RIVER TURTLE REPRODUCTIVE DEMOGRAPHY AND EXPLOITATION PATTERNS IN BELIZE: IMPLICATIONS FOR MANAGEMENT

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ABSTRACT

Dermatemys mawii is a large river turtle restricted to the Atlantic drainages of southern Mexico, Belize, and Guatemala. Because *Dermatemys* lays its eggs in scattered locations during the high water periods of the late rainy season, exploitation of nesting females and their eggs by humans is inconsequential. Exploitation is primarily for meat, and is most intense during the latter part of the dry season. All three methods of capture (harpoons, nets, and free-diving) select for the larger size classes. The effects of relentless large-scale removals are reduced densities and lower proportions of adults, which results in reduced recruitment. These dynamics do not appear to be as severe in populations subjected to histories of intermittent and/or small-scale exploitation. By removing adults and subadults, human exploitation introduces high predation rates to size classes that have experienced high survival rates over evolutionary time. Stability in populations of large freshwater turtles is maintained by extreme iteroparity accomplished through high adult survival rates and extended longevity, both of which are disrupted by exploitation. If we attempt to manage *Dermatemys* harvests we should do so conservatively. Though socioeconomic and law enforcement constraints need to be considered when developing harvest prescriptions, it is the biological constraints that will determine if those levels are sustainable.

KEY WORDS: Belize, *Dermatemys*, exploitation, reproductive demography, river turtle

RESUMEN

Dermatemys mawii es una tortuga ribereña de gran tamaño, restringida a la cuenca Atlántica del sur de México, Belice y Guatemala. Debido a su tendencia a anidar en lugares dispersos al final de la estación lluviosa, cuando los ríos registran niveles máximos de agua, la explotación para las hembras anidadoras y sus huevos por humanos es muy baja. La explotación para carne tiene mayor importancia y es más intensiva al final de la estación seca. Las tres técnicas de pesca (harpón, red y buceo) seleccionan por los ejemplares más grandes. El efecto de la pesca a gran escala son densidades reducidas y proporciones bajas de adultos, que resulta en un reclutamiento reducido de la población. Tal dinámica no parece tan severa en las poblaciones sujetas a la explotación intermitente y/o a pequeña escala. La explotación de adultos y subadultos por humanos presenta una alta taza de depredación de la tortuga, que ha mostrado una alta taza de sobrevivencia durante tiempos evolutivos. La estabilidad de las poblaciones de tortugas de agua dulce de gran tamaño se mantiene por la iterparidad lograda por la alta taza de sobrevivencia de adultos y la longevidad extendida, ambos de los cuales son interrumpido por la explotación. Si se trata de manejar las cosechas de *Dermatemys*, debe hacerse en forma conservadora. Aunque se deben considerar limitaciones socioeconómicas y cumplimiento de la legislación cuando se elaboran las regulaciones para la cosecha, son las limitaciones biológicas las que determinarán si los niveles pueden sostenerse.

PALABRAS CLAVES: Belice, demografía de reproducción, *Dermatemys*, explotación, tortuga de agua dulce

RESUMO

Dermatemys mawii é uma tartaruga lacustre de tamanho grande, restringida às vertentes Atlânticas do sul do México, Belize e Guatemala. Devido à sua tendência de aninhar em lugares dispersos ao final da estação de chuvas, quando os rios registram os níveis máximos de água, a exploração de fêmeas aninhando e de ovos por humanos é muito baixa. A exploração para carne tem maior importância e é mais intensiva no final da estação seca. As tres técnicas de pesca (arpão, rede e mergulho) selecionam os exemplares maiores. A pesca em grande escala causa uma densidade mais baixa e menores proporções de adultos, o que resulta em um recrutamento menor. Estas dinâmicas não parecem ser tão severas em populações sujeitas à exploração intermitente e/ou de pequena escala. Através da remoção de adultos e subadultos, a exploração humana introduz uma alta taxa de predação a classes de tamanho que têm tido altas taxas de sobrevivência no tempo evolucionário. A estabilidade das populações de tartarugas de água doce de tamanho grande se mantém pela iteroparidade alcançada pela alta taxa de sobrevivência de adultos e pela grande longevidade. Se trata-se de manejar a caça de *Dermatemys*, deveríamos de fazê-lo conservadoramente. Apesar de que se devem considerar os limites sócio-econômicos e a capacidade de se fazer cumprir a lei quando se elaboram os regulamentos para a caça, são os limites biológicos que determinarão se os níveis são sustentáveis.

PALAVRAS-CHAVE: Belize, demografia de reprodução, *Dermatemys*, exploração, tartaruga de agua doce

VIDA SILVESTRE NEOTROPICAL 4(1):10-19

The Central American river turtle *Dermatemys mawii* is an economically important threatened species. This large, highly aquatic, herbivorous, freshwater turtle is restricted to the Atlantic lowlands of southern Mexico, Belize and northern Guatemala (Álvarez del Toro 1982, Álvarez del Toro *et al.* 1979, Iverson 1986, Iverson and Mittermeier 1980). In Spanish-speaking countries it is referred to as tortuga blanca. In Belize it is called hickatee. Throughout its range, *Dermatemys* is harvested for its meat (Álvarez del Toro *et al.* 1979, Holman 1964, Lee 1969, Mittermeier 1970, 1971, Moll 1986a, 1988) which is used by rural people and sold in urban markets. As a result of intense hunting pressure, *Dermatemys* is listed in: a) Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); b) as endangered under the provisions of the U. S. Endangered Species Act; and c) as a high priority species in the IUCN Species Survival Commission Action Plan for the Conservation of Tortoises and

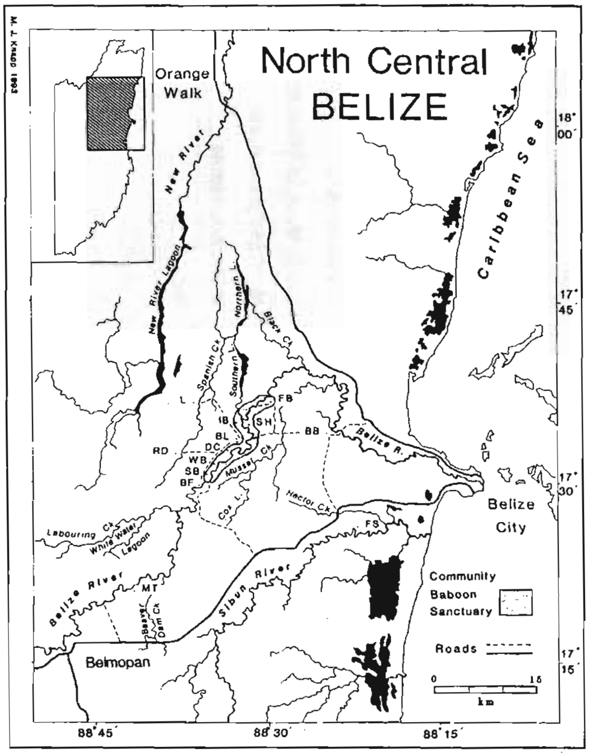

Figure 1. Villages and waterways of the primary study area in north-central Belize. Community Baboon Center (CBS) straddles the Belize River. Village names: Bermudian Landing (BL); Big Falls (BF); Burrell Boom (BB); Doublehead Cabbage (DC); Flowers Bank (FB); Freetown Sibun (FS); Isabella Bank (IB); Lemonal (L); More Tomorrow (MT); Rancho Dolores (RD); Scotland Halfmoon (SH); St. Paul's Bank (SB); and Willows

Freshwater Turtles (CITES 1984, Code of Federal Regulations 1987, IUCN/SSC/TFTSG 1991).

Information on the biology and ecology of *Dermatemys* was anecdotal in nature (Álvarez del Toro 1982, Álvarez del Toro *et al.* 1979, Campbell 1972, Holman 1964, Iverson and Mittermeier 1980, Lee 1969, Smith and Smith 1979) until the early 1980's (Moll 1986a, 1986b, 1988, 1989, Vogt and Flores-Villela 1992a, 1992b). Moll (1986a) found *Dermatemys* common to abundant in many areas of Belize, but vulnerable and declining in harvested areas. He suggested that biological data be collected and based on this, scientific management of the species begin.

In response to that need, in 1989 I initiated a field study on the reproductive biology and exploitation of *Dermatemys* in northern Belize. This report will discuss: a) exploitation patterns; b) interaction of these patterns with reproductive demography; and c) implications for sustainable use management. Reproductive biology, presented only briefly here, is detailed in Polisar (1992, in press) and Vogt *et al.* (in press).

STUDY AREA

Belize is a small (22,953 km^2), sparsely populated country lying between 15-19° north latitude on the Caribbean coast of Central America (GOB 1989, Hartshorn *et al.* 1984). The research took place in the northern half of the country, which contains a broad coastal plain dissected by numerous rivers and freshwater and brackish lagoons. The research was requested by members of the Community Baboon Sanctuary, a small, grassroots conservation project managing 32 km of riparian forest habitat along the Belize River for black howler monkeys, *Alouatta pigra* (Horwich 1990). Community Baboon Sanctuary members were concerned that local consumption of the hickatee had reached unsustainable levels. Inhabitants from the eight villages involved in the howler sanctuary agreed to supply *Dermatemys* reproductive organs for analysis. As the project evolved, four additional villages became involved, and the primary study area expanded to include an additional 54 km of the Belize River, and 39 km of its tributary systems (Spanish Creek, Mussel Creek, Cox Lagoon, and White Water Lagoon, Fig. 1). Although precise elevations are unavailable, probably no part of this area exceeds 50 m above sea level.

Winter, mean, monthly air temperature minimums in this core area were 16°-17°C. Summer, mean monthly maximums were 32°-33°C. The dry season typically lasts 3-4 months (early February through May). However, dry season initiated late in 1990 (mid-March to early June), and terminated late in 1991 (February until July). Total annual precipitation was 2,404 mm in 1990 and 1,911 mm in 1991. Average annual precipitation is 1,500-2,000 mm, thus during the study period, a wetter than normal year (1991) was followed by a drier year (1992).

Dermatemys inhabits three types of streams in the primary study area. Mussel Creek and Spanish Creek are sluggish darkwater streams. These systems contrast with blackwater streams of the Amazon (Goulding 1980, Payne 1986, Sioli 1984) in that they contain a productive fishery. The deepest sections are 4.6-6 m. The water in White Water Lagoon stays clear nearly year-round. While clearwater systems in the Amazon are nutrient poor (Goulding 1980), White Water Lagoon possesses a rich community of aquatic macrophytes, but vegetation is absent in the deepest pools (9 m).

All three of the aforementioned systems are tributaries of the Belize River (Fig. 1). This river is often turbid, but during the dry season the sediment load is reduced and underwater visibility improves. In contrast to the sluggish tributaries, the current of the Belize River is relatively swift. Highest water levels occur between September and December. Lowest water levels occur in April and May. Channel widths are 35-60 m. During the dry season many river sites

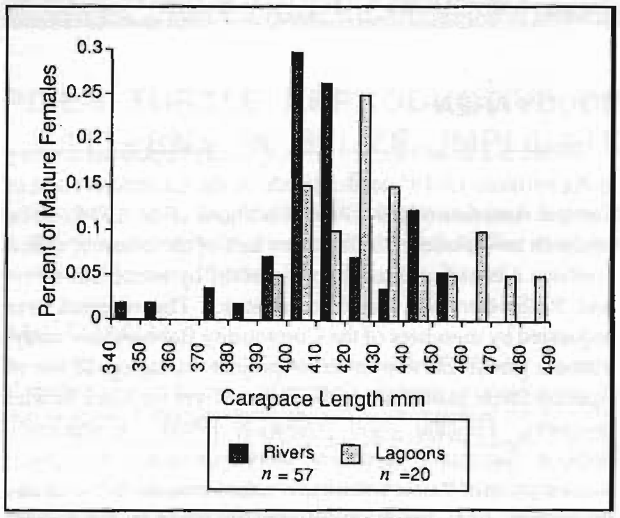

Figure 2. Significant contrasts (P<0.0009) in minimum size at maturity: body sizes of mature females from rivers and lagoons. Rivers include Belize River and Río Bravo. Lagoons include Spanish Creek, Mussel Creek, White Water Lagoon, and New River Lagoon.

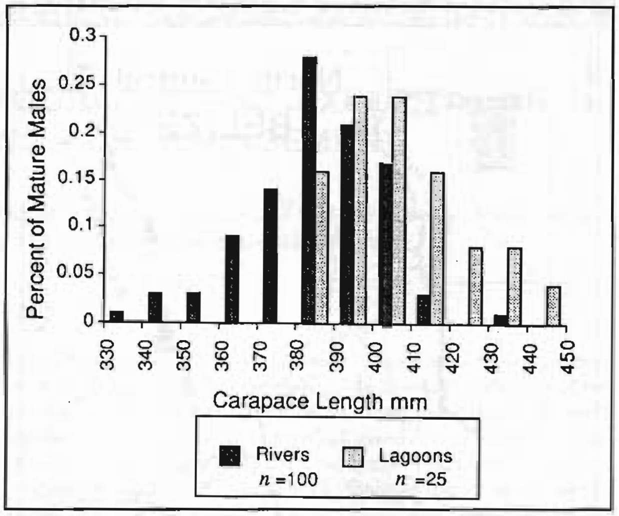

Figure 3. Significant contrasts (P<0.0009) in minimum size at maturity: body sizes of mature males from rivers and lagoons. Rivers include Belize River and Río Bravo. Lagoons include Spanish Creek, Mussel Creek, White Water Lagoon, and New River Lagoon.

are over 9 m in depth. During floods, river depth doubles, and surface area expands several-fold, flooding vast sections of riparian forests and savannas.

Observations made during inventory work in the Río Bravo Conservation and Management Area in northwest Belize complemented the more detailed work in the primary study area. Information obtained directly and through cooperators provided familiarity with other *Dermatemys* waters of northern Belize: the New River, Hector Creek Lagoon, the Hondo Branch, and the Sibun River.

METHODS

Reproductive Biology

Reproductive chronology and parameters were measured from reproductive organs of adult turtles slaughtered locally for consumptive purposes. The nesting ecology study involved opportunistic and focused searches for nests, rewards for located nests, intensive capture efforts with nets in multiple waterways, and radiographs of four adult females.

Exploitation Patterns

Exploitation data was collected from September 1989 to December 1990 (Polisar 1992). This information was collected in several ways. I attempted to keep abreast of imminent slaughters in 12 villages. Although an important function of that activity was to salvage reproductive organs, it also provided documentation of the timing and methods of exploitation, as well as water bodies, body sizes, and number of turtles involved. Even when it was impossible to schedule an organ salvaging date for a turtle, villagers still allowed us to measure their catch. During April and May of 1990, project personnel and I accompanied commercial diving operations to document the composition of the catch. The Community Baboon Sanctuary provided numerical estimates of diving removals for 1988-1989. Between August 1989 and November 1990, observers regularly checked the numbers of turtles for sale in the open air market on the waterfront in Belize City. Linear measurements of turtle shells were made with tree calipers and dial vernier calipers. Numerous measurements were obtained from the 567 turtles handled (Polisar 1992; Polisar, in press; Vogt *et al.*, in press), but only straight mid-line (nuchal-pygal) carapace length (CL), measured with calipers, is referred to here.

RESULTS AND DISCUSSION

Summary of Reproductive Biology

Reproductive chronology and parameters were measured from reproductive organs of 51 adult male and 27 adult female turtles slaughtered locally for consumptive purposes from September 1989 to September 1991 (Polisar 1992).

In northern Belize, *Dermatemys* mates between March and September. It exhibits a solitary nesting pattern, laying multiple, moderate-sized clutches of large brittle-shelled eggs during the latter part of the rainy season (late September through December) when flooding is most probable. Based on 49 nests studied (37 from collected ovaries, 4 from

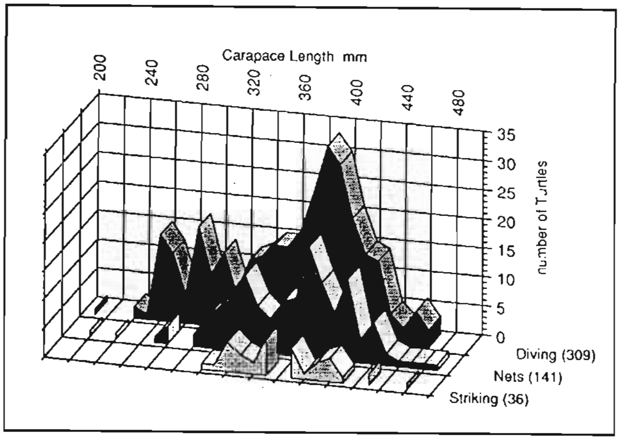

Figure 4. Comparison of numbers caught and size-class selection of three *Dermatemys* hunting methods.

radiographs, and 8 from uncollected ovaries), mean clutch size was 10.98 eggs, with a range of 2 to 20 (SD=3.68). Approximately equal proportions of 21 active females laid one clutch (33%), two clutches (33%), and three clutches (29%) yearly. Only one out of 21 active females laid four clutches in a year. Mean clutch frequency was 2.05 eggs. Total annual reproductive output (number of eggs laid in a year) varied from 0 to 47 eggs. Mean total reproductive output (direct estimates from 27 specimens) was 21 eggs. Nearly all mature adult females examined (30 of 31) were reproductively active in 1989-1990 (Polisar 1992).

Although no nesting activity was directly observed, 11 nests of varying ages were studied, and three accounts from old hunters indicated that *Dermatemys* nests near the water's edge. The nesting season coincides with the long-term annual high water levels, which frequently inundate riparian forests and savannas. Within that period water levels are dynamic, with frequent and sometimes extreme oscillations. Nests laid prior to floods are subsequently submerged under meters of water. The existence of a post-ovipositional diapause is suggested by the ability of the eggs to withstand over 30 days of flooding with no reduction in viability (Polisar 1992; Polisar, in press; Vogt and Flores-Villela 1992a). *Dermatemys* is essentially a winter-nesting turtle of the subtropics: river and nest temperatures occasionally dropped to 20°-22°C between November and February. Nest temperatures between March and May (dry months) are more conducive to development (>25°C). Hatchling emergence is timed to coincide with the resumption of summer rains in June and July. Local hunters rarely found *Dermatemys* nests. None had witnessed hatchling emergence.

Minimum body size at maturity varied between sexes and among water bodies (Figs. 2, 3). The smallest mature female was 342 mm CL. The largest immature female was 420 mm CL (Fig. 2). The smallest male exhibiting the external characteristics of maturity (dorsal head coloration and enlarged tail) was 338 mm CL. The largest immature male was 386 mm CL (Fig. 3). The largest female was over 480 mm CL. The largest male was under 450 mm CL. Larger immature animals of both genders were found in the sluggish waterways and lagoons than in the Belize River (t-test: females, P=0.0009; males, P=0.0001). The majority (~70%) of river males over 370 mm CL were mature. A similar percentage of lagoon males attained maturity between 380 and 390 mm. Most (~70%) females from the Belize River were mature at 400 mm CL. A similar percentage of lagoon females attained maturity between 410 and 420 mm. The regression slope of total annual reproductive output against body size was steep for a sample of small females (342-401 mm CL) from the Belize River (n=5, R^2=0.9205), but deteriorated for larger females (399-483 mm CL lagoon females, n=8, R^2=0.7519, 406-451 mm CL Belize River females n=12, R^2=0.3298), primarily due to variation in clutch frequency (Polisar 1992).

Exploitation

Seasonality and scale of hunting techniques.- In Belize, *Dermatemys* are caught by harpooning (striking with a peg), nets, and free-diving (Polisar 1990, 1992).

Striking with a peg. A peg harpoon consists of two elements: a) a 3-4 m long cylindrical wooden staff; and b) a single, detachable, barbed metal tip made of an old triangular file attached to the staff by a strong thin twine. Hunters in canoes harpoon ("strike") turtles when they surface to breathe, or when they forage at the water's surface.

Proggers are men who hunt at night from canoes. They usually take any edible or marketable animal, hunting turtles with a peg harpoon, or fish with a "wire" harpoon, or game with a shotgun. When encountered, turtles (including sympatric *Trachemys scripta* or *Staurotypus triporcatus*) are opportunistically collected. Most harpooning is done at night except during the dry season, when water visibility improves and animals are less dispersed. Harpooning peaks in April and May, when men station their dories over deep areas and wait for hickatees to rise to breathe. *Dermatemys* can be harpooned the rest of the year during the day when water is rising, because downstream flushing of turbid water stimulates unwary foraging activity. There are more harpooners than net men and divers. Harpooning usually is done for family consumption or local trade.

Nets. Three net types are employed for *Dermatemys*: a) river nets; b) lagoon nets; and c) hoop nets. River nets (polypropylene or braided nylon headline, sinkerless, 2.7 m long, 2.4 m deep, 12.6 cm mesh) and lagoon nets (polypropylene or braided nylon headline, sinkerless, 13.5-74 m long, 3.6-6.8 m deep, 13-13.5 cm square mesh) are locally constructed. River nets are set in short, calm stretches in flowing water, baited with a natural food source eaten by *Dermatemys*

Table 1. Free-diving capture rates in the Belize River during the 1990 dry season. Turtles were collected by crews of 1-4 men making repetitious deep dives while drifting downstream.

Section of Belize River	Village density	Historic hunting intensity	Sampling interval	Turtles/ man-dive-days	Turtles/man-dive-day
Upper	None, only several camps, & milpas	Light to medium	19-23 April	124/9.75	12.7
Middle	1/5.3 river km	Heavy & recurrent	9 April-11 May	23/10.5	2.19
Lower	1/11 river km	Medium to heavy	13-17 May	117/10:0	11.7

Note: Sections of river were designated as follows.
Upper: Big Falls to More Tomorrow
Middle: Flowers Bank to Big Falls
Lower: Burrel Boom to Flowers Bank

(*e.g.* leaves and fruit of *Ficus* sp. or *Inga edulis*). They are infrequently used, normally yielding few turtles for local consumption and trade. They are most efficient with rising water, but totally inefficient during flooding.

Lagoon nets are set, unbaited, in slow-moving or still water bodies where they function as a lightweight and responsive, wall-like surface that entangles moving turtles. High water reduces capture efficiency because turtles disperse into flooded areas. These nets don't work under strong current conditions. Consequently, lagoon nets are used often during the dry season, but only sporadically during the rainy season. The scale and destination of lagoon net captures varies from occasional small-scale use for family subsistence needs to larger-scale commercial use.

Hoop nets (consisting of seven fiberglass 122 cm diameter hoops, 488 cm long, 7.6 cm square mesh) were imported from the United States during catfish *Ictalurus furcatus* export operations. To capture turtles, researchers have typically set staked baited or unbaited hoop nets, partially submerged in shallow water (Vogt 1980). In Belize, hoop nets are used to capture *Dermatemys* by tying a long cord from an overhanging tree to the closed end of the trap, baiting it with *Ficus* sp. leaves, and allowing the trap to sink mid-channel. Facing downstream, the open throat of the deeply submerged net rests on the river bottom and is held open by the current. These nets catch *Dermatemys* "walking" on the substrate, especially in rapidly flowing turbid water. Occasional large numbers of small *Dermatemys* sold in the Belize City market during high water were probably caught in hoop nets. The catfish cooperatives had disbanded and the few remnant hoop nets were deteriorating. They were uncommon upstream in the more remote villages and played a minimal role in my exploitation analysis.

Free-diving. Free-diving involves repeated deep dives without airtanks to examine stream substrates for resting turtles. This method has become much more efficient with the use of masks, fins and boats with outboard motors. It is undoubtedly the best method under optimum water clarity conditions, but is mostly restricted to the dry season. Turtles are located while they rest, supposedly secure, on the river bottom. Well-organized diving efforts can result in nearly exhaustive harvesting of turtles in an area.

Free-diving is most effective in rivers where seasonal turbidity and floods keep the main channels free of vegetation. When water levels drop, lack of submergent vegetation and increased water clarity allow observations of turtles resting in deep water, oftentimes in association with woody debris. Some diving occurs in clear streams, but success is hampered by extensive underwater grass beds, which provide hiding cover for turtles. White Water Lagoon was the only sluggish stream in the primary study area exploited by free-diving. In the deeper pools of the lagoon, turtle captures were facilitated by sparse submergent vegetation.

In the primary study area, free-diving for *Dermatemys* was often a well-organized activity. Most of the diving in the Belize River was done by two teams from two villages in the Community Baboon Sanctuary. Diving parties typically involved one or more boats with 3 or 4 divers who gave their captures to men on the boats, and one or more canoes with strikers, or men who captured alarmed turtles that surfaced for air while fleeing downstream. Six continuous hours of repetitious 6-9 m deep unassisted dives, including periodic underwater sprints to catch particularly wary turtles, is a physically demanding activity. Thus, good divers are well-respected in their communities, adding personal identity to income as an incentive to perpetuate the activity. In the past, trammel nets weighted with stones had been used to block downstream routes of escape, allowing what would appear to be a consummate collection of turtles in a stretch of river. The latter activity alarmed riverside residents, who feared depletion of the resource for their own use. Peer pressure and net attrition had eliminated this practice during our study. There were some casual divers who collected the animals for personal use, but the primary objective was profit.

Free-diving resulted in more captures than any other method (Fig. 4). Although hunters using pegs outnumbered net men and divers, they took far fewer animals. Turtle numbers taken by hickatee nets was intermediate. The greatest number of turtles taken by all three methods occurred during April, partly because hickatee and white rice is a traditional Easter meal in northern Belize. Heavy January

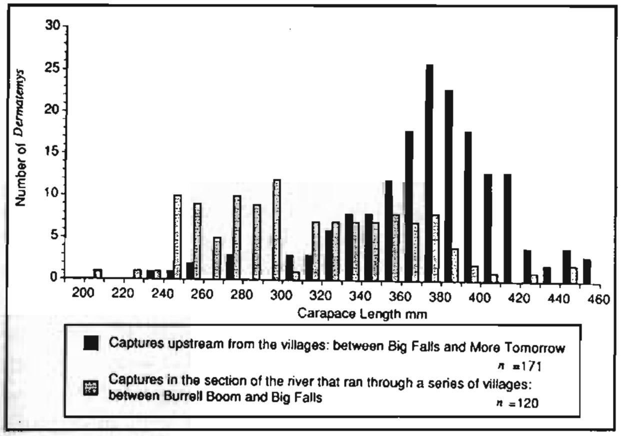

Figure 5. Significant differences in *Dermatemys* size-class distributions (P<0.0001) between two sections of the Belize River exposed to contrasting levels of hunting intensity.

rains and a late dry season in 1990 resulted in a reduced period of low water levels compared to the norm. A more typical dry season could probably have resulted in more intense exploitation than was documented in 1990.

Because *Dermatemys* nests are very difficult to locate they are less vulnerable to exploitation than those of synchronous colonial-nesting turtles. This study's exploitation data were dominated by free-diving captures because of the project's central location on the Belize River, which lent itself to diving. In areas dominated by lagoon systems, net captures are more abundant.

Market checks. Results of the Belize City market counts departed from the seasonal patterns described above and the market's long-term pattern, as reported by Belician residents. The short dry season in 1990 resulted in higher water levels than usual, reducing capture efficiency throughout northern Belize. Because supply never exceeded the demand in the rural area, a greater profit was made by selling turtles retail in the villages than wholesale in Belize City.

Dermatemys numbers in the Belize City market did not peak during the dry season. Mean numbers of *Dermatemys* per market check were 0.428 in March, 1.43 in April, and 0 in May of 1990. The highest counts relative to numbers of visits occurred during August 1989 (2.22) September 1989 (6.67) and February 1990 (8.67). During the rainy months, the large numbers of relatively small turtles sold in the market had no peg scars and were probably caught in hoop nets. Large females were never encountered in the Belize City market.

Size Classes Selected by Different Hunting Methods

Each of the three hunting methods accounted for a slightly different size-class distribution of *Dermatemys* (Fig. 4). Striking caught large juveniles and adults, because it was difficult to hit smaller targets. Hickatee nets collected a broader size range of turtles, however their large mesh size (13 cm^2) allowed small turtles to avoid capture. All size classes were vulnerable to free-diving, as proportionally more small animals (250-300 mm CL) were collected this way than by nets or pegs. However, *Dermatemys* below 200 mm CL had little meat and no financial value, so were never pursued by free-divers. Despite contrasts in size-class distribution, most animals collected using all three methods were large juveniles and adults (Figs. 2, 3, 4).

Adult sex ratios were similar between hunting methods. The 36 *Dermatemys* collected by striking were 30% adult males, 17% adult females, and 53% juveniles. Hickatee nets collected 141 turtles, of which 24% were males, 14% females, and 62% juveniles. The 309 turtles collected by free-diving were 24%, 16%, and 60% males, females, and juveniles, respectively. Turtles taken during free-diving operations should provide the most accurate description of the actual population because they are unbiased towards more mobile animals. Although males may have been more visible due to dorsal head coloration, turtles were detected from close-range, examination of substrate (5-9+ m).

Effects of Exploitation

In the absence of long-term data, indirect assessments of exploitation effects can be provided by capture rates and population structure. In the section of the Belize River with the highest village density, between Flowers Bank (FB) and Big Falls (BF), free-diving capture rates were less than one-fifth those in the humanly unpopulated and sparsely populated river sections (Fig. 1, Table 1). On three occasions, a half-day of diving yielded no turtles between FB and BF. In contrast, two days of diving yielded 114 turtles in the most remote section of river between Labouring Creek (LC) and More Tomorrow (MT) (Fig. 1). Thirty to 40 turtles were collected daily between FB and Burrell Boom (BB) (Fig. 1). The humanly unpopulated section of river above Big Falls had been exposed to occasional strikers and diving. Exploitation downstream from FB was assumed greater than the wilderness section above BF, but less intense than the river section (FB to BF) amidst several villages. This village area had experienced several dives per dry season (some with trammel nets set across the river), regular harpooning and yearly net captures.

For several years prior to this study, free-diving teams from villages were hunting turtles in White Water Lagoon (Fig. 1). Diving trips to White Water Lagoon took divers progressively farther up the Belize River, where both more and larger animals were captured than in other areas. The lagoon's clear waters allowed diving earlier in the dry season, while the main river was still turbid. During the study period, removals by a combination of free-diving and lagoon nets

Table 2. Comparison of population structure in contrasting sections of the Belize River.

Status	Unpopulated[a]	Populated[b]
Adult females	22%	4%
Adult males	34%	14%
Juveniles	44%	82%
n =	171	120

[a]Big Falls to More Tomorrow
[b]Burrell Boom to Big Falls

significantly reduced capture rates in White Water Lagoon. Diving capture rates were lower in April (1.14 turtles/person-dive-day) than in December (5.33 turtles/person-dive-day). Net capture rates were an order of magnitude lower in March (0.0182 turtles/net-day) than in February (1.82 turtles/net-day). By May, when capture rates should have been highest, net capture rates were zero.

In 1952, 72 net-captured *Dermatemys* were removed from White Water Lagoon in one trip, and in a two-day dry spell in December 1989, three divers caught 32 turtles. At an undetermined point in the past, a "truckload" of net-caught *Dermatemys* were removed from the "hickatee hole" in the upper Rio Bravo (a long, deep pool in an otherwise small river). Adult and juvenile *Dermatemys* were present in the hickatee hole I sampled in July 1990, and small juveniles and remnant egg shells provided evidence of reproduction. Although stories of historical large harvests may lack precision, their basic content is probably true. Thus, evidence indicates that intense exploitation can lower population densities; less documented information suggests that heavily exploited populations can at least partially recover.

Comparing harvests made by free-diving from humanly unpopulated and populated sections of the Belize River provides strong evidence of the effects of exploitation (Fig. 5). These samples were collected by the same crew, in the same river, using the same methods. Large adult turtles were much more abundant in the humanly unpopulated section of the Belize River between BF and MT (Fig. 5) than in the humanly populated section of the Belize River below BF (Fig. 5) (t-test: P=0.0001). Only 4% of the sample in the humanly populated area were adult females, compared to 22% upstream from the villages (Table 2). Pooled capture rates in humanly populated areas were half those in unpopulated areas, indicating lower densities. The greatest proportion of captures were juveniles.

Comparisons of turtle exploitation from different sections of the Belize River demonstrated effects of repeated harvesting. Densities were lower in the most intensely exploited section, and selective removal of large juveniles and adults resulted in fewer large turtles (Fig. 5). The proportion of adult females was particularly low (Table 2). Small capture samples in Mussel Creek, the branch of the Hondo, and sections of Spanish Creek (SC) suggested the same response to heavy exploitation. In less intensely exploited areas, large females constituted a greater proportion of the catch. Because smallest size classes were untouched by all three methods, intermittent hunting presumably could allow those turtles to mature and restock an area. This is one explanation for persistence of populations inhabiting areas subject to sporadic large removals.

Belize City market counts of turtles were an unreliable index of numerical trends because of variable weather, effort, and marketing patterns. However, they suggested the same trends observed in the field. Larger turtles bring more profit for effort expended, yet large females were never encountered in the market. The preponderance of young turtles sold in the market suggests that adults were becoming rare.

If adult females and nests have become scarce, harvesting remnant cohorts of maturing juveniles may create an illusion of resiliency in populations where recruitment is actually low. Their removal inhibits replacement of reproductive classes, hastening the decline of the population. The data from the humanly populated section of the Belize River (Fig. 5, Table 2) fit this description.

Turtle exploitation levels by villages in the Community Baboon Sanctuary were unsustainable. Heavy exploitation had resulted in low recruitment. If all adult and maturing juvenile hickatees were removed, only immigration from dispersal, originating in less-disturbed sections of the river could prevent local population extinctions.

A less intensely exploited section of SC had a more sustainable pattern. Peg and net collecting in the creekside villages of Lemonal (L) and Rancho Dolores (RD) peaked during April and May (Fig. 1). The netting was generally small scale, and the harvest was usually distributed within the communities. Composition of a small sample (n= 48) of net captures was 19% adult females, 19% adult males, and 62% juveniles. The primary difference between this example and the preceding one was probably scale of removal. At most, a Lemonal net man may have caught 10 turtles a week (it was usually one or two). In the years preceding this study, free-divers had removed hundreds of turtles from the more accessible parts of the Belize River every dry season.

Exploitation and Demography

Life history traits of freshwater turtles places biological constraints on the level of harvest that populations can withstand. These traits include delayed maturity and subsequent iteroparity, which requires extended longevity (Congdon *et al.* 1993). Even the smallest and fastest maturing turtle species do not lay eggs until they are 4 years old (Gibbons 1987). Females of many turtle species mature between 6 and 12 years of age (Gibbons 1987). This includes

Trachemys scripta, sympatric with *Dermatemys*, but half the size (Gibbons *et al.* 1981, Mitchell and Pague 1990, Moll and Moll 1990). Blandings turtle, *Emydoidea blandingi*, takes 15 years to mature (Congdon *et al.* 1983). Lifespans over 40 years have been recorded in field studies of freshwater turtles, while captive turtles over 50 years have been recorded (Congdon *et al.* 1983, 1987; Gibbons 1987).

Freshwater turtle eggs usually have low survivorship (mean egg deposition to hatching survivorship=0.229, n=15 species, Iverson 1991). Survivorship increases (0.539) during *Trachemys scripta* hatchling's first year (Frazer *et al.* 1990). That increase typically continues through the juvenile years (mean=0.672, n=7 species, Iverson 1991) culminating with high subadult (mean=0.837, n=4 species, Iverson 1991) and adult survivorships (mean=0.879, n=8 species, Iverson 1991). The probabilities of attaining reproductive maturity are low. Frazer *et al.* (1990) estimated a 2.1% probability that a female *Trachemys scripta* would survive from egg deposition to first maturity. However, the few animals that attain maturity are subject to low predation levels. While data for *Dermatemys* lacks the preceding level of detail, a dramatic departure from the general pattern is unlikely.

Extended iteroparous longevity compensates for both delayed maturation (Gibbons 1987) and high egg and hatchling mortality (Frazer *et al.* 1990, Wilbur 1975). Because adult survivorship is high, sporadic years of high egg or juvenile mortality may not affect population stability (Congdon *et al.* 1983, 1987).

Solitary nesting habits of *Dermatemys* makes headstart programs impractical. Nesting beaches are unavailable for easy collection of large numbers of eggs. Although eggs may be obtained by inducing oviposition in wild-caught females, considerable labor and expense is involved. *Dermatemys* females in flood waters are difficult to catch (*e.g.* 369 net days to catch four gravid females) because they are widely dispersed. In heavily exploited areas, adult females constitute a small proportion of the catch, requiring large investments of time and labor.

With limited financial and human resources dedicated to conservation, it is important to address the source of population declines. Exploitation by humans, a recent development in *Dermatemys* history, has introduced high predation rates to size classes accustomed to high survival rates. This will likely disrupt the longitudinal interaction of iteroparity and longevity that maintains stability in turtle populations. Increasing adult survival should be the focus of an management program, and harvest should be conservative. If the source of decline is adequately addressed, and riparian habitats maintained, rivers and lagoons can provide cost effective natural turtle nurseries.

In April 1993, Belize approved legislation to conserve and protect *Dermatemys* (Statutory Instrument No. 55 of 1993). The legislation includes year-round possession limits, a closed season during the month of May, a prohibition on selling or purchasing of *Dermatemys*, and an extensive series of completely closed zones in major waterways of northern Belize. One intent of the legislation was to increase survivorship of larger size classes by reducing the number of *Dermatemys* removals. The means selected were those judged functional within the context of socio-economic and law enforcement constraints. Complex fine-tuned prescriptions were considered impractical for a pioneering exercise. The cultural factors considered in drafting the legislation were described in Polisar (1994) and Polisar and Horwich (1994). Completely closed zones were included as insurance, and to enhance any possibility of dispersal-aided recovery of diminished stocks.

The data and examples presented here emphasize the importance of considering biological constraints when developing sustainable-use harvest schemes and directly addressing the origin of management dilemmas, such as excessive adult mortality levels causing declines. Finally, be prepared for a long commitment. Production of research-based recommendations is a quick process compared to the long-term monitoring and adaptive management of both people and game that must follow.

ACKNOWLEDGEMENTS

The research was funded by NYZS-The Wildlife Conservation Society, Chelonia Institute, Programme for Belize, Lincoln Park Zoo, the Office of International Programs and the Program for Studies in Tropical Conservation at the University of Florida, Manomet Bird Observatory, and Sigma Xi. Support for follow-through work came from the Chelonia Institute, Crystal Channel Foundation, Fossil Rim Foundation, and the Tropical Conservation and Development Program at the University of Florida. Logistical assistance was provided by the Community Baboon Sanctuary, Belize Audubon Society, Belize Center for Environmental Studies, Chau Hiix Lodge, Belize Meteorological Service and Hydrology Department, Lighthawk, and British Forces Belize. The Belize Forestry and Fisheries Departments cooperated in many ways.

R. Horwich and F. Young helped start this project. P. C. H. Pritchard, M. W. Klemens, J. L. Behler, and A. Carr III provided administrative assistance. L. Diekman of St. Johns College provided space for specimen storage. R. Young, R. Horwich, and J. Lyon participated in market counts.

J. D. Congdon, M. W. Ewert, J. B. Iverson, K. Bjorndahl, J. P. Ross, D. Moll, and R. C. Vogt increased my understanding of turtle biology and conservation. F. W. King, L. J. Guillette, Jr., J. F. Eisenberg, and H. F. Percival reviewed the thesis from which this paper is excerpted. B. Godshalk, and the anonymous reviewers are thanked for editorial comments.

Special credit is due to over 75 residents of rural northern Belize; without their cooperation and assistance, the study would have been impossible. Thanks to R. Young and R. Brooks, and the Herrera, Lanza, Hulse, Joseph, Young, Flowers, Thompson, and Soler families. The village of Freetown Sibun deserves recognition for their request for regulations on turtle harvesting.

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Associate Editor: Christopher Vaughan
received: October 10, 1993
accepted: November 4, 1994