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Clutch Size and Frequency in Florida Box Turtles (*Terrapene carolina bauri*): Implications for Conservation

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Abstract. – **From 1992 to 1995 I radiographed 515 Florida box turtles, *Terrapene carolina bauri*, residing on an island off the west coast of Florida. Shelled eggs were observed from late March through early August in females from 124 to 153 mm carapace length. Clutch size varied between 1 and 5 eggs ($\bar{x}$ = 2.4), with a mode of 2. Florida box turtles may produce 2 or 3 clutches annually although some individuals appeared to skip reproduction in some years. From 1.7 to 54.2% were gravid in any month sampled. Mean clutch size did not vary among months or sampling periods. The relationship between clutch size and both carapace and plastron lengths was linear and positive, although r^2 values were small. I suggest that variation in annual clutch size and frequency of the population result from differential resource availability among years rather than from morphological constraints, and I suggest a field study to test this hypothesis. Only a small percentage of the population produces multiple clutches, and clutch sizes are smaller than in northern conspecifics. The data suggest that the simple number of potential clutches is not a good measure of reproductive output in box turtles and is not a reliable estimator of the effects of removing individuals from a reproductively viable population.**

Key Words. – **Reptilia; Testudines; Emydidae; *Terrapene carolina bauri*; turtle; reproduction; clutch frequency; clutch size; fecundity; conservation; Florida; USA**

The number of eggs that a female turtle produces and the percentage of the population reproducing each year have important implications for the evolution of life-histories and for population persistence (Tinkle et al., 1981; Schwarzkopf and Brooks, 1986; Iverson, 1992; Scribner et al., 1993). Prior to the last 20 years or so, data on freshwater and terrestrial turtle reproduction came from museum specimens collected randomly in space and time, from the sacrifice of live individuals, from opportunistic observations, or from captive individuals. Each technique has biases that preclude reliable estimates of annual reproductive output at both the individual and population levels. The widespread use of radiographs (Gibbons and Greene, 1979) coupled with long-term data sets (e.g., Congdon and Gibbons, 1990a; Congdon and van Loben Sels, 1991; Iverson and Smith, 1993), allows researchers to investigate reproductive variables more reliably and to develop hypotheses of how turtles package their eggs in terms of morphological and resource allocation constraints.

Abdominal space obviously limits reproductive potential (Jackson, 1988) because turtles possess a rigid shell within which eggs must develop. The eggs then must pass through the pelvic girdle which may restrict egg width (Congdon and Tinkle, 1982; Congdon et al., 1983a; Congdon and Gibbons, 1987). For theoretical reasons, one might predict that selection would favor a trade-off between egg size and clutch size resulting in an optimal egg size (Brockelman, 1975), but this does not seem to have occurred in the many species of turtles that have been examined (Congdon et al., 1983a; Congdon and Gibbons, 1985; Rowe, 1994).

In addition to morphological constraints, other biotic and abiotic conditions may affect clutch size and frequency. Egg production requires a relatively expensive energy allocation. For example, reproduction consumes approximately 14% of the annual energy budget of the freshwater turtle *Chrysemys picta* in Michigan (Congdon et al., 1982). Congdon et al. (1987) suggested that factors affecting habitat quality and individual history might lower the ratio of energy available for reproduction to total maintenance energy. Thus, the amount of energy allocated to reproduction might be limited and result in "low frequency reproduction" (Bull and Shine, 1979).

Parental investment in turtles involves providing sufficient yolk not only for embryogenesis, but also to sustain the hatchling immediately after hatching, sometimes throughout the winter (Gibbons and Nelson, 1978) or during other adverse environmental conditions (Ewert, 1991). Given these constraints, the ability to produce large or multiple clutches in some species might be resource-constrained, especially in variable environments. If reproductive behavior itself is energetically expensive, females should maximize reproductive output during each nesting attempt (Hays and Speakman, 1991).

In addition to a resource constraint, a temporal constraint also may be involved. In order for turtles to produce multiple clutches, there must be enough time to complete embryonic development prior to the onset of harsh climatic conditions, or hatchlings must have sufficient yolk reserves for overwintering. The length of the nesting season, and thus the potential for multiple clutches, also might be limited by the number of warm days available for the initial vitellogenesis of follicles (Congdon et al., 1987). Clutch size, mass, and frequency are thus in a balance between individual and environmental constraints. Selection should maximize reproductive output given these constraints.

Clutch size and frequency are important considerations in conservation programs because fecundity is sometimes used as a measure of a population's resilience to disturbance (see below). By such reasoning, a species with a large per capita fecundity should recover faster from a decline than a species with a small per capita fecundity, assuming all else (e.g., aspects of population structure, survivorship) is equal. All else is seldom equal, however. For turtles, large numbers of eggs *per se* do not automatically bestow resilience to perturbations. For example, the large number of eggs produced by snapping turtles and sea turtles does not make them resilient to commercial take, since all life stages are important for population persistence and stability (Crouse et al., 1987; Congdon et al., 1994).

The box turtle, *Terrapene carolina*, is a ubiquitous species in eastern North America (Ernst et al., 1994). Although it is sometimes called the "common" box turtle, this name is a misnomer. Perceptions of commonness are rarely supported by reliable field data, and many populations have undergone substantial declines (Dodd and Franz, 1993). Box turtles are threatened by many factors, particularly habitat destruction and collection for the pet trade (Salzberg, 1994). Somewhat surprisingly there are few long-term data on box turtle reproduction (Messinger and Patton, 1995); indeed, information on even common characteristics, such as clutch size and frequency, is lacking among many subspecies or populations (Iverson, 1977; Ernst et al., 1994).

North American box turtles were listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) at the Ninth Meeting of the Conference of the Parties in Fort Lauderdale, Florida, in November 1994. Under USA law, the listing became effective early in 1995. As a result of CITES listing, permits are required before box turtles (all *Terrapene* sp.) can be exported from the USA. Prior to issuance, a scientific determination must be made that issuing the permit will not be biologically detrimental to wild populations and that the box turtles have been obtained legally.

For U.S. species, the U.S. Fish and Wildlife Service's Office of CITES Management Authority (OMA) issues export permits. However, the scientific determination is made by the Interior Department's Office of CITES Scientific Authority (OSA). According to Lieberman (1994), "OMA will work closely with State wildlife agencies to ensure that commercial exports will be considered only from States that allow exports and have sustainably managed populations."

In March 1995 OSA issued a memorandum recommending that the State of Louisiana be granted a permit to export 9750 *T. c. major* and *T. c. triunguis*. Although acknowledging the life-history traits of long-lived species that would argue against export (Congdon et al., 1993, 1994), the recommendation was based, in part, on the premise that since *T. c. major* was multiple-brooded, it would be more resistant to population perturbations than the species studied by Congdon et al. (1993, 1994). The memorandum acknowledged that the degree of resilience would depend on population parameters "for which we do not have any information."

Very few data on clutch size and frequency in *T. c. major* (Tucker et al., 1978, $n = 18$; Jackson, 1991, $n = 1$) are available, and I am aware of only two studies that report data on *T. c. triunguis* (Messinger and Patton, 1995; St. Clair, 1995). Hence, data gathered on other southeastern *T. carolina* populations might assist in making management and conservation decisions on these long-lived chelonians. In this paper, I present clutch size and frequency data on a population of Florida box turtles, *T. c. bauri*, based on 4 yrs of data collection. I then relate these findings to recent recommendations for box turtle export.

STUDY AREA AND METHODS

Egmont Key is a 180 ha island located in the mouth of Tampa Bay, Hillsborough Co., Florida (27°36'04"N, 82°45'40"W). The island has a long history of human occupation (Franz et al., 1992) and island habitats are highly modified by the introduction of many exotic plants. The primary vegetation types include sea oat (*Uniola paniculata*) meadows, Australian pine (*Casuarina equisetifolia*) groves, and extensive forests with a mixed cabbage palm (*Sabal palmetto*) – Australian pine – Brazilian pepper (*Schinus terebinthifolius*) overstory. Dodd et al. (1994) provide a detailed description of the island. Egmont Key is a National Wildlife Refuge presently leased to the State of Florida for

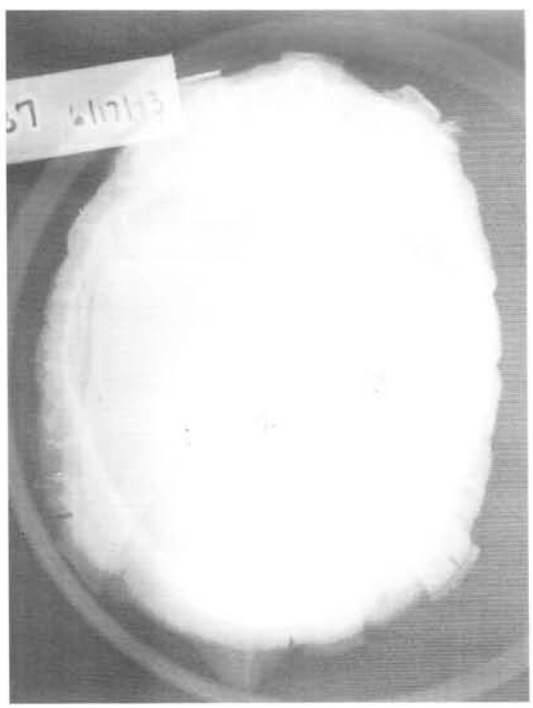


Figure 1. Radiograph of female box turtle # 687 (128 mm CL, 525 g) taken 17 June 1993. Three eggs are clearly visible.

use as a state park. Twelve species of amphibians and reptiles currently are known from the island (Franz et al., 1992; Smith et al., 1993).

Box turtles were collected on 11 three-day trips in 1992 (19–21 June), 1993 (23–25 April, 17–19 May, 16–18 June, 27–29 July), 1994 (7–9 June, 12–14 July, 9–11 August), and 1995 (19–21 March, 12–14 April, 22–24 May) from the southern 36.4 ha of the island. The turtles were taken to a field house where they were kept at ambient temperatures until radiographed, usually within 12–16 h of capture. Turtles were radiographed for 1 sec at 90 kV using a MinXray Model 903 portable X-ray machine (Fig. 1).

In addition to a variety of habitat and activity information (Dodd et al., 1994), data on carapace length (CL), plastron length (PL), and body mass (in g using a Pesola spring scale) were recorded. Turtles were shell notched (Cagle, 1939) for future recognition and released at or near their point of capture. I recorded egg number from the developed film (Gibbons and Greene, 1979) but made no attempt to measure egg size (see Graham and Petokas, 1989). Statistical procedures were carried out using the SAS program for microcomputers (SAS Institute, Inc., 1988). The level of significance was set at $\alpha < 0.05$.

RESULTS

A total of 515 radiographs were taken of 257 female turtles; data from an additional female captured while covering her nest (Dodd et al., 1994) are included in the results. The females ranged between 104 and 153 mm CL ($n = 258$, $\bar{x} = 133.2$, SD = 8.0), 90 to 138 mm PL ($n = 258$, $\bar{x} = 117.6$, SD = 8.7) and 195 to 605 g body mass ($n = 257$, $\bar{x} = 444.2$, SD = 83.4). There were no significant differences in CL among either months ($F_{5,135} = 1.71$, $p = 0.136$) or sampling periods ($F_{10,130} = 1.13$, $p = 0.345$). Although there were no significant differences in body mass among sampling periods (F[illegible] = 1.61, $p = 0.111$), there was significant variation in mass among months ($F_{5,134} = 2.74$, $p = 0.021$). However, no trends were apparent: the range of means spanned only 8.8 g, and standard deviations were high (64.5 to 93.7). There also were no significant differences in CL, PL, or body weights in all between-year comparisons in any one month (Table 1).

Shelled eggs were observed in all months sampled from late March through early August. Ninety-eight different turtles were found to be gravid at some point during the study (CL: 124–153 mm, $\bar{x} = 136.5$, SD = 5.9; PL: 107–137 mm, $\bar{x} = 122.1$, SD = 6.9; mass: 355–615 g, $\bar{x} = 486.7$, SD = 54.6, $n = 97$). The smallest gravid female measured 124 mm CL (117 mm PL, 385 g mass, 1 egg) whereas a 131 mm CL turtle weighed the least (355 g), although she contained a clutch of 4 eggs. Clutch size varied between 1 and 5 eggs with a mode of 2 (Table 2). The frequency distribution of clutch sizes varied among sampling periods (Likelihood ratio $\chi^2 = 118.08$, df = 50, $p < 0.001$). Both carapace and plastron lengths were positively correlated with clutch size (Fig. 2) (CL: $F_{1,139} = 11.14$, $p = 0.001$, regression equation $y = -2.40 + 0.04x$; PL:

Table 1. Comparison of clutch size (CS), carapace length (CL), plastron length (PL), and body mass (M) of female *Terrapene carolina bauri* on Egmont Key, Florida, between and among years by month. F = ANOVA results.

Month	Years Compared	Variable	F	df	*p*
April	1993 vs. 1995	CS	3.12	1,24	0.09
		CL	0.01	1,24	0.94
		PL	0.28	1,24	0.60
		M	0.89	1,24	0.36
May	1993 vs. 1995	CS	0.10	1,31	0.76
		CL	1.81	1,31	0.19
		PL	0.00	1,31	0.98
		M	0.64	1,30	0.43
July	1993 vs. 1994	CS	0.25	1,16	0.62
		CL	0.15	1,16	0.70
		PL	0.34	1,16	0.57
		M	0.05	1,16	0.82
June	1992, 1993, 1994	CS	0.35	2,57	0.71
		CL	0.62	2,57	0.54
		PL	0.41	2,57	0.67
		M	0.51	2,57	0.60

Table 2. Clutch size by sampling period for *Terrapene carolina bauri* on Egmont Key, Florida. Overall mean clutch size = 2.44 ± 0.77.

Month/Year	Number of Eggs 0	1	2	3	4	5	Percent Gravid	Mean Clutch Size	Total Radiographed
June 1992	37	1	4	4	1	0	21.3	2.50	47
April 1993	15	0	5	3	4	0	44.4	2.91	27
May 1993	32	1	7	8	2	0	36.0	2.61	50
June 1993	27	0	23	8	1	0	54.2	2.31	59
July 1993	35	1	11	2	1	0	30.0	2.20	50
1993 Summary	109	2	46	21	8	0	41.4	2.45	186
June 1994	35	1	11	4	1	1	34.0	2.44	53
July 1994	47	0	3	0	0	0	6.0	2.00	50
August 1994	57	0	1	0	0	0	1.7	2.00	58
1994 Summary	139	1	15	4	1	1	13.7	2.36	161
March 1995	24	1	0	1	1	0	11.1	2.67	27
April 1995	36	3	5	5	1	0	28.0	2.29	50
May 1995	30	0	8	6	1	0	33.3	2.53	45
1995 Summary	90	4	13	12	3	0	26.2	2.44	122
Total	373	8	78	41	13	1	27.3	2.44	516

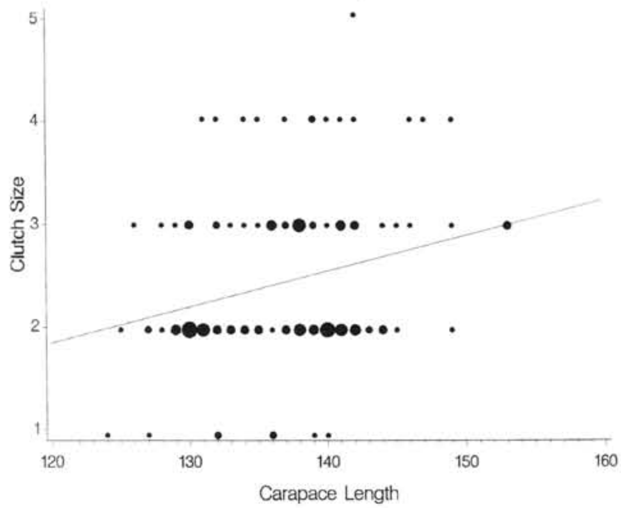


Figure 2. Relationship between carapace length (straight-line in mm) and clutch size in *Terrapene carolina bauri* on Egmont Key, Florida. There may be more than one record per carapace length; the larger the size of the dots, the greater the number of observations. See text for regression equation ($n = 141$).

$F_{1,139} = 8.70$, $p = 0.004$, regression equation $y = -0.79 + 0.026x$) although r^2 values were very small (CL, 0.074; PL, 0.059).

From 1.7% to 54.2% of turtles were gravid in any one month (Table 2). Mean clutch size did not vary monthly ($F_{5,135} = 1.01$, $p = 0.42$) nor among sampling periods ($F_{10,130} = 1.03$, $p = 0.42$). Mean clutch size decreased, although barely significantly, as the season progressed ($F_{1,139}=3.81$, $p = 0.053$; regression equation: $y = 3.04 - 0.004x$, $r^2 = 0.027$; Fig. 3). Although the decline was statistically significantly different from zero when analyzed by month ($F_{1,139} = 4.46$, $p = 0.036$; regression equation: $y = 3.16 - 0.132x$), the r^2 value also was quite small (0.031). In any one year, between 13.7% and 41.4% of the individual turtles examined were gravid (Fig. 4) although unequal sampling effort among individuals may bias these results.

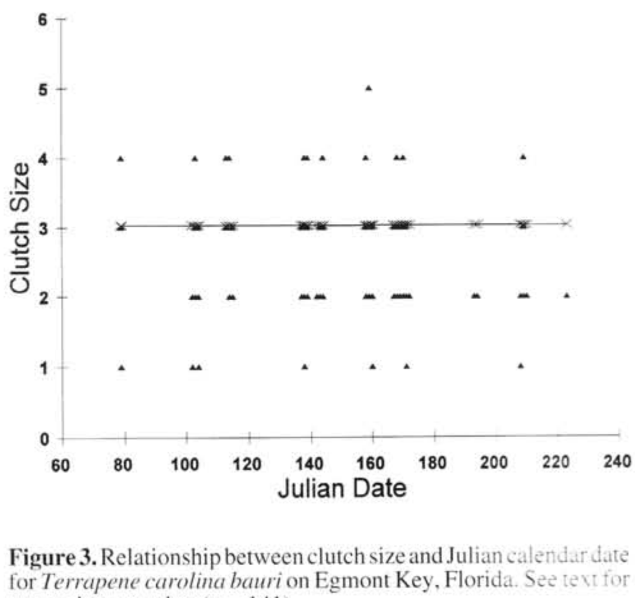


Figure 3. Relationship between clutch size and Julian calendar date for *Terrapene carolina bauri* on Egmont Key, Florida. See text for regression equation ($n = 141$).

Inasmuch as sampling periods were generally spaced so as to minimize the potential for counting the same clutch twice (see Messinger and Patton, 1995; L. Guillette, *pers. comm.*), the production of multiple clutches among some female turtles was evident. Nine females deposited at least two clutches in 1993, one female deposited two clutches in 1994, and two females deposited two clutches in 1995. Two females showed evidence of producing three clutches in 1993.

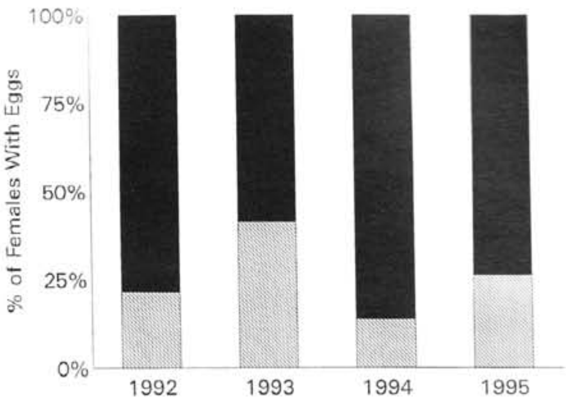
Based on radiographs in at least three consecutive months, three females appeared to deposit only one clutch in 1994, and a few turtles may not have deposited any eggs within a year (1 in 1993, 5 in 1994, 1 in 1995). However, the lack of early and late month samples in 1994 and 1995 makes it difficult to rule out the possibility that these turtles deposited at least one clutch outside the sampling period.

A few turtles were confirmed nesting in consecutive years: two in 1992 and 1993, one in 1993 and 1994, one in 1994 and 1995, and three in 1993, 1994, and 1995. For the vast majority of females, however, there were too few data to make conclusive statements as to the extent of nesting in consecutive years. The year with the highest reproductive output relative to sampling effort (1993 – 54.9% of all eggs observed compared with 36% of the sampling effort during the study) had the highest amounts of rainfall in the months immediately preceding reproduction (Fig. 5), although more data over a longer time frame are needed to determine the effects, if any, of rainfall on reproduction.

DISCUSSION

Clutch Size and Frequency in Southern Box Turtles. — Circumstantial evidence in the literature has suggested that box turtles are capable of laying multiple clutches (Legler, 1958; Tucker et al., 1978; Jackson, 1991), and at least one paper (Tucker et al., 1978) proposed that *T. c. major* could deposit up to five clutches per season. Captive *T. c. triunguis* in Louisiana deposited from 2 to 6 clutches per season (Messinger and Patton, 1995). On the other hand, Iverson (1977) hypothesized that *T. carolina* in north Florida laid only one clutch per season as opposed to aquatic emydids which normally lay multiple clutches. The gopher tortoise (*Gopherus polyphemus*), the only other terrestrial turtle on Egmont Key and a species sympatric with box turtles throughout most of Florida, also deposits only one clutch per season (Diemer and Moore, 1994). On Egmont Key, Florida box turtles lay between one and three clutches annually. No evidence yet available demonstrates that wild Florida box turtles deposit more than three clutches per year.

It seems clear that whereas the production of multiple clutches is probably common in *T. c. bauri*, not all turtles deposit multiple clutches each year. Clutch number may vary from one year to the next, and some turtles may skip annual reproduction, a phenomenon recorded in a variety of other turtles (Gibbons and Greene, 1978; Tinkle et al., 1981; Congdon et al., 1983b, 1987; Iverson, 1991; Diemer and Moore, 1994). Some box turtles on Egmont Key lay in



	1992	1993	1994	1995
Not Gravid	37	109	139	90
Gravid	10	77	22	32

Figure 4. Minimum percentage of female *Terrapene carolina bauri* that were gravid in any one year on Egmont Key, 1992 to 1995. Total *n* sampled = 516, total *n* gravid = 141.

consecutive years, but others do not. Thus, schedules of reproduction vary considerably both at the individual and population levels. More long-term data are required to determine the proportion of the population that deposits multiple clutches annually and the proportion that reproduces in consecutive years.

Body Size Effects. — In many turtle populations, clutch size increases with maternal body size, no matter whether body size is measured in carapace length, plastron length, mass, or some measure of volume (Jackson, 1988; Iverson, 1992). However, the relationship is not uniform among populations, where site effects can be important (Iverson and Smith, 1993; Rowe, 1994). Thus, it is not particularly surprising that there was a positive relationship between clutch size and female carapace length in Egmont Key's box turtles, although St. Clair (1995), based on a much smaller sample size, found no such relationship in *T. c. triunguis*. However, r^2 values were small, suggesting that there are other more important determinants of clutch size in this population.

Iverson (1992) and Iverson et al. (1993) noted the effect of latitude on turtle reproduction. After adjusting for the effects of body size, turtles from northern latitudes laid fewer clutches than those in southern populations. Clutch size was positively correlated with latitude, although egg size was negatively correlated with latitude. He suggested that southern turtles matured at a smaller body size than northern turtles because of the longer growing season.

At least some box turtles on Egmont Key deposit two or three clutches a season, although the variation among seasons is unknown. Northern *T. carolina* appear to lay larger and perhaps fewer clutches, but among-year variation in reproductive output is unknown. Thus, Iverson's (1992) hypothesis of latitudinal effects on reproduction cannot yet be verified for box turtles. In any case, there does not appear to be support for the effects of latitude on female body size. For example, the smallest *T. c. bauri* found gravid on Egmont Key (124 mm CL) was much larger than the smallest size at which North Carolina *T. c. carolina* have been found to be gravid (105 mm CL; Palmer and Braswell, 1995).

Resource Allocation and Multiple Clutches. — More northern populations of *T. carolina* routinely deposit four or more eggs (Warner, 1982; Ernst et al., 1994; Messinger and Patton, 1995; Palmer and Braswell, 1995; St. Clair, 1995), yet the carapace length of mature females is nearly identical

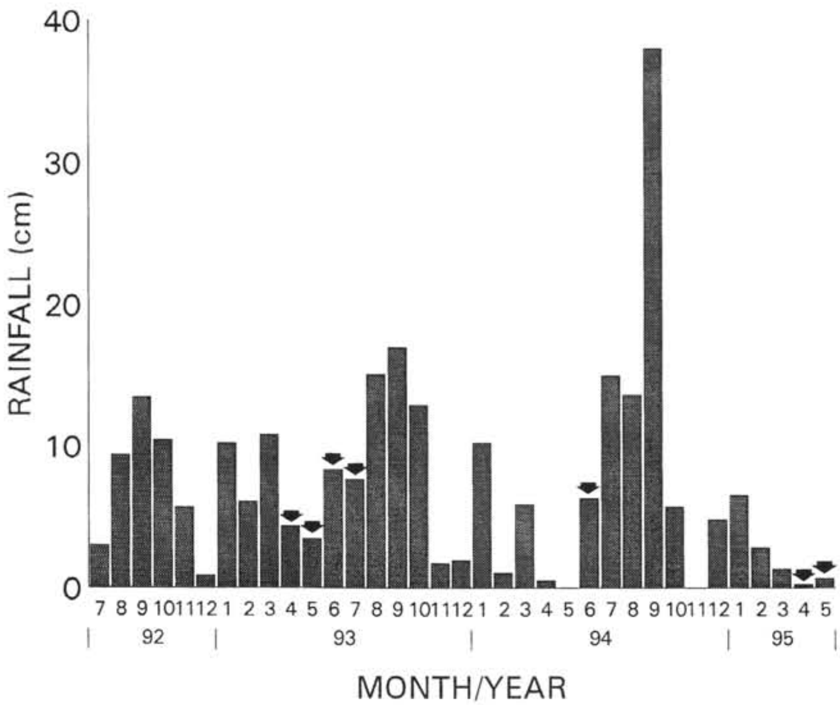


Figure 5. Monthly rainfall on Egmont Key, July 1992 to May 1995. The arrows show the months when more than 20% of the turtles were gravid.

to *T. c. bauri* on Egmont Key (Stickel and Bunck, 1989). Box turtles on Egmont Key can easily package four or more eggs within their body cavity but rarely do so; both small and large females occasionally contained clutches of four eggs. The length of the potential reproductive season (late March through mid-August) and the fact that box turtles are active year-round on Egmont Key (Dodd et al., 1994) suggest that the activity season does not limit the time available for intrauterine egg development.

Although speculative, I suggest that resources limit clutch size and frequency on Egmont Key. Reproductive characteristics appear to have a strong environmental component in the painted turtle *Chrysemys picta* (Iverson and Smith, 1993) and in other reptiles (Tinkle et al., 1970; Seigel and Fitch, 1985; James and Shine, 1988; Ford and Seigel, 1989; Seigel and Ford, 1991). Northern populations of box turtles, i.e., those with the best data on reproduction (see Ernst et al., 1994) generally occur in rich mesic woodlands where resources, particularly soil arthropods, earthworms, and fungi, are abundant and readily available (e.g., Stickel, 1950; Klimstra and Newsome, 1960; Reagan, 1974). On Egmont Key, however, potential food resources seem subjectively to be much less seasonally and spatially available. The soils are thin and sandy or composed of compact shells with a very shallow organic layer and support a much reduced arthropod/fungus community. The soils are also much drier than those of an eastern deciduous forest floor and are prone to rapid desiccation. Although cockroaches are abundant and fruit is available seasonally (Dodd et al., 1994), food availability is likely subject to a great deal of variation, particularly as a result of variation in rainfall and moisture.

Rainfall might prove a measure of resource availability and quality on Egmont Key. For example, 1993, a year in which many box turtles reproduced, had a substantial amount of rainfall, especially in the spring; whereas in 1994, a year with reduced rainfall during the spring, reproduction seemed to be curtailed. Autumn rainfall was plentiful from 1992 to 1994, suggesting that it is not a reliable predictor of reproductive output the following year. On the other hand, drought is common on Egmont Key (R. Baker, *pers. comm.*; Fig. 5). Drought and decreased humidity not only restrict box turtle activity (Reagan, 1974; Strang, 1983; Dodd et al., 1994), such as foraging, but also limit the activity of prey, such as snails and earthworms. Snails, in particular, can make up a substantial proportion of a box turtle's diet (Stuart and Miller, 1987). Drought thus could have an indirect effect on reproduction by limiting the activity of prey and the time available for the acquisition of energy reserves. This situation would result in conditions conducive to low frequency reproduction (Bull and Shine, 1979).

A relatively simple test could be made to determine if resources are limiting clutch size and frequency in Florida box turtles on Egmont Key. Rainfall is very sporadic on the island compared with the nearby mainland, where rainfall is higher and more evenly distributed. Soils where box turtles occur on the mainland are much more mesic (Carr, 1940; *pers. obs.*), presumably with a more stable food resource base. Therefore, mainland populations at similar latitudes should have higher average clutch sizes and a more evenly distributed pattern of clutch frequency than the island's population. There should also be a higher percentage of females reproducing every year.

Conservation Implications. — Conservation and management decisions must be made on the basis of sound biological data. In the case of the export of Louisiana box turtles, it appears as if government agencies assumed that the "increased" fecundity implied by the production of multiple clutches in Louisiana box turtles would somehow offset the loss of reproductively mature adults in the population, thus allowing a measure of population resilience. Although the presence of multiple clutches recently has been documented for Louisiana *T. c. triunguis* (Messinger and Patton, 1995), I can find no literature reference to support the assumption that "increased" annual frequency of reproduction allows resilience to ecological disturbance.

Reproductive output involves more than simply the number of clutches produced per year per female. In order to know the reproductive output within a population, it is necessary to know the proportion of females reproducing each year, the total number of females based on reliable population estimates (e.g., Langtimm et al., 1996), size and age-specific reproductive characters, variation in clutch size and offspring size, the quality of eggs (e.g., fertility, lipid content, mass), and the effect of resource availability on reproductive output. Even with this information, it may be impossible to determine whether the production of multiple clutches *per se* offsets other life-history characteristics of long-lived chelonians (Congdon et al., 1993, 1994) which make them vulnerable to exploitation. If survivorship in southern juvenile turtles is lower than in northern turtles (perhaps because of increased levels of predation during a longer activity period), one could even argue that the production of multiple clutches only serves to compensate for the low survivorship rates.

In addition to fecundity, the survivorship of offspring and adults, age at sexual maturity, reproductive longevity, and a host of other demographic variables combine to determine whether a population of organisms can respond to exploitation without detrimental effects. Variation in many life-history traits, especially those related to reproduction, is a result of natural selection (Wilbur and Morin, 1988; Congdon and Gibbons, 1990b). Hence, the presence of multiple clutches in Louisiana turtles is not a character that can be assumed to respond plastically to high levels of exploitation and thus compensate for the removal of reproductively mature adults.

Although multiple clutches may be produced in southern box turtles, the smaller clutch size (Egmont Key $\bar{x}$ = 2.4; Louisiana *T. c. triunguis* $\bar{x}$ = 3.3, Messinger and Patton, 1995) may not result in any greater net annual reproductive output per female compared with northern conspecifics, much less with other species. By making management decisions that ignore the reaction norms associated with the co-evolved life history traits of long-lived chelonians, complex evolutionary processes are confused with the simple tabulation of numbers of eggs and clutches.

The data from the Egmont Key *T. c. bauri* population confirm that reproductive output may be far different from simply the number of clutches that turtles can potentially produce per year. Although many data are not yet available (e.g., precise estimates of the age at first reproduction and the percentage of the population reproducing each year or producing two or three clutches), it is clear that whereas box turtles are capable of producing multiple clutches, 1) only a small percentage of the population actually may do so, 2) clutch sizes are smaller in southern turtles than in northern conspecifics, and 3) only a portion of the population likely reproduces in any one year. On Egmont Key circumstantial evidence suggests that resource availability may play an important role in annual reproduction. It is reasonable to suspect that these reproductive traits are equally variable in Louisiana box turtles.

For reasons previously discussed in relation to turtle life history evolution (Dunham et al., 1989; Congdon et al., 1993, 1994), the number of clutches individuals of a long-lived species can lay in any one year is only a fraction of the information that must be available before attempting to predict a species' response to exploitation. My data suggest that the simple number of potential clutches is not a good measure of reproductive output in box turtle populations and, hence, is not a reliable estimator of the effects of removing individuals from a reproductively viable population. Before exploitation could be allowed on a so-called sustained yield basis (but see Larkin, 1977; Holt and Talbot, 1978), many more quantitative life history data are necessary.

Addendum. — Because of the lack of data on the effects of the removal of box turtles from wild populations, export quotas for *Terrapene carolina* from the USA under CITES were set at 0 for 1996. The State of Louisiana is appealing this decision.

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