increased scute variation in olive ridleys (Hill, 1971), and has been shown to induce mortality in embryos (Limpus, Baker and Miller, 1979). Thus, there is evidence to suggest that several different environmental factors may influence scute pattern variation during incubation.

There also exists a possibility that there is sexual dimorphism in scute counts as suggested by Hill (1971). As most studies of adult turtles are based predominantly on observations of nesting females, perhaps our concept of a "normal" scute pattern is biased by lack of data from adult males. Given the strong influence of incubation temperature on sex in sea turtles, and the example cited above of temperature-induced scute pattern variations in garter snakes, perhaps incubation temperature could be influencing sex and scute pattern in a parallel manner. However, Frazier (1984) examined a series of olive ridleys from Mexico and concluded that there were no significant differences between the sexes in any of the meristic characters he compared, including carapacial scutes.

The typical chelonian carapacial scutation consists of a median longitudinal series of unpaired elements (the vertebral scutes), flanked on each side by a series of bilaterally paired scutes (the costals), which are bordered exteriorly by another series of bilaterally paired scutes (the marginals). Situated anteriorly between the first pair of marginals is a single nuchal. Thus, midline elements consist of a nuchal scute anteriorly, followed posteriorly by a series of vertebral scutes. The paired marginal scutes border the periphery of the carapace except where the nuchal separates them anteriorly. The costal scutes occupy the region lateral to the vertebrals and medial to the marginals on each side. Some workers consider the posterior-most pair of carapacial scutes (the supracaudals) apart from the marginals (e.g., Frazier, 1984; Pritchard and Trebbau, 1984), but for the purposes of this study we have considered these scutes as part of the marginal series.

Among the sea turtles, the most deviance from the scute pattern common to most individuals of a species as well as the greatest variability in pattern are found in the genus *Lepidochelys*. The olive ridley possesses such a high frequency of scute pattern anomalies that it is considered by Pritchard (1969b) to be "unique among turtles in having a truly polymorphic carapace" (i.e., essentially having no "normal" pattern). Though it does not possess carapace polymorphism to the degree of its congener, Kemp's ridley has nevertheless been shown to exhibit some carapacial scute variation (Chávez, Contreras and Hernández, 1967, 1968; Pritchard, 1969b). The modal carapacial scutation for Kemp's ridley consists of 13 pairs of marginal scutes, five pairs of costal scutes and five vertebral scutes, with a single nuchal (Figure 1).

The intent of our study was to describe and document scute anomalies in Kemp's ridley from two perspectives:

1. meristic variation with each series of scutes (left marginals, left costals, vertebrals, right costals and right marginals), and
2. variation among individual turtles from the modal scutation pattern (Figure 1).

Further, we attempted to relate variation in Kemp's ridley scutation to the various types of natural and artificial conditions under which our study animals were incubated and handled and also to the ontogenetic stages represented in our study animals.

Continued research into the causes of scute pattern variation in turtles is necessary to elucidate possible relationships of such variation to viability. An improved understanding of these relationships could greatly assist management and conservation of endangered and threatened species of turtles. Zangerl (1969) has commented that "the morphogenetic controls that determine the bone and shield patterns of the turtle shell are unquestionably complex." It is hoped that the present study will enhance the knowledge of these complex processes.

Materials and Methods

The carapacial scutes of 5,919 specimens of Kemp's ridley hatchlings and juveniles were examined. The study animals were grouped both by ontogenetic stage and conditions under which they were incubated and handled (Table 1). During the 1981 nesting season at the Kemp's ridley rookery near Rancho Nuevo, Tamaulipas, Mexico, 4,114 live hatchlings were examined and later released. Another 298 hatchlings and embryos, either dead in the egg, dead in the nest, or alive but severely deformed or underdeveloped and unable to rupture the egg, were examined at Rancho Nuevo during the same nesting season. Those that were unable to rupture the egg were included as dead hatchlings because they would have died naturally had they not been used in our study. Dead hatchlings and embryos were considered a younger ontogenetic stage than live hatchlings. The remaining 1,507 were juveniles examined at the National Marine Fisheries Service (NMFS) Southeast Fisheries Center (SEFC) Galveston Laboratory during head starting of the 1980 year-class. The specimens examined at Rancho Nuevo came from nests that had been handled or incubated, or both, in four different ways:

1. The largest group of hatchlings came from 37 nests incubated in corrals at Rancho Nuevo. This category will be referred to hereafter as the corral nest category. These eggs were dug by hand from their natural nests on the beach, then transported in bags to the corrals where they were reburied in holes carefully fashioned to

closely resemble the depth and shape of natural nests. The corrals were located high on the dune to lessen the risk of inundation during spring tides and were fenced to protect the eggs from large predators such as coyotes. Due to the large number of turtles nesting during *arribadas*, eggs replanted in this fashion often remained *in situ* for up to seven hours before replantation. These nests were sometimes subjected to bouncing and heat during transportation from their natural nests to the corrals, and were at times left out of the substrate for several hours prior to replantation. We authors consider the eggs replanted to the corral in this manner to have received the roughest or least careful handling of any of the incubation-handling groups.

2. The second largest group of hatchlings came from 11 nests replanted using the special handling techniques of the international effort to establish a new nesting colony on Padre Island, Tex., through head starting. Padre Island boxes will be the category used in this paper to refer to these nests. Padre Island eggs were collected in clean plastic bags as they dropped from the cloacas of ovipositing females, thus avoiding contact with Rancho Nuevo sand. They were immediately transported to a shaded area where they were placed by hand into polystyrene foam boxes filled with sand collected from Padre Island. These boxes containing Padre Island sand and the eggs were placed on elevated shelves in a concrete block building at the Rancho Nuevo turtle camp where they were carefully monitored to prevent their dessication or infestation of any kind. The intended destination of these 11 nests was the Padre Island National Seashore, where the eggs were to be incubated by the National Park Service to provide hatchlings for the Kemp's Ridley Head start Research Project at the NMFS SEFC Galveston Laboratory. Due to numerous delays, these eggs hatched at Rancho Nuevo before they could be flown to the National Seashore. The hatchlings used in our study were released offshore of Rancho Nuevo. The eggs that produced this group of 894 hatchlings were exposed to virtually no rough handling and were expeditiously transplanted.
3. Seven nests were incubated in Rancho Nuevo sand in polystyrene foam boxes in the same concrete block building, concurrently and under the same conditions as the 11 originally destined for Padre Island. However, these Rancho Nuevo nests were transplanted as much as 24 hours after oviposition. This group will be referred to as the Rancho Nuevo boxes category. In all but one of the Rancho Nuevo nests, special handling techniques were used to avoid changing the orientation of the eggs as they were removed from the natural nest. These eggs produced 549 hatchlings used in our study.
4. The 151 hatchlings that represented a sample of five natural nests at Rancho Nuevo were discovered as they were entering the sea. We categorized this group as natural nests. The exact number of hatchlings from each nest therefore was unknown. One of the five nests was severely infested with ants and contained many dead hatchlings that might otherwise have emerged alive. This may have biased that portion of the sample of natural nests represented by dead hatchlings; i.e., some of the hatchlings that died due to attack by ants may have had scutation characteristics nearer those of the live hatchlings than those that died from other causes. Though there were fewer hatchlings from natural nests than in any of the other three categories from eggs incubated at Rancho Nuevo, we included the data for naturally incubated nests due to the paucity of such information in the literature for Kemp's ridley and because of its value in comparative studies.
5. In addition to the four categories of hatchlings examined at Rancho Nuevo, 1,507 living juvenile Kemp's ridleys of the 1980 year-class were examined in April 1981 at the NMFS SEFC's Galveston Laboratory. They were categorized as Galveston head starts. These juveniles were presumably handled and incubated in the same

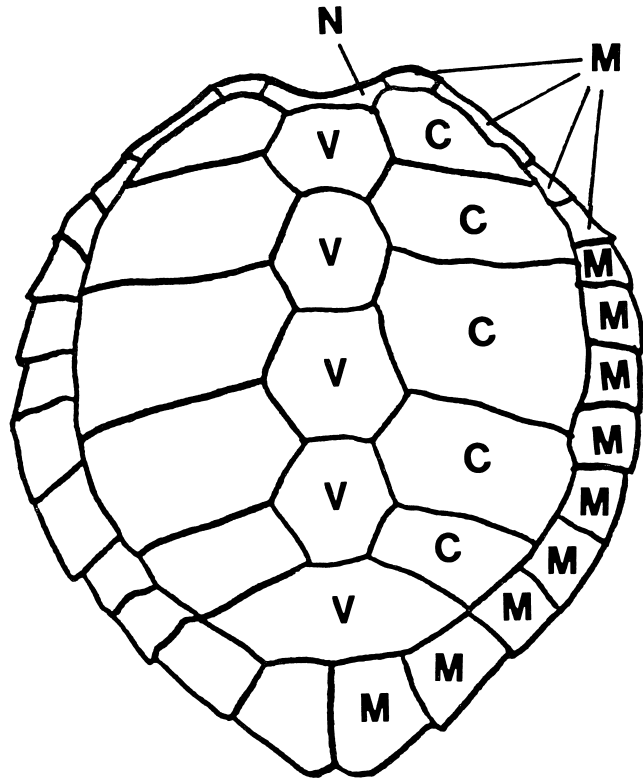


Figure 1. Modal carapacial scute arrangement for Kemp's ridley sea turtle including 13 pairs of marginals (M), 5 pairs of costals (C), 5 vertebrals (V) and 1 nuchal (N).

manner as described in item 2 above for the Padre Island sample incubated at Rancho Nuevo, except that the boxed eggs from which the 1980 year-class hatchlings were produced were transported from Mexico to the Padre Island National Seashore where they were incubated, and where the hatchlings were imprinted before being transferred to Galveston.

Temperature regime, including mean temperature and temperature range, differed between the corrals and the concrete block building at the Rancho Nuevo turtle camp. Levels of humidity and their fluctuation also doubtlessly varied between these two environments, as the nests incubated in polystyrene foam boxes were sheltered from precipitation, receiving only occasional and intentional sprinklings to prevent desiccation of the eggs. Because of these humidity and temperature differences, as well as differences in internal nest conditions brought about by incubation in boxes, the environmental conditions acting on the eggs and embryos incubated for various periods in the concrete block house (i.e., Padre Island boxes, Rancho Nuevo boxes and Galveston head starts) were substantially different from those for the beach-incubated nests (i.e., corral nests and natural nests).

For each turtle, the number of carapacial scutes in each series was recorded from left to right, including left marginals, left costals, vertebrae, right costals and right marginals (e.g., 13-5-5-5-13). Also recorded for each turtle was whether or not it had the normal single nuchal scute. Each five-element array constituted a scute pattern or scutation. Frequencies of each pattern variation were also recorded by nest. Variation in frequencies within each scute series (left marginals, left costals, vertebrae, right costals and right marginals) as well as nuchals, was examined separately from that of scute pattern. This approach to analysis of scute variations did not recognize abnormal seam placement unless it also entailed a change in the number of scutes in a particular series. For instance, a specimen may have had the usual five vertebrae, but with the seams positioned in such a way as to clearly indicate a non-normal arrangement. In our analysis, such abnormality would not be recognized. In this sense our data are conservative with regard to levels of variability, because a specimen such as that described above was recorded as normal with regard to vertebrae.

Statistical procedures generally follow the recommendations and procedures of Sokal and Rohlf (1981). Because of the disparity in magnitude between marginal counts and costal or vertebral counts, direct comparisons among coefficients of variation for these different series are misleading. While the significance of each unit deviation from the mode is no different for marginals than for costals or vertebrae, the coefficients of variation for marginal counts are smaller as a result of the larger denominator (i.e., 13 instead of 5). Therefore, the standard deviation is the best indicator of relative variation among scute series in a given incubation-handling category. In comparing different incubation-handling categories with regard to a given scute series, the coefficient of variation was a valuable indicator. The magnitude of the standard deviation for a given scute series within an incubation-handling category was an indicator of relative variability in that scute series because of the discrete nature of the data. Paired comparison t-tests were used to test for asymmetry in counts of costals and marginals. G-tests of independence were used to test the goodness of fit of cell frequencies to expectations in examining the frequencies of individuals exhibiting the modal scute pattern in the various incubation-handling categories and ontogenetic stages.

Results

Variation in the Nuchal Scute Series

Nuchal scute variation from the normal single nuchal was confined to a small number of turtles in which this scute had either split to form a double nuchal or was fused with adjacent scutes from the marginal or vertebral series. The double nuchal was the more common of these two departures from the norm. However, such variations in the nuchal were rare, because 99.5 percent of the 5,919 turtles possessed a single nuchal scute.

Variation in the Vertebral Scute Series

The number of scutes in the vertebral series ranged from 3 to 9 with a mode of five (Table 2). The standard deviation and coefficient of variation were higher for the vertebral series than for any other scute series. The magnitude of variation in vertebral counts, as indicated by standard deviations and coefficients of variation, ranked highest in the corral category, followed by the Galveston head starts, Padre Island boxes, Rancho Nuevo boxes and natural nests (Table 3).

Ranges in vertebral scute counts in live turtles show similar rankings with the widest range for corral nests, followed by the Galveston head starts, Padre Island boxes, Rancho Nuevo boxes and natural nests (Table 4). A similar ranking by range is mirrored in the dead turtles except that no dead Galveston head start turtles were examined.

The proportion of turtles possessing the modal count of five vertebrae is another criterion useful in comparing incubation-handling categories. For live turtles, Galveston head starts exhibited the smallest proportion (62.4 percent) with five vertebrae followed by corral nests (67.4 percent), Padre Island boxes (85.9 percent), Rancho Nuevo boxes (90.7 percent) and natural nests (97.5 percent). In all categories, except Galveston head starts which had no dead turtles, the frequency of the modal vertebral count was greater for live turtles than for dead.

Table 1. Number of live and dead specimens of Kemp's ridley sea turtles in each incubation-handling category.

Ontogenetic stage and incubation-handling category*	Number of specimens		
	Live	Dead	Total
<i>Hatchlings</i>			
Corral nests (37)	2,677	141	2,818
Padre Island boxes (11)	874	20	894
Rancho Nuevo boxes (7)	483	66	549
Natural nests (5)	80	71	151
<i>Juveniles</i>			
Galveston head starts (unknown)	1,507	0	1,507
Total	5,621	298	5,919

*Number of nests is shown in parentheses.

Table 2. Summary statistics for carapacial scute counts by scute series for 5,919 Kemp's ridley hatchlings and juveniles.

Scute series	Range	Minimum	Maximum	Mode	Mean	Standard deviation	Coefficient of variation (%)
Left marginals	7	9	16	13	13.27	0.512	3.86
Left costals	5	3	8	5	5.13	0.381	7.44
Vertebrales	6	3	9	5	5.35	0.628	11.75
Right costals	5	3	8	5	5.10	0.336	6.59
Right marginals	7	9	16	13	13.28	0.532	4.01

Table 3. Summary statistics for carapacial scute counts of Kemp's ridley hatchlings and juveniles, by incubation-handling categories and scute series.

Incubation-handling category and scute series	Range	Minimum	Maximum	Mode	Mean	Standard deviation	Coefficient of variation (%)
<i>Corral nests (n=2,818)</i>							
Left marginals	7	9	16	13	13.26	0.532	4.01
Left costals	5	3	8	5	5.16	0.426	8.27
Vertebrales	6	3	9	5	5.41	0.682	12.61
Right costals	4	4	8	5	5.13	0.383	7.46
Right marginals	7	9	16	13	13.28	0.554	4.17
<i>Padre Island boxes (n=894)</i>							
Left marginals	5	10	15	13	13.23	0.473	3.58
Left costals	3	4	7	5	5.10	0.317	6.22
Vertebrales	3	5	8	5	5.16	0.416	8.07
Right costals	1	5	6	5	5.08	0.265	5.23
Right marginals	5	10	15	13	13.27	0.482	3.63
<i>Rancho Nuevo boxes (n=549)</i>							
Left marginals	2	12	14	13	13.17	0.393	2.98
Left costals	1	5	6	5	5.05	0.227	4.50
Vertebrales	3	4	7	5	5.09	0.320	6.29
Right costals	3	3	6	5	5.04	0.219	4.34
Right marginals	3	11	14	13	13.12	0.530	4.04
<i>Natural nests (n=151)</i>							
Left marginals	1	13	14	13	13.17	0.393	2.98
Left costals	1	5	6	5	5.05	0.225	4.45
Vertebrales	1	5	6	5	5.07	0.261	5.14
Right costals	1	5	6	5	5.04	0.196	3.89
Right marginals	2	13	15	13	13.25	0.450	3.40
<i>Galveston head starts (n=1,507)</i>							
Left marginals	5	11	16	13	13.37	0.532	3.98
Left costals	3	4	7	5	5.12	0.379	7.39
Vertebrales	5	4	9	5	5.46	0.680	12.45
Right costals	3	4	7	5	5.09	0.320	6.29
Right marginals	4	12	16	13	13.35	0.513	3.84

Table 4. Frequency distribution of vertebral scute counts for dead and live Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Number of vertebral scutes	Corral nests		Incubation-handling category						Galveston head starts		Total	
	frequency	%	Padre Island boxes frequency	%	Rancho Nuevo boxes frequency	%	Natural nests frequency	%	frequency	%	frequency	%
Dead Turtles												
3	1	0.7	0		0		0		0		1	0.3
4	4	2.8	0		1	1.5	0		0		5	1.7
5	65	46.1	13	65.0	59	89.4	62	87.3	0		199	66.8
6	47	33.3	5	25.0	4	6.1	9	12.7	0		65	21.8
7	20	14.2	2	10.0	2	3.0	0		0		24	8.1
8	3	2.1	0		0		0		0		3	1.0
9	1	0.7	0		0		0		0		1	0.3
Subtotal	141		20		66		71		0		298	
Live Turtles												
4	17	0.6	0		1	0.2	0		5	0.3	23	0.4
5	1,804	67.4	751	85.9	438	90.7	78	97.5	941	62.4	4,012	71.4
6	669	25.0	114	13.0	43	18.9	2	2.5	440	29.2	1,268	22.6
7	157	5.9	6	0.7	1	0.2	0		105	7.0	269	4.8
8	27	1.0	3	0.3	0		0		15	1.0	45	0.8
9	3	0.1	0		0		0		1	0.1	4	0.1
Subtotal	2,677		874		483		80		1,507		5,621	
Combined												
3	1	0.0	0		0		0		0		1	0.0
4	21	0.7	0		2	0.4	0		5	0.3	28	0.5
5	1,869	66.3	764	85.5	497	90.5	140	92.7	941	62.4	4,211	71.1
6	716	25.4	119	13.3	47	8.6	11	7.3	440	29.2	1,333	22.5
7	177	6.3	8	0.9	3	0.5	0		105	7.0	293	5.0
8	30	1.1	3	0.3	0		0		15	1.0	48	0.8
9	4	0.1	0		0		0		1	0.1	5	0.1
Total	2,818		894		549		151		1,507		5,919	

Table 5. Frequency distribution of left costal scute counts for live and dead Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Number of left costal scutes	Corral nests		Incubation-handling category						Galveston head starts		Total	
	frequency	%	Padre Island boxes frequency	%	Rancho Nuevo boxes frequency	%	Natural nests frequency	%	frequency	%	frequency	%
Dead												
3	1	0.7	0		0		0		0		1	0.3
4	8	5.7	1	5.0	0		0		0		9	3.0
5	97	68.8	17	85.0	61	92.4	63	88.7	0		238	79.9
6	30	21.3	2	10.0	5	7.6	8	11.3	0		45	15.1
7	4	2.8	0		0		0		0		4	1.3
8	1	0.7	0		0		0		0		1	0.3
Subtotal	141		20		66		71		0		298	
Live												
4	25	0.9	0		0		0		15	1.0	40	0.7
5	2,238	83.6	794	90.8	458	94.8	80	100.0	1,301	86.3	4,871	86.7
6	392	14.6	75	8.6	25	5.2	0		180	11.9	672	12.0
7	20	0.7	5	0.6	0		0		11	0.7	36	0.6
8	2	0.0	0		0		0		0		2	0.0
Subtotal	2,677		874		483		80		1,507		5,621	
Combined												
3	1	0.0	0		0		0		0		1	0.0
4	33	1.2	1	0.1	0		0		15	1.0	49	0.8
5	2,335	82.9	811	90.7	519	94.5	143	94.7	1,301	86.3	5,109	86.3
6	422	15.0	77	8.6	30	5.5	8	5.3	180	11.9	717	12.1
7	24	0.9	5	0.6	0		0		11	0.7	40	0.7
8	3	0.1	0		0		0		0		3	0.1
Total	2,818		894		549		151		1,507		5,919	

Table 6. Frequency distribution of right costal scute counts for dead and live Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Number of right costal scutes	Corral nests		Incubation-handling category								Total	
	frequency	%	Padre Island boxes frequency	%	Rancho Nuevo boxes frequency	%	Natural nests frequency	%	Galveston head starts frequency	%	frequency	%
Dead												
3	0		0		1	1.5	0		0		1	0.3
4	7	5.0	0		0		0		0		7	2.3
5	105	74.5	18	90.0	60	90.9	65	91.5	0		248	83.2
6	26	18.4	2	10.0	5	7.6	6	8.5	0		39	13.1
7	3	2.1	0		0		0		0		3	1.0
Subtotal	141		20		66		71		0		298	
Live												
4	19	0.7	0		0		0		15	1.0	34	0.6
5	2,307	86.2	808	92.4	465	96.3	80	100.0	1,351	89.6	5,011	89.1
6	337	12.6	66	7.6	18	3.7	0		138	9.2	559	9.9
7	13	0.5	0		0		0		3	0.2	16	0.3
8	1	0.0	0		0		0		0		1	0.0
Subtotal	2,677		874		483		80		1,507		5,621	
Combined												
3	0		0		1	0.2	0		0		1	0.0
4	26	0.9	0		0		0		15	1.0	41	0.7
5	2,412	85.6	826	92.4	525	95.6	145	96.0	1,351	89.6	5,259	88.8
6	363	12.9	68	7.6	23	4.2	6	4.0	138	9.2	598	10.1
7	16	0.6	0		0		0		3	0.2	19	0.3
8	1	0.0	0		0		0		0		1	0.0
Total	2,818		894		549		151		1,507		5,919	

Table 7. Frequency distribution of left marginal scute counts for dead and live Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Number of left marginal scutes	Corral nests		Incubation-handling category								Total	
	frequency	%	Padre Island boxes frequency	%	Rancho Nuevo boxes frequency	%	Natural nests frequency	%	Galveston head starts frequency	%	frequency	%
Dead												
9	2	1.4	0		0		0		0		2	0.7
10	0		1	5.0	0		0		0		1	0.3
11	2	1.4	1	5.0	0		0		0		3	1.0
12	5	3.5	1	5.0	3	4.5	0		0		9	3.0
13	86	61.0	13	65.0	55	83.3	63	88.7	0		217	72.8
14	37	26.2	3	15.0	8	12.1	8	11.3	0		56	18.8
15	8	5.7	1	5.0	0		0		0		9	3.0
16	1	0.7	0		0		0		0		1	0.3
Subtotal	141		20		66		71		0		298	
Live												
11	0		0		0		0		1	0.1	1	0.0
12	29	1.1	3	0.3	1	0.2	0		4	0.3	37	0.7
13	1,988	74.3	669	76.5	394	81.6	60	75.0	975	64.7	4,086	72.7
14	606	22.6	195	22.3	88	18.2	20	25.0	498	33.0	1,407	25.0
15	52	1.9	7	0.8	0		0		28	1.9	87	1.5
16	2	0.0	0		0		0		1	0.1	3	0.1
Subtotal	2,677		874		483		80		1,507		5,621	
Combined												
9	2	0.1	0		0		0		1	0.1	2	0.0
10	0		1	0.1	0		0		4	0.3	1	0.0
11	2	0.1	1	0.1	0		0		975	64.7	4	0.1
12	34	1.2	4	0.4	4	0.7	0		498	33.0	46	0.8
13	2,074	73.6	682	76.3	449	81.8	123	81.5	28	1.9	4,303	72.7
14	643	22.8	198	22.1	96	17.5	28	18.5	1	0.1	1,463	24.7
15	60	2.1	8	0.9	0		0		0		96	1.6
16	3	0.1	0		0		0		0		4	0.1
Total	2,818		894		549		151		1,507		5,919	

Table 8. Frequency distribution of right marginal scute counts for dead and live Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Number of right marginal scutes	Incubation-handling category											
	Corral nests		Padre Island boxes		Rancho Nuevo boxes		Natural nests		Galveston head starts		Total	
	frequency	%	frequency	%	frequency	%	frequency	%	frequency	%	frequency	%
Dead												
9	2	1.4	0		0		0		0		2	0.7
10	1	0.7	1	5.0	0		0		0		2	0.7
11	0		0		1	1.5	0		0		1	0.3
12	6	4.3	0		1	1.5	0		0		7	2.3
13	89	63.1	17	85.0	57	86.4	58	81.7	0		221	74.2
14	39	27.7	2	10.0	7	10.6	13	18.3	0		61	20.5
15	4	2.8	0		0		0		0		4	1.3
Subtotal	141		20		66		71		0		298	
Live												
9	1	0.0	0		0		0		0		1	0.0
10	0		0		0		0		0		0	
11	1	0.0	0		0		0		0		1	0.0
12	25	0.9	3	0.3	44	9.1	0		8	0.5	80	1.4
13	1,923	71.8	628	71.9	333	68.9	56	70.0	972	64.5	3,912	69.6
14	658	24.6	237	27.1	106	21.9	23	28.8	515	34.2	1,539	27.4
15	67	2.5	6	0.7	0		1	1.2	9	0.6	83	1.5
16	2	0.1	0		0		0		3	0.2	5	0.1
Subtotal	2,677		874		483		80		1,507		5,621	
Combined												
9	3	0.1	0		0		0		0		3	0.1
10	1	0.0	1	0.1	0		0		0		2	0.0
11	1	0.0	0		1	0.2	0		0		2	0.0
12	31	1.1	3	0.3	45	8.2	0		8	0.5	87	1.5
13	2,012	71.4	645	72.1	390	71.0	114	75.5	972	64.5	4,133	69.8
14	697	24.7	239	26.7	113	20.6	36	23.8	515	34.2	1,600	27.0
15	71	2.5	6	0.7	0		1	0.7	9	0.6	87	1.5
16	2	0.1	0		0		0		3	0.2	5	0.1
Total	2,818		894		549		151		1,507		5,919	

Table 9. Mean values of the differences between paired left and right counts for costal and marginal scute series of Kemp's ridley hatchlings and juveniles, by incubation-handling category.

Scute series and incubation-handling category	n	Mean	Standard error	P ^a
Marginal Scutes				
Dead ^b	298	0.017	0.038	0.656
Live	5,621	-0.015	0.007	0.039*
Corral nests	2,677	-0.030	0.011	0.007*
Padre Island boxes	874	-0.046	0.018	0.012*
Rancho Nuevo boxes	483	0.052	0.024	0.035*
Natural nests	80	-0.063	0.060	0.300
Galveston head starts	1,507	0.011	0.012	0.349
Total	5,919	-0.013	0.007	0.062
Costal Scutes				
Dead ^b	298	0.030	0.031	0.335
Live	5,621	0.027	0.005	< 0.001*
Corral nests	2,677	0.025	0.008	0.002*
Padre Island boxes	874	0.022	0.009	0.013*
Rancho Nuevo boxes	483	0.014	0.010	0.162
Natural nests	80	0.000	0.000	1.000
Galveston head starts	1,507	0.038	0.010	< 0.001*
Total	5,919	0.027	0.005	< 0.001*

^aProbability that the observed mean difference between paired left and right scute counts was significantly different from zero; i.e., that there was significant departure from bilateral symmetry in a matched pairs t-test. *Indicates significance at alpha ≤ 0.05.
^bNot subdivided by incubation-handling category because of small sample size.

Table 10. Summary statistics for carapacial scute counts of dead and live Kemp's ridley hatchlings from 37 corral nests.

Scute series	Range	Minimum	Maximum	Standard		Coefficient of		
				Mode	Mean	deviation	variation (%)	
Dead (n=141)								
Left marginals		7	9	16	13	13.28	0.895	6.74
Left costals		5	3	8	5	5.22	0.656	12.56
Vertebrals		6	3	9	5	5.67	0.908	16.02
Right costals		3	4	7	5	5.18	0.538	10.40
Right marginals		6	9	15	13	13.21	0.826	6.25
Live (n=2,677)								
Left marginals		4	12	16	13	13.26	0.506	3.82
Left costals		4	4	8	5	5.15	0.411	7.97
Vertebrals		5	4	9	5	5.40	0.666	12.34
Right costals		4	4	8	5	5.13	0.373	7.27
Right marginals		7	9	16	13	13.29	0.536	4.04

Table 11. Summary statistics for carapacial scute counts of dead and live Kemp's ridley hatchlings from 11 Padre Island boxes.

Scute series	Range	Minimum	Maximum	Mode	Mean	Standard deviation	Coefficient of variation (%)
Dead (n=20)							
Left marginals	5	10	15	13	12.95	1.050	8.11
Left costals	2	4	6	5	5.05	0.394	7.80
Vertebrals	2	5	7	5	5.45	0.686	12.59
Right costals	1	5	6	5	5.10	0.308	6.04
Right marginals	4	10	14	13	12.95	0.759	5.86
Live (n=874)							
Left marginals	3	12	15	13	13.24	0.451	3.41
Left costals	2	5	7	5	5.10	0.315	6.18
Vertebrals	3	5	8	5	5.15	0.406	7.88
Right costals	1	5	6	5	5.08	0.264	5.21
Right marginals	3	12	15	13	13.28	0.472	3.56

Table 12. Summary statistics for carapacial scute counts of dead and live Kemp's ridley hatchlings from seven Rancho Nuevo boxes.

Scute series	Range	Minimum	Maximum	Mode	Mean	Standard deviation	Coefficient of variation (%)
Dead (n=66)							
Left marginals	2	12	14	13	13.08	0.404	3.09
Left costals	1	5	6	5	5.08	0.267	5.25
Vertebrals	3	4	7	5	5.11	0.434	8.50
Right costals	3	3	6	5	5.05	0.369	7.32
Right marginals	3	11	14	13	13.06	0.425	3.26
Live (n = 483)							
Left marginals	2	12	14	13	13.18	0.390	2.96
Left costals	1	5	6	5	5.05	0.222	4.39
Vertebrals	3	4	7	5	5.09	0.302	5.93
Right costals	1	5	6	5	5.04	0.190	3.76
Right marginals	2	12	14	13	13.13	0.543	4.13

Table 13. Summary statistics for carapacial scute counts of dead and live Kemp's ridley hatchlings from five natural nests.

Scute series	Range	Minimum	Maximum	Mode	Mean	Standard deviation	Coefficient of variation (%)
Dead (n=71)							
Left marginals	1	13	14	13	13.11	0.318	2.43
Left costals	1	5	6	5	5.11	0.318	6.23
Vertebrales	1	5	6	5	5.13	0.335	6.54
Right costals	1	5	6	5	5.08	0.280	5.51
Right marginals	1	13	14	13	13.18	0.390	2.95
Live (n=80)							
Left marginals	1	13	14	13	13.25	0.436	3.29
Left costals	0	5	5	5	5.00	0.000	0.00
Vertebrales	1	5	6	5	5.03	0.157	3.13
Right costals	0	5	5	5	5.00	0.000	0.00
Right marginals	2	13	15	13	13.31	0.493	3.70

Table 14. Frequencies of the modal scute number for Kemp's ridley sea turtles.

Group	13 left marginals		5 left costals		5 vertebrales		5 right costals		13 right marginals	
	frequency	%	frequency	%	frequency	%	frequency	%	frequency	%
Hatchlings^a										
Corral nests (n=2,677)	1,988	74.3	2,238	83.6	1,804	67.4	2,307	86.2	1,923	71.8
Padre Island boxes (n=874)	669	76.5	794	90.8	751	85.9	808	92.4	628	71.9
Rancho Nuevo boxes (n=483)	394	81.6	458	94.8	438	90.7	465	96.3	333	68.9
Natural nests (n=80)	60	75.0	80	100.0	78	97.5	80	100.0	56	70.0
Juveniles^a										
Galveston head starts (n=1,507)	975	64.7	1,301	86.3	941	62.4	1,351	89.6	972	64.5
Subadults^b										
(n=96)			95	99.0			96	100.0		
Adult Females^c										
(n=154)	89	57.8	151	98.1	135	87.7	148	96.1	123	79.9

^aThis study; live turtles only.

^bFrom Carr and Caldwell (1956).

^cFrom Chávez *et al.* (1967, 1968).

Clearly, the most interesting observation regarding variation in vertebral scute count was its apparent relation to incubation-handling technique. Various aspects of the data suggested greatest departure from normal vertebral counts in the corral nests and Galveston head starts, least in naturally incubated turtles, and intermediate in the Padre Island and Rancho Nuevo boxes. This same trend recurs in other scute series, as well as in overall scute pattern.

Variation in the Costal Scute Series

Patterns of variation in left and right costal scute series were very similar (Tables 2 and 3), reflecting their bilateral symmetry. Among the 5,919 specimens, left and right costals exhibited the same range (5), minimum (3), maximum (8) and mode (5). The two costal series exhibited the least variation in count among the carapacial scute series (with the exception of the nuchal), as indicated by the low ranges and standard deviations (Tables 2 and 3). The means and modes for each costal series were closer to one another in all incubation-handling categories than the means and modes of any other scute series, further depicting the stability of costal scute counts as compared to counts in the other scute series.

Variability in scute counts within both costal series was greatest in the corral nest category, followed by the Galveston head starts, Padre Island boxes, Rancho Nuevo boxes and natural nests as shown by the standard deviations and ranges (similar in Padre Island and Rancho Nuevo boxes, Table 3). There was greater variation among dead turtles than among live turtles (Tables 5 and 6). The proportion of turtles exhibiting the modal count of five costals, whether left or right, was lower for dead turtles than for live ones in all incubation-handling categories. This suggested greater stability in costal scute count in live turtles than in those that died as hatchlings or embryos.

Variation in the Marginal Scute Series

Bilateral symmetry between counts of left and right marginals was evidenced by their identical ranges (7), minima (9), maxima (16) and modes (13) among the 5,919 turtles (Table 2). The greatest range in marginal scute counts occurred in the corral category, followed in descending order by Galveston head starts, Padre Island boxes, Rancho Nuevo boxes and natural nests. Mean scute numbers and standard deviations indicated that marginal scutes were the most variable scute series in Padre Island box, Rancho Nuevo box and natural nest categories, and were exceeded in variability only by the vertebral series in the corral nest and Galveston head start categories (Table 3).

As was the case with vertebrals and costals, the corral nest and Galveston head start categories exhibited the greatest variation in counts of marginals as contrasted with natural nests which exhibited the least. However, the differences in variability of marginal counts among the incubation-handling categories were slight, suggesting more stability in marginal scute counts among the five incubation-handling categories than for the other scute series.

Dead versus live comparisons for marginal count variability were not as clearly differentiated as were the cases for the costal and vertebral series. Marginal scute counts showed generally greater variability in dead than in live turtles, but the percentages of turtles exhibiting the modal count of 13 marginals (left or right) followed a different rank order among incubation-handling categories (Tables 7 and 8) than for other scute series (Tables 4-6).

Tests of Symmetry in Paired Counts of Scute Series

A series of t-tests was performed on mean differences between left and right counts of costals and marginals for all 5,919 turtles, and for various subgroupings (Table 9). Tested was the null hypothesis of bilateral symmetry in left and right counts. The difference was obtained for each specimen by subtracting the right scute count from the left scute count, for marginal and costal series separately.

For marginals, the mean difference for the entire sample of 5,919 turtles was not significantly different from zero, suggesting bilateral symmetry in scute counts, though certain groupings exhibited significant asymmetry (Table 9). For example, marginal counts were significantly asymmetric in live turtles, but the dead specimens showed no significant asymmetry. The live turtles from corral nests, Padre Island boxes and Rancho Nuevo boxes had significantly asymmetric marginal counts, even though Galveston head starts and turtles from natural nests did not.

In contrast, left and right costals for the entire sample of 5,919 turtles were significantly asymmetric (Table 9). Yet, only the live turtles exhibited significant asymmetry in costal counts, while the dead turtles did not. Substantial differences in sample size between the live and dead subgroupings may have contributed to the difference in costal scute results for these two subgroupings. The dead subgroup was the smaller of the two, so its t-test of the mean difference between counts of left and right costal scutes was more conservative than that for the live subgroup.

For costals and marginals, the natural nest and Rancho Nuevo box categories did not have significant mean differences between left and right counts, whereas corral nest, Padre Island box and Galveston head start categories exhibited significantly asymmetric counts. In those incubation-handling categories exhibiting costal count asymmetry, the greater number of scutes occurred in the left series (Table 9). Among the incubation-handling categories displaying asymmetrical marginal counts, corral nest and Padre Island box categories had a greater number of scutes in the right series, while the Rancho Nuevo category had the greater number in the left series. It is tempting to suggest, based on the corral nest and Padre Island box categories, that there is a relationship between the increase in right

marginals and left costals. This may reflect some developmental mechanism that balances combined costal and marginal scute counts on left and right sides of the carapace such that overall symmetry in left and right counts is maintained. However, this balance was not evident in the Rancho Nuevo box category.

Variation in Scute Series by Incubation-Handling Category

Corral Nests – Several of the preceding analyses indicated that hatchlings from corral nests exhibited a higher degree of variability than those from any of the other incubation-handling category. Corral nest hatchlings had the greatest ranges, standard deviations (with one exception: left marginals for Galveston head starts), and coefficients of variation for scute counts in each of the scute series (Table 3). However, corral nests represented the largest incubation-handling category (2,818 turtles), or 48 percent of all turtles examined. Also, greater variability in dead than in live turtles from corral nests for all scute series (Tables 4 and 10) contributed to the overall variability in the corral nest category. Within the corral nest category, the most variable scute series was the vertebral, followed by the marginal, then the costal.

Galveston Head Starts – Juvenile turtles from the Galveston head start category were second to the corral nest category in degree of variability within scute series. Based on ranges, standard deviations and coefficients of variation for each scute series (Table 3), Galveston head starts had slightly lower scute variability than hatchlings in the corral nest category, though consistently higher variability than Rancho Nuevo box, Padre Island box and natural nest categories. Galveston turtles, like hatchlings from corral nests, showed greatest variation in the vertebral series, followed by the marginal then the costal series.

The reader is cautioned about drawing broad conclusions based on our observations of the 1980 year-class of Galveston head start juveniles as compared to hatchlings of the 1981 year-class. We only witnessed the incubation-handling techniques used in 1981, and not those used for the 1980 year-class of Kemp's ridleys head started at the Galveston Laboratory. We had no data to compare environmental conditions between the two years, thus raising the possibility that the observed differences between the Galveston head starts from the 1980 year-class and the other incubation-handling categories from the 1981 year-class might be due to differences in environmental variables other than incubation-handling techniques. Also, we had no dead subgroup to compare to the live subgroup from the Galveston head start category, thus there was no opportunity to investigate changes during ontogeny within this category. Finally, we had no way of determining whether incubation-handling was consistent from year to year for those nests destined to provide hatchlings for head starting.

Padre Island Boxes – Hatchlings from the Padre Island boxes were consistently intermediate in scute series variability between the two extremes represented by the highly variable corral nest and Galveston head start categories and the slightly variable Rancho Nuevo box and natural nest categories. This is shown by ranges, standard deviations and coefficients of variation for the scute series (Table 3). Costals were the least variable of the scute series for both live and dead hatchlings in the Padre Island box category, with marginals showing greatest variability in the dead subgroup, and vertebrales showed greatest variability in the live subgroup.

The mean marginal scute counts of dead hatchlings in the Padre Island box category were lower than those for live turtles in that category (Table 11). This tendency toward lower counts of marginals in dead Padre Island hatchlings (Table 11) was unique among all live-dead contrasts, scute series and incubation-handling categories (Tables 4-8 and 10-13). However, only 20 dead specimens in the Padre Island box category were examined.

Rancho Nuevo Boxes – In general, both live and dead turtles in the Rancho Nuevo box category exhibited the least amounts of variability in scute counts (Table 12) as judged by ranges, standard deviations and coefficients of variation in scute counts for all incubation-handling categories except the natural nests. The dead turtles showed greatest variability in the vertebral series, while live turtles show greatest variability within the marginal series. Costals were the most stable series for both live and dead hatchlings in the Rancho Nuevo box category.

Natural Nests – The least overall variation in scute counts was observed in the natural nest category (Table 13), no doubt due in part to the small sample size for this category. Indeed, in nearly all scute series, the turtles from natural nests showed the lowest variation of all among the incubation-handling categories. The greatest variation for natural nest turtles was in the marginal series, followed by the vertebral and costal series (which exhibited 100 percent modal counts in the live subsample).

Departures from Modal Scute Counts

Table 14 provides for comparisons among scute series and incubation-handling categories of our study, as well as within sub-adult (Carr and Caldwell, 1956) and adult female Kemp's ridleys (Chávez *et al.*, 1967, 1968) from other studies. Only live turtles were used in this comparison because the other studies were based on live specimens.

Costals showed less departure from the mode than vertebrales or marginals, the latter of which had the lowest percentage of turtles with the modal count. An exception to this was that the corral nest and Galveston head start categories exhibited a high percentage of turtles with modal counts for costals, and percentages for modal counts of

vertebrals similar to those for marginals. In general, corral nest and Galveston head start categories exhibited greater departures from modal counts for all scute series than did the other categories.

Adult female Kemp's ridleys (Chávez *et al.*, 1967, 1968) also exhibited higher proportions of modal scute counts for costals and vertebrals than for marginals. The percentages of adult females exhibiting modal counts for vertebrals and costals fell within the range of comparable percentages for the Rancho Nuevo box, Padre Island box and natural nest categories. In the adult females, the proportion with modal counts for left marginals was considerably lower than that for the right marginals. It was also the lowest of the percentages for any group of turtles in Table 14. On the other hand, the proportion with modal counts for the right marginal series was higher in the adult female than for any of the categories in our study. Only costal scute counts were available for subadult Kemp's ridleys (Carr and Caldwell, 1956), and the proportions of turtles with modal counts were on the high end of the range, similar to those of the Rancho Nuevo box and natural nest categories of our study.

Variation in Scutation

Among the 5,919 turtles examined in our study, 264 different scute patterns or scutations were recorded: 77 patterns among the dead turtles ($n = 298$) and 233 patterns among the live turtles ($n = 5,621$). Included among the 77 scute patterns found in the dead specimens were 31 patterns that did not occur in live turtles. The modal scute pattern (13-5-5-5-13) was observed in 2,646 (44.7 percent) turtles. The next most common patterns were: 13-5-5-5-14 (in 444 turtles or 7.5 percent), 13-5-6-5-13 (in 438 turtles or 7.4 percent), 14-5-5-5-14 (in 384 turtles or 6.5 percent) and 14-5-5-5-13 (in 373 turtles or 6.3 percent). It is interesting that the most common of the aberrant scute patterns involved additional marginal or vertebral scutes. A scute count lower than the mode was a much rarer occurrence than one higher than the mode for any scute series. In cases in which there were above-modal vertebral and costal scute counts, the additional scutes most often appeared at the posterior end of the scute series as a split fifth costal or fifth vertebral scute, or as a supernumerary scute between the fourth and fifth vertebrals. Extra marginal scutes, on the other hand, nearly always appeared at the anterior end of the series as a split second, third or fourth marginal scute.

The mean number of different scute patterns per nest (i.e., per clutch) within each incubation-handling category provided another measure of relative variability in scutation. The mean number of scute patterns per clutch was highest in the corral nest category (20.8 patterns), followed by the Padre Island box (11.2 patterns) and Rancho Nuevo box (9.1 patterns) categories. The small amount of information available for natural nests suggested even fewer variants per nest (approximately 4.5 patterns). We were unable to make such calculations for the Galveston head starts, because we had no data on how many clutches were represented in our sample.

Departures from Modal Scute Patterns

The proportion of turtles exhibiting the modal scute pattern (13-5-5-5-13) was not significantly different in live and dead subgroupings in the 5,919 specimens in our study (Table 15). In that regard, the only significant difference occurred for the corral nests in which more of the live turtles (41.7 percent) exhibited the modal scute pattern than did the dead turtles (26.2 percent), as shown in Table 15 and Figure 2. The greatest percentage of individuals showing the modal scute pattern was in the Rancho Nuevo box category, followed closely by natural nests, with the Padre Island box category being about 10 percent less. Live turtles from corral nest and Galveston head start categories had nearly the same proportions (about 42 percent) of individuals with modal scute patterns.

Discussion

While most earlier researchers examined carapacial scute variation in Kemp's ridley only with regard to individual scute series, we expanded our examinations to include variation in frequencies of scute patterns as a whole. Comparisons among the five different incubation-handling categories of our study, each of which was exposed to different environmental conditions during ontogeny, provided tests of the working hypothesis that scute variability might be related to environmental circumstances during ontogeny. To determine if there were differences in scute variation within a given incubation-handling category during development, we examined different ontogenetic stages represented by dead (younger hatchlings and embryos) and live specimens (later stage). One might expect increased variability to be evidenced in the dead turtles relative to the live ones if selection were acting to remove extreme phenotypes from the population. Evidence in support of this hypothesis would indicate that scute variation may be related to the survivability of the individual. This could act through underlying problems of viability associated with some scute pattern variants (Zangerl, 1969; Hill, 1971).

We have no reason to believe that scute pattern itself is a selective factor. Pritchard (1969a) commented that the hydrodynamics of a turtle's shell would be little affected by the arrangement or quantity of scute seams and the overall appearance of a turtle's shell is little affected by scute variation. Therefore, it seems more likely that an abnormal scute pattern is an external phenotypic expression of some underlying physiological or morphological problem which may affect the viability of the turtle. The senior author has noted, on several occasions, that extreme deformity and albinism

Table 15. G-tests of the null hypothesis of independence between scute pattern and incubation-handling category for Kemp's ridley hatchlings and juveniles.

Pairwise contrasts between incubation-handling categories	G ^a
Dead vs. Live ^b	
Corral nests	13.9956*
Padre Island boxes	0.5418
Rancho Nuevo boxes	1.6555
Natural nests	0.0424
Combined (total)	0.1838
Live only	
Corral nests vs. Padre Island boxes	11.4840*
Corral nests vs. Rancho Nuevo boxes	55.3000*
Corral nests vs. Natural nests	7.7996*
Corral nests vs. Galveston head starts	0.1186
Padre Island boxes vs. Rancho Nuevo boxes	17.3342*
Padre Island boxes vs. Natural nests	2.4970
Padre Island boxes vs. Galveston head starts	8.0904*
Rancho Nuevo boxes vs. Natural nests	0.1830
Rancho Nuevo boxes vs. Galveston head starts	46.4818*
Natural nests vs. Galveston head starts	7.1012*

* indicates significance at $\alpha \leq 0.05$, leading to rejection of the null hypothesis; i.e., concluding that the two groups being compared are significantly different.

^bThere were no dead turtles in the Galveston head start category, so no tests were possible with that category.

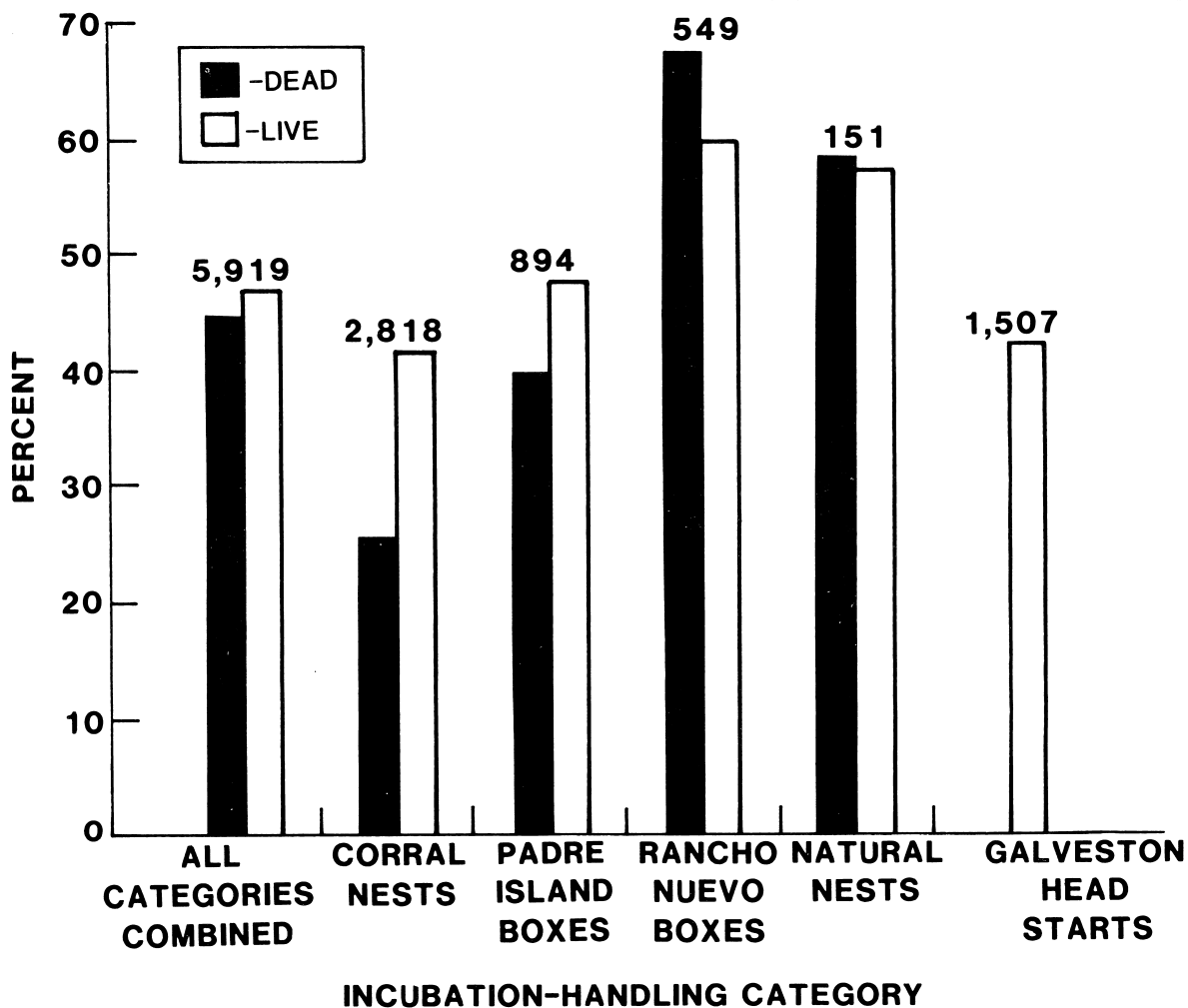


Figure 2. Proportions of live and dead Kemp's ridley hatchlings and juveniles that exhibited the modal scute pattern (13-5-5-13), by incubation-handling category (sample size is shown above the vertical bars for each category).

in dead hatchling sea turtles is nearly always accompanied by aberrant scute pattern, yet the abnormal scute pattern itself was certainly not the cause of death. Certain abnormal scute patterns were never observed in live turtles, but only in dead specimens. There were 31 of these "lethal scute patterns" observed in this study.

A high degree of carapacial scute variation was encountered in the young Kemp's ridleys in our study, despite various statements in the literature regarding the great stability of scutation in Kemp's ridley as compared to olive ridley (Pritchard and Márquez, 1973; Frazier, 1984). Though the most common carapacial scute pattern we observed in Kemp's ridley was 13-5-5-5-13, it occurred in only 44 percent of the 5,919 turtles we examined, thus it constituted less than half of our relatively large sample.

Differences in amounts of carapacial scute variation among the five incubation-handling groups we examined were notable. Based on our qualitative judgements in ranking the five incubation-handling categories, the most carefully handled and undisturbed eggs (Padre Island boxes and natural nests) produced turtles with less carapacial scute variability, and the most roughly handled eggs (Corral nests) produced turtles with higher levels of scute variation. Even if the 1980 year-class represented by the Galveston head starts is ignored, the trend from higher variability in carapacial scutes of turtles from roughly handled eggs to lower variability in turtles from carefully handled eggs or unhandled eggs appears in nearly all analyses of the data. For the Galveston head starts we possessed the least complete information regarding actual incubation conditions and no dead subgroup for this sample. Indeed, large and significant differences in amount of variability were present among the groups of turtles derived from eggs incubated or handled in different ways. These results suggest that environmental circumstances during incubation affect scute variability of the resultant hatchlings.

Several environmental factors have been implicated as agents causing scute pattern variation (see review by Ewert, 1979), all of them acting during the embryonic phase of the life cycle. Handling is merely one of these factors (Hill, 1971), so we have considered both incubation and handling together rather than handling alone. Incubation temperatures and humidity regimes varied greatly among our five incubation-handling categories, with the widest differences in this regard being between the concrete block house and the natural beach. There was no great disparity in carapacial scute variability within the 1981 year-class hatchlings derived from the two incubation-handling categories incubated in the concrete block house (*viz.* Rancho Nuevo and Padre Island). Both of these categories were considered to be carefully handled eggs. The greatest disparity in carapace scute variation occurred between the two groups of eggs incubated on the Rancho Nuevo beach, with roughly handled eggs represented by corral nests producing turtles with the greatest amount of scute variation and untouched eggs represented by natural nests which produced turtles with far less scute variability. Though there were numerous factors, like temperature and humidity, that may have affected embryonic development of the turtles from our five categories, we had no quantitative measurements of these potentially significant factors. Instead our conclusions are based on qualitative judgements of the environmental differences and obvious distinctiveness among the five incubation-handling categories. While no cause and effect relationship has been demonstrated, we believe that the differences in the degrees of scute variability among the categories are attributable, at least in part, to the ways in which the eggs were treated or not treated after oviposition.

Comparisons of carapacial scute variability between dead and live individuals were made among the four incubation-handling categories examined in Mexico. On the whole, dead turtles exhibited somewhat more variation than live turtles, and correspondingly lower relative frequencies (percentages) in the modal scute class (for a given series) than live turtles. This is particularly notable in the corral nest category, as this was the only category with a large sample of dead individuals. Our results suggest that dead animals (the youngest ontogenetic stage in our study) had more variability in carapacial scutes than live animals, indicating that selection was acting to remove extreme phenotypes from the younger age classes. Nevertheless, these results are no more than suggestive. Comparisons between categories of Kemp's ridley hatchlings in our study and categories represented by juveniles (Carr and Caldwell, 1956) and adult females (Chávez *et al.*, 1967 and 1968) revealed no marked differences. Confirmation that selection acts on the extremes of carapacial scutation phenotypes in Kemp's ridleys awaits further study.

Interest in possible significance of carapacial scute variation as an index of the effects of differences in incubation-handling techniques may increase now that we have demonstrated considerable variation in carapacial scute counts among turtles obtained from eggs incubated and handled in a variety of ways. The process in which phenotypic variation occurs as a consequence of physical environmental factors acting on sensitive portions of a developing organism was referred to by Smith-Gill (1983) as phenotypic modulation. Scutes or scales are phenotypic variables that are easily quantified and which have been presumed to reflect, at least in underlying genetic variation (Fox, 1975). Several studies of squamate reptiles have examined the evolutionary significance of scale count variation at different ontogenetic stages (see review by Simbotwe, 1981). However, the carapacial scutes of turtles do not seem to have

received such attention, possibly due to the relatively low frequencies of individual variations, and to the phylogenetic stability of the overall scute pattern (Zangerl and Johnson, 1957; Zangerl, 1969). The large extent to which phenotypic modulation appears to determine the degree of variability in carapacial scutes of turtles brings into question the role that heritability plays in the observed variation. It seems likely that the extent of phenotypic modulation present is itself a heritable feature. Nevertheless, each generation may be subject anew to selection on the variety of carapacial scute phenotypes produced by phenotypic modulation. As noted by Smith-Gill (1983), this variation may not necessarily be adaptive, or it may be non-adaptive. Hill (1971) found that adult olive ridleys (*L. olivacea*) in Surinam were less variable in scutation than hatchlings, and he implied that increased variation was not desirable. A study of green turtles (*Chelonia mydas*) by Le Toquin, Gamel and Trotignon (1980) also implied that the scutes of adult sea turtles were less variable than those of hatchlings. These previous studies support the hypothesis that selection acts against extremes in carapacial scutation phenotypes.

Conclusions

Implications of our findings to the conservation of endangered sea turtles such as Kemp's ridley are numerous. We have presented evidence confirming that the manner in which eggs of Kemp's ridley are handled after oviposition has a marked effect on carapacial scute variability. Further, it is apparent that increased variability is undesirable, with more extreme variants being less viable and selectively removed from the population over the course of ontogenetic development. Therefore, transplantation, translocation and artificial incubation of sea turtle eggs should be evaluated with concern for their possible effects on viability of hatchlings.

When the mechanisms of scute abnormality are better understood, scute patterns may become useful external indicators of phenotypic or genotypic deficiencies related to future viability. Many selective pressures are removed by artificial incubation but are replaced by others, so any external indicator of phenotypic or genotypic deficiency would be a useful tool in determining the long-term effects and suitability of artificial incubation and various other techniques involving the incubation and handling of eggs. For example, culling of abnormal individuals based on the presence of certain known, lethal scute patterns might be an effective means of maintaining healthy stocks.

Developmental plasticity is the process whereby environmental input alters the phenotype of an organism (Smith-Gill, 1983). Environmentally determined sex in turtles is a well documented example of this sort of alteration (Bull, 1980, 1983). The possible consequences of artificially altering sea turtle sex ratios through control of conditions during incubation of eggs have been widely publicized (Mrosovsky and Yntema, 1980; Yntema and Mrosovsky 1980, 1982; Morreale *et al.*, 1982; Mrosovsky, 1982). Smith-Gill (1983) reviewed the concept of critical period during development with regard to phenotypic plasticity. It holds that organs are most susceptible to environmental influences during periods when they are most actively differentiating. The critical period during which temperature influences gonadal differentiation in turtles is the middle third of incubation (Bull and Vogt, 1981; Yntema and Mrosovsky, 1982). Similarly, the carapacial scute pattern must also have a critical period for differentiation (Ewert, 1979). Research to determine when this critical period occurs could aid conservationists in making wise choices about when to move eggs, if at all, and would doubtless help in determining linkages between aberrant scute patterns and other organ system abnormalities which are more directly related to long-term viability.

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Literature

- Brongersma, L.D. 1968. Notes upon some turtles from Surinam. *Koninklijke Nederlandse Akademie van Wetenschappen, Proceedings, Series C, Biological and Medical Sciences* 71(12):114-127.
- Bull, J.J. 1980. Sex determination in reptiles. *Quarterly Review of Biology* 55:3-21.
- Bull, J.J. 1983. **Evolution of sex determining mechanisms**. The Benjamin/Cummings Publishing Company, Inc., Menlow Park, California, xx plus 316 pp.
- Bull, J.J. and R.C. Vogt. 1979. Temperature dependent sex determination in turtles. *Science* 206:1186-1188.
- Bull, J.J. and R.C. Vogt. 1981. Temperature-sensitive periods of sex determination in emydid turtles. *Journal of Experimental Zoology* 218:435-440.

- Carr, A.F. and D.K. Caldwell. 1956. The ecology and migrations of sea turtles: 1. results of fieldwork in Florida, 1955. *American Museum Novitates* 1793, 23p.
- Chávez, H., M. Contreras G. and T.P.E. Hernández D. 1967. Aspectos biológicos y protección de la tortuga lora *Lepidochelys kempi* (Garman), en la costa de Tamaulipas, Mexico. *Instituto Nacional de Investigaciones Biológicas Pesquera, Publicación Número 17*, 40 p.
- Chávez, H., M. Contreras G. and T.P.E. Hernández D. 1968. On the coast of Tamaulipas. *International Turtle & Tortoise Society Journal* 2(4):20-29, 37 and 2(5):16-19, 27-34.
- Coker, R.E. 1905a. Diversity in the scutes and bony plates of Chelonia. *Science* 21:384-385.
- Coker, R.E. 1905b. Gadow's hypothesis of "orthogenetic variation" in Chelonia. *Johns Hopkins University Circular* 178, p. 9-24.
- Coker, R.E. 1905c. Orthogenetic variation? *Science* 22:873-875.
- Coker, R.E. 1910. Diversity in scutes of Chelonia. *Journal of Morphology* 21:1-75.
- Deraniyagala, P. E. P. 1939. **The tetrapod reptiles of Ceylon, I. Testudinates and Crocodylians.** Colombo Museum, Colombo, Ceylon, xxxii plus 412 pp.
- Ewert, M.A. 1979. The embryo and its egg: development and natural history, p. 333-413. *In: Harless, M. and H. Morlock (Editors), Turtles: Perspectives and Research*, John Wiley and Sons, N.Y., xvi plus 695 p.
- Fox, W. 1948. Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. *Copeia* 1948: 252-262.
- Fox, S.F. 1975. Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. *Evolution* 29:95-107.
- Fox, W., C. Gordon and M.H. Fox. 1961. Morphological effect of low temperature during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica* 46:57-71.
- Frazier, J.G. 1984. Analisis estadístico de la tortuga golfina *Lepidochelys olivacea* (Escholtz) de Oaxaca, Mexico. *Ciencia Pesquera* 4:49-75.
- Gadow, H. 1899. Orthogenetic variation in the shells of Chelonia, p. 207-222, Part 3. *In: Willey, A. (Editor) Zoological Results Based on Material from New Britain, New Guinea, Loyalty Islands and Elsewhere, Collected During the Years 1895, 1896, and 1897.* Cambridge University Press, Cambridge, England.
- Hildebrand, S.F. 1930. Duplicity and other abnormalities in diamond-back terrapins. *Journal of the Elisha Mitchell Scientific Society* 46:41-53.
- Hildebrand, S.F. 1938. Twinning in turtles. *Journal of Heredity* 29:243-253.
- Hill, R.L. 1971. Surinam turtle notes - 1. Polymorphism of costal and vertebral laminae in the sea turtle *Lepidochelys olivacea*. *Stichting Natuurbehoud Suriname (STINASU), Mededelingen* 2:1-9.
- Le Toquin, A., E. Gamel and J. Trotignon. 1980. Morphologie, croissance individuelle et dynamique des populations de la tortue verte (*Chelonia mydas* L.) au Banc D'Arguin (Republique Islamique de Mauritanie). *Revue d'Ecologie (La Terre et la Vie)* 34:271-302.
- Limpus, C.J., V. Baker and J.D. Miller. 1979. Movement induced mortality of loggerhead eggs. *Herpetologica* 35:335-338.
- Lynn, W.G. and M.C. Ullrich. 1950. Experimental production of shell abnormalities in turtles. *Copeia* 1950:253-262.
- Morreale, S.J., G.J. Ruiz, J.R. Spotila and E.A. Standora. 1982. Temperature dependent sex determination: current practices threaten conservation of sea turtles. *Science* 216:1245-1247.
- Mrosovsky, N. 1982. Sex ratio bias in hatchling sea turtles from artificially incubated eggs. *Biological Conservation* 23:309-314.
- Mrosovsky, N. and C.L. Yntema 1980. Temperature dependence of sexual differentiation in sea turtles: implications for conservation practices. *Biological Conservation* 18:271-280.
- Newman, H.H. 1906. The significance of scute and plate "abnormalities" in Chelonia. *Biological Bulletin* 10: 68-114.
- Parker, G.H. 1901. Correlated abnormalities in the scutes and bony plates of the carapace of the sculptured tortoise. *American Naturalist* 35:17-24.
- Pritchard, P.C.H. 1969a. Sea turtles of the Guianas. *Bulletin of the Florida State Museum* 13:85-140.
- Pritchard, P.C.H. 1969b. Studies of the systematics and reproductive cycle of the genus *Lepidochelys*. Ph.D. Dissertation, University of Florida, Gainesville, xii plus 196 p.
- Pritchard, P.C.H. and R. Márquez M. 1973. Kemp's ridley turtle or Atlantic ridley *Lepidochelys kempi*. *International Union for the Conservation of Nature and Natural Resources Monograph No. 2:* 30 p.
- Pritchard, P.C.H. and P. Trebbau. 1984. The turtles of Venezuela. *Contributions to Herpetology* 2: 1-403.
- Simbotwe, M.P. 1981. Natural selection in the lizard *Eumeces obsoletus* (Lacertilia: Scincidae). *Amphibia-Reptilia* 2:143-151.
- Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. *American Zoologist* 23: 47-55.
- Sokal, R. and F.J. Rohlf. 1981. **Biometry.** Second Edition, W.H. Freeman and Company, San Francisco, California, 849 p.
- Wandolleck, B. 1904. Eine bucklige *Testudo graeca* L. *Zoologische Jahrbucher, Abtheilung für Systematik* 20:151-166.

- Yntema, C.L. 1976. Effects of incubation temperatures on sexual differentiation in the turtle *Chelydra serpentina*. *Journal of Morphology* 150:453-462.
- Yntema, C.L. and N. Mrosovsky. 1980. Sexual differentiation in hatchling loggerhead (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36:33-36.
- Yntema, C.L. and N. Mrosovsky. 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Canadian Journal of Zoology* 60:1012-1016.
- Zangerl, R. 1969. The turtle shell, p. 311-339. *In*: Gans, C. (Editor), **Biology of the Reptilia**, Volume 1, Morphology A, Academic Press, London, xvi plus 373 p.
- Zangerl, R. and R.G. Johnson. 1957. The nature of shield abnormalities in the turtle shell. *Fieldiana, Geology* 10:341-362.