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ONTOGENETIC SHIFTS AND SEX DIFFERENCES IN CAUDAL LURING IN THE DUSKY PYGMY RATTLESNAKE, *SISTRURUS MILIARIUS BARBOURI*

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ABSTRACT: Caudal luring is a behavior used by many ambush-foraging snakes that increases their encounter rate with prey. In this study, we used the dusky pygmy rattlesnake, *Sistrurus miliarius barbouri*, in a series of trials involving prey and measured the frequency and duration of caudal luring. This behavior varied ontogenetically, with adults never performing caudal luring. Juveniles that lured for longer durations were more successful in attracting prey. Males and females caudal lured in equal frequency but females took longer time periods to achieve a similar level of foraging success. Because the tails are sexually dimorphic in this species, we suggest that the longer tail of the male may be a more effective luring device. This is the first quantification of a sex difference in caudal luring, and the results suggest important differences in foraging ecology among males and females.

Key words: Behavior; Caudal luring; Foraging; Ontogeny; Rattlesnake

CAUDAL luring by ambush-foraging snakes can increase their encounter rates with prey (Neill, 1960). The wiggling of a brightly colored tail presumably mimics the movements made by insect larvae, which are prey items of frogs and lizards (Greene and Campbell, 1972). Frogs and lizards are attracted to the lure and become prey themselves when they move within striking distance of the snake (Greene and Campbell, 1972). The use of this behavior as a foraging strategy has been well documented in viperids, but previous studies did not test whether this behavior varies among age classes or sexes.

In most species that caudal lure, including pygmy rattlesnakes, ontogenetic shifts in diet from anuran and lizard prey as juveniles to small mammalian prey as adults parallel ontogenetic shifts in tail color from bright yellow in juveniles to dark brown in adults (Heatwole and Davison, 1976; Rabatsky and Farrell, 1996). Because most small mammals do not consume insect larvae, the use of a lure by adult snakes presumably would not be effective in attracting mammalian prey. The observation that caudal luring occurs primarily in juvenile snakes (Heatwole and Davison, 1976) supports this hypothesis. Comparing the frequency (number of individuals) and duration of caudal luring among cohorts when experimentally offered prey, may indicate whether this behavior varies among age classes.

Anecdotal evidence suggests that some snakes that caudal lure may exhibit sex differences in this behavior as a result of sexual dimorphism in the tail (Neill, 1960). Neill (1960) suggested that the reproductive organs in the tail of the male give the tail a longer and more tapered appearance relative to females. Therefore, the tails of male snakes may be morphologically more similar to insect larvae and thus more effective as a lure. Furthermore, in the majority of species that caudal

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lure, the tails of males are brighter and more conspicuous (Neill, 1960). Male *Acanthophis antarcticus* and *Bothrops atrox* and female *Cerastes vipera* possess more conspicuous tail colors than their counterparts, but sex differences in behavior have not yet been observed in these species (Carpenter et al., 1978; Heatwole and Davison, 1976). Pygmy rattlesnakes are sexually dimorphic in tail morphology to accommodate the reproductive organs in males, but are not dichromatic in tail color (Bishop et al., 1996). Comparing the frequency (number of individuals) and duration of caudal luring between the sexes, as well as the luring success of each individual, when experimentally offered prey, may indicate whether a sex difference occurs in this behavior and whether the longer tails of the males are more effective luring devices.

In this study, we used a combination of field observations and laboratory trials to test for ontogenetic and sex effects on the frequency, duration, and success of individuals performing caudal luring in dusky pygmy rattlesnakes, *Sistrurus miliarius barbouri*. If age and related ontogenetic shifts in diet and tail color affect the frequency of caudal luring, then we predicted that a larger number of neonate and juvenile snakes would caudal lure and lure for longer durations than adults. Furthermore, we predicted that neonates and juveniles would attract more prey to move within striking distance than adults. Because male snakes possess longer, more tapered tails than females, and therefore should be more effective in attracting prey, we predicted that males would caudal lure less often and for shorter durations than females, and attract more prey within striking distance than females.

MATERIALS AND METHODS

For laboratory experiments, we collected snakes from Rock Springs Run State Reserve in Lake County, Florida, by visual survey between June and November of 2001 and 2002. After capture, we determined age based on body size as in Bishop et al. (1996). Snakes that were one year old we considered juveniles and snakes that were two years old and older we considered adults. We used 20 captive-born neonates from six clutches because no neonates were found in the field. We did not determine sex for neonates.

In the laboratory, we housed the snakes individually in 37.7-l glass terraria with leaf litter, a water dish, a nonilluminating heat source and a natural photoperiod. All snakes were kept in a room that was only visited at the start or end of an experimental trial. We allowed snakes 72 h to acclimate to the enclosure before beginning trials. Each snake was used in two randomized trials, one in the presence of prey and one in the absence of prey. If a snake had fed recently, as indicated by an externally palpable bolus, we waited seven days for digestion to occur (or until the bolus was no longer detectable) before beginning trials. We did not feed snakes between trials.

We also collected the lizard, *Anolis sagrei*, from Rock Springs to use as prey in trials because it is readily preyed upon by *S. m. barbouri* and it elicits caudal luring in this species (A. M. Rabatsky, personal observation). Lizards were provided the same amenities as the snakes, but several lizards were housed in a single terrarium and all lizards were kept in a separate room from the snakes. Lizards were not fed until after they were used in a trial and no lizard was used more than once. Although not quantified, smaller lizards were used for trials with smaller snakes and larger lizards were used for trials with larger snakes so that the size of the lizard did not exceed the gape of the snake.

During trials with prey, we placed a lizard in the corner of the terrarium opposite the snake. An incandescent light bulb mounted 1 m above the terrarium was dimmed to 2.7 lux (the approximate lighting at dawn and dusk). This light level induces the most caudal luring in this species (Rabatsky and Farrell, 1996). After 30 min, we removed the lizard from the terrarium. The same procedure was used for trials without prey except that no lizard was placed in the terrarium. We separated trials by 24 h and recorded them using a video camera mounted 1 m above the terrarium. We noted how long the snake undulated its tail, and if and when the lizard moved within striking distance of the snake (0.33 of the total length of the snake) using a scale marked on the terrarium.

We used nonparametric statistics because the data were nonnormal and heteroschodastic. Because some cell counts were zero values, we used a Pearson's chi-square test with a
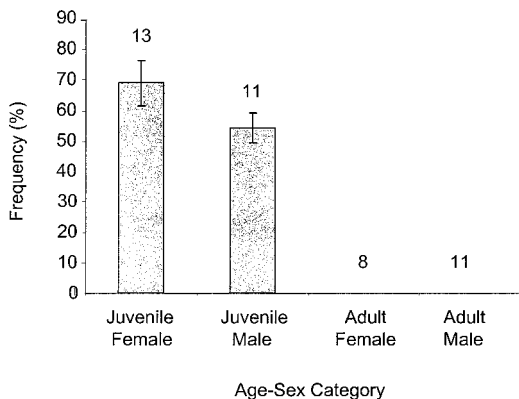
FIG. 1.—Frequency ($\pm$ 1 SE) of snakes performing caudal luring in trials with prey by age-sex categories. Numbers above bars denote sample sizes.
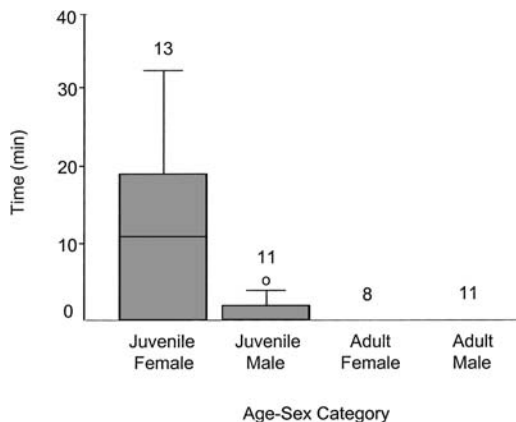

FIG 2.—Median and interquartile range for duration of caudal luring in trials with prey by age-sex categories. Circle denotes outlier and numbers above bars denote sample sizes.

Monte Carlo convergence approach (10,000 iterations) for frequency data. An adjusted Bonferroni approach was used to control for type I error rate (Rice, 1989). For duration data, we used a Kruskal-Wallis test. Several tests of interaction were considered, but again, a large number of zero values were problematic. In a concurrent study, we determined that the number of rattle segments possessed by a snake did not significantly influence luring success, and therefore was not controlled for statistically. Statistical analyses were performed using SAS (SAS Institute Inc., 2003).

RESULTS

Snakes never lured in the absence of prey and only young snakes (24 juveniles and 20 neonates) caudal lured when prey were present. Adults (n = 19) never lured in the presence of prey and therefore failed to lure prey to move within striking distance. Thus, there was a significant difference in the frequency (χ^2_2 = 18.74, P_{exact} < 0.0001, n = 63) and duration (χ^2_1 = 17.76, P < 0.0001, n = 63) of caudal luring among age classes. Young snakes also lured more lizards to move within striking distance than adults (χ^2_1 = 11.41, P_{exact} = 0.0006, n = 63). When only juveniles were considered, there was no significant difference in the frequency of caudal luring between the sexes (χ^2_1 =1.39, P_{exact} = 0.41, n = 24), but females spent significantly more time caudal luring than males (χ^2_1 = 4.82, P_{exact} = 0.03, n = 24). However, females did

not lure more lizards to move within striking distance than males (χ^2_1 = 1.73, P_{exact} = 0.19, n = 24). A summary of the frequency and duration of caudal luring by age-sex categories is given in Fig. 1 and Fig. 2. A total of nineteen lizards moved to within striking distance of a snake and only one lizard was struck within the 30 min trial period.

DISCUSSION

Ontogenetic shifts in diet and luring behavior are thought to be related in many species, but this relationship has been questioned in *S. m. barbouri* (Rabatsky and Farrell, 1996). Jackson and Martin (1980) reported one observation of caudal luring in an adult *S. m. barbouri* and suggested that because these snakes consume insectivorous prey into adulthood, they might benefit by retaining luring behavior as adults. However, Rabatsky and Farrell (1996) observed a significant ontogenetic shift in foraging posture in *S. m. barbouri*, with more young-of-the-year snakes found coiled with their tails exposed in the field. In this laboratory study, I found that caudal luring occurred exclusively in young snakes, which further suggests that luring is rare in adults. However, individual variation in when caudal luring behavior is no longer exhibited probably exists, and may contribute to conflicting observations.

Sistrurus miliarius barbouri is sexually dimorphic in tail length (Bishop et al., 1996).

Based on Neill's (1960) hypothesis, the longer tails of males in this species should be more effective as luring devices. In this study, males and females caudal lured with equal frequency but females took significantly longer than males to achieve the same foraging success. This result indicates that the tails of males are more effective as luring devices, which supports Neill's hypothesis. This finding is ecologically important because it indicates that males may spend less time exposing a conspicuously colored tail, and therefore may benefit from reduced predation.

Schuett et al. (1984) suggested that increasing segmentation of the tail may have enhanced the optical attractiveness of the lure and could have been the first step in the evolution of the rattle. This implies that adult snakes caudal lure and that adults, who have more time to accumulate segments, may be more effective in attracting prey when caudal luring. In this study, adults never caudal lured and therefore failed to lure prey within striking distance. Thus, my findings do not support Schuett's hypothesis. However, trials in which both the behavior and the morphology are present (e.g., juveniles with a variable number of rattle segments) are needed for a more robust test of this hypothesis.

Reiserer (2002) used caudal luring in a study designed to assess the perceptual mechanisms and cognitive functions of vipers. He found that *Sistrurus catenatus*, the closest relative of *Sistrurus miliarius*, demonstrated intraspecific variation in caudal luring among populations; *S. c. edwardsii* lured for lizards but not frogs, while *S. c. catenatus* and *S. c. tergeminus* lured for frogs but not lizards. Based on the observations of Jackson and Martin (1980) of *S. m. barbouri* (from south Florida), Reiserer stated that this species will lure for frogs (*Acris* spp.), but not for lizards. Results obtained in my study contrast with this observation. *Sistrurus miliarius barbouri* lured for lizards, and in a previous study, I showed that *S. m. barbouri* (also obtained from central Florida) lures for *Hyla* spp. (Rabatsky and Farrell, 1996). Thus, it appears that *S. m. barbouri* lures for both frogs and lizards and/or exhibits geographic variation in caudal luring.

The variation in luring behavior observed in this study indicates that the costs and benefits of this behavior differ among age classes and between sexes. Currently, frequent luring and luring for multiple prey types may enhance foraging success in *Sistrurus miliarius* and may partially explain the accelerated life history traits that are observed in this species, including rapid growth rates of juveniles, early age at first reproduction, and frequent reproduction in females (Bishop et al., 1996; Farrell et al., 1995). Males also may have increased survivorship compared to females due to reduced risk of predation. At present, the rattle appears to serve little function as a defensive mechanism in this species (Rowe et al., 2002). Historically, however, the enhanced defense and survival due to rattling may have been more important than enhanced foraging for adults, especially if a lure was less effective in attracting mammalian prey. Further investigation of luring behavior may reveal additional costs and benefits that influence the foraging ecology of this species.

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SURVIVAL PROBABILITY ESTIMATES FOR LARGE JUVENILE AND ADULT GREEN TURTLES (*CHELONIA MYDAS*) EXPOSED TO AN ARTISANAL MARINE TURTLE FISHERY IN THE WESTERN CARIBBEAN

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ABSTRACT: The largest remaining green turtle (*Chelonia mydas*) population in the Atlantic is potentially threatened by the resurgence of a commercial artisanal green turtle fishery in Nicaragua. Nicaragua is the site of the principal feeding ground for adults from the Tortuguero, Costa Rica, rookery. Little is known about the life history parameters of this population away from the nesting beach. To better understand the potential impact of harvesting in Nicaragua on the Tortuguero population, we estimated survival rates of adult females tagged on the nesting beach at Tortuguero, and a mixed group of large juveniles and adults tagged at turtle fishing sites in Nicaragua. Based on band recovery analysis, large juvenile and adult green turtles tagged at Nicaragua turtle fishing sites have a very low annual survival probability, 0.55. Adult females tagged on the nesting beach, which may forage at a broad range of Caribbean feeding grounds, had an annual survival probability of 0.82. These survival rate estimates are likely too low to sustain the population and have important implications for the future of the Tortuguero rookery.

Key words: Band recovery; Caribbean; *Chelonia mydas*; Green turtle; Nicaragua; Survival rates; Tortuguero, Costa Rica

ESTIMATES of stage- or age-specific survival probabilities of wildlife populations are necessary to understand life cycles and to evaluate population dynamics, threats, and potential management strategies for the conservation of the target species (Lebreton et al., 1992; Williams et al., 2002). Most populations of sea turtles are declining and in need of strong conservation actions (Limpus, 1995). Sea turtle life histories are only generally un-

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derstood: they are long-lived, slow to mature, exhibit low survivorship in the early life stages and high survivorship in the later life stages. Specific life history parameters, however, are not well known for all life stages of any sea turtle population, and consequently, the effects of management practices are unclear. Furthermore, because they are highly migratory throughout their life cycle, continued harvest of some sea turtle populations may compromise conservation efforts of other nations with which this resource is shared. Estimates of current demographic parameters for sea turtle populations and a better understanding of the principal threats affecting their dynamics are needed to develop effective strategies to conserve them.

Among the most serious threats to green turtle (*Chelonia mydas*) populations in the greater Caribbean are artisanal turtle fisheries. Of particular importance is a large, legal turtle fishery on the Caribbean coast of Nicaragua. An unknown number of green turtles is also captured in shrimp trawls fishing along the east coast of Nicaragua, and some of these turtles are brought to commercial centers and consumed along with turtles from the turtle fishery (C. J. Lagueux, unpublished data). The commercial artisanal turtle fishery in Nicaragua occurs in one of the most important developmental and foraging habitats for green turtles in the Caribbean. The expansive seagrass pastures in this region attract green turtles of both sexes and from multiple rookeries (Bass et al., 1998). It appears to be particularly important to large juveniles and adults that recruit into this habitat from numerous developmental habitats throughout the region (e.g., Bahamas, Bermuda, and Florida). In addition, Nicaragua comprises the most important foraging ground for the green turtle rookery at Tortuguero, Costa Rica (Carr et al., 1978), which is the largest remaining green turtle rookery in the Atlantic.

The Tortuguero population has been subjected to intense, but variable, harvest pressure on adult females and their eggs at the nesting beach, and on large juveniles and adults on feeding grounds in Nicaragua and elsewhere. After many years of harvest, numbers of nesting females showed signs of decline in the 1960's (Carr, 1969), although specific data on harvest levels are sparse. A severe decline in nesting was observed at Tortuguero in the 1970's, only a few years after three turtle processing plants began operations on the Caribbean coast of Nicaragua. The demand for green turtles during this time resulted in an estimated harvest of 5000 to 10,000 turtles annually (Groombridge and Luxmoore, 1989; Nietschmann, 1973, 1979). In the mid-1970's, this population was afforded some protection on the nesting beach in Costa Rica, and harvesting also decreased in Nicaragua due to the closing of the turtle processing plants and in the 1980's because of civil unrest, which limited fishing activities. Recent evaluations of the nesting population at Tortuguero showed a trend of increasing nesting activity (Bjorndal et al., 1999; Troëng and Rankin, 2005). Intensive harvest pressure in Nicaragua, however, returned in the early to mid-1990's, where currently a minimum of 11,000 green turtles are harvested annually (Lagueux, 1998). To better understand how this recent increase in harvesting may affect the Tortuguero nesting population in the future, and the population as a whole, an examination of current life history parameters and population status is needed.

The only estimates available on survival rates for any life-history stage of the Tortuguero population are for nesting females (Bjorndal, 1980), and for eggs and emergence success of hatchlings (Fowler, 1979; Horikoshi, 1992). From Bjorndal's (1980) data, where an enumeration method was used on cohorts, annual survival of nesting females was estimated at 0.61 from 1959 to 1972, which includes a period of heavy exploitation. However, these data are more than 30 years old and the current annual survival rate could be significantly different, as could the population growth rate. In addition, more appropriate methods for parameter estimation (such as mark-recapture and band recovery models) are now available and widely used. No information has been published on survival rates of large juveniles from this population, which comprises the majority of animals harvested in the Nicaragua turtle fishery (Lagueux, 1998). In this study, we estimate current annual survival rates of nesting females at Tortuguero, and of large juvenile and adult turtles targeted in the turtle fishery in Nicaragua.
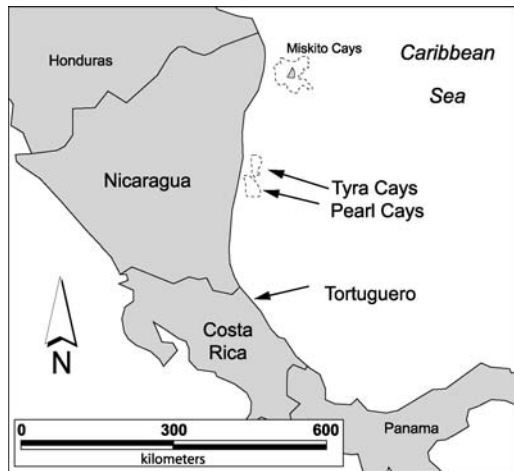
FIG. 1.—Location of study sites in Costa Rica (Tortuguero nesting beach) and Nicaragua (foraging grounds near the Pearl Cays and Tyra Cays) where green turtles were captured, tagged, and released. Dashed lines show the general turtle fishing areas.

MATERIALS AND METHODS

Capture-Mark-Release

Nicaragua foraging grounds.—The Nicaragua field study was conducted from March 1999 to May 2002, whenever weather conditions permitted. Field work was conducted by a team of three to four local fishers, and often one or both of the authors. We used large-mesh entanglement nets to capture turtles, the most common technique used by turtle fishers of the Caribbean coast of Nicaragua (Lagueux, 1998); see Campbell (2003) for a detailed description. We used established turtle fishing sites located off the central Caribbean coast of Nicaragua, primarily near the Pearl Cays (Fig. 1), to capture green turtles. Specific capture locations included Crow Cam, Crowning Spot, Cynthia's Bank, Little Middle Set, Seal Cay (Southwest Bank), and South Compass (Fig. 2).

Turtles were examined, measured, weighed, marked (tagged), and then released near the original capture location on the same day of capture (with a few exceptions). Straight-line carapace length (SCL) was measured from the nuchal notch to the longest posterior marginal tip. Curved carapace length (CCL) was measured along the mid-line from the nuchal notch to the posterior notch. Sex was determined by external characteristics (principally using tail length) whenever possible. Turtles smaller
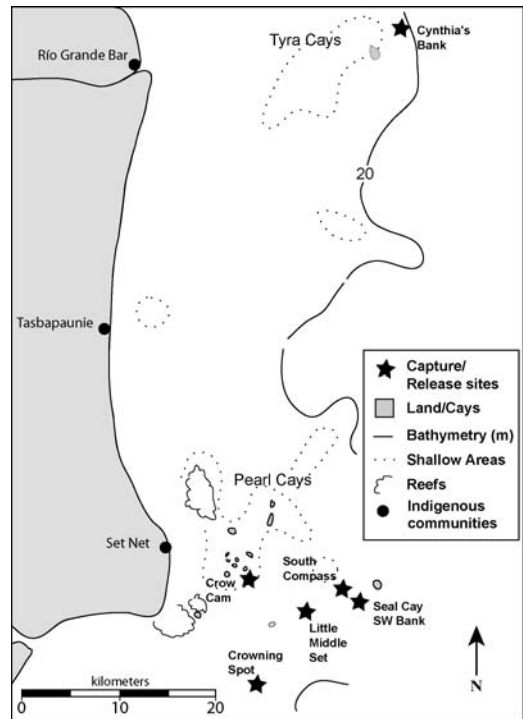

FIG. 2.—Capture/release locations of green turtles on the southern foraging grounds off the central Caribbean coast of Nicaragua.

than approximately 86 cm CCL, without observable external male characteristics, were deemed of "unknown" sex, while turtles larger than this size without observable male characteristics were deemed female, with a few exceptions. In a few cases where our assignment of sex disagreed with morphometric data presented by Lagueux (1998) on the relationship between carapace and tail lengths of green turtles of known sex, we assigned sex based on her results. In doing so, we avoided potentially misidentifying immature male turtles as females. Turtles were double-tagged with either monel or inconel metal tags (style #681, National Band and Tag Company [NBTC], Freeport, Kentucky, U.S.A.). Each tag (bearing a unique number) was placed proximal to the first scale on the trailing edge of each front flipper.

Local Nicaragua fishers were encouraged to return tags to project personnel from any marked turtles they captured. For each tag return, information was recorded on the fate of the turtle and how, when, and where the turtle

was captured. The fishers then received a specially designed t-shirt or hat for their cooperation.

Costa Rica nesting beach.—The Caribbean Conservation Corporation (CCC) conducts a green turtle research and tagging program annually at Tortuguero, Costa Rica (Fig. 1). Research on the green turtle population at Tortuguero was initiated in 1955 (Carr and Giovannoli, 1957) and has continued for almost 50 years. For this study, we used data from the 1995 to 2000 nesting seasons, provided by the CCC, to estimate survival rates of Tortuguero nesting females.

Prior to 1998, the green turtle tagging program was conducted from early-July to mid-September. Since 1998, however, the program has expanded and is now conducted from early-June to late-October. For logistical and historical reasons, the tagging program focuses on turtles that nest primarily on the northern 8 km of the 35 km-long nesting beach. This 8 km-section is patrolled nightly by teams of people who tag the turtles subsequent to egg deposition. Nesting turtles were tagged in both front flippers (in the same location as described for turtles in the Nicaragua study); however, there has been some experimental tagging in various combinations of front and rear flippers. Primarily inconel metal tags (style #681, NBTC) were used during the study period, but in some seasons monel metal tags also were used (style #49, NBTC).

Fishers and others from throughout the Caribbean have returned turtle tags from the CCC's tagging program primarily, to the Archie Carr Center for Sea Turtle Research, University of Florida, and in Nicaragua to CJL (where the majority of tag recoveries occur). A small monetary reward ($5.00 USD) is provided by the CCC for each tag recovery.

Model Structure, Model Selection, and Parameter Estimation

To generate the band (tag) recovery histories necessary for analysis, we assigned each tagged animal to a marking period and each tagged animal that was reported dead to a recovery period. A marking period (MP) is the period in which a group of animals are captured, tagged, and released. We assigned a mid-point (a single date) to each MP in order to define the recovery periods (RP, the time interval between MPs when tags from marked animals are recovered) and assigned each recovery accordingly. A recovery refers exclusively to the recovery of tag(s) from a marked animal that was killed.

The tag and recovery histories of green turtles tagged in Nicaragua (representing a mixed group of large juveniles and adults of both sexes) and Costa Rica (representing only adult females) were analyzed using recovery models implemented in Program MARK (White and Burnham, 1999) to estimate survival rates for each group. On a few occasions, turtles were reported recaptured and not killed; these recaptures were not included in the recovery analysis. The modeling used for tag recoveries follows the following scenario for one marking and one recovery period:
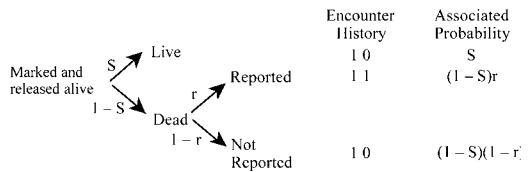
where a marked animal either (i) survives (with probability S and an encounter history of 1 followed by 0 for being alive at release and not encountered later), (ii) dies and is recovered and reported (with probability $(1 - S)r$ and an encounter history of 1 1 for being alive at release and being reported when recovered), or (iii) dies and is not reported (with probability of $(1 - S)(1 - r)$ and an encounter history of 1 0 for being alive at release and not being reported when recovered) (Cooch and White, 2001). The parameters estimated in this recovery model include a survival probability, S, and a recovery probability, r (the probability that a dead marked animal is reported). Maximum likelihood estimates of these probabilities are calculated through an iterative process in Program MARK from the recovery data, i.e., the numbers of tagged animals and subsequent recoveries by time period.

Assumptions of modeling tag recoveries include: (i) the sample is representative of the population under investigation; (ii) there is no

tag loss; (iii) the date of recovery is correctly tabulated; (iv) survival rates are not affected by tagging; (v) rate parameters for all individuals within a group are homogeneous; and (vi) fates of tagged individuals are independent of each other (Brownie et al., 1985).

A set of four candidate models for the data set for adult females (nesting beach) and five candidate models for the data set for mixed large juveniles/adults (foraging ground) were developed. The global model (model with the most parameters) is a fully time-dependent (t) model, $S_t r_t$, that allows for S to differ between release periods and r to differ among recovery periods. The other three models used for both data sets are reduced parameter models that allow for combinations of time-dependence and constant rates for S and r. An additional model, $Sr(d)$, for the mixed large juvenile/adult data set is a model in which S is assumed constant (per unit time) and r is a function of the duration of the interval until the next release period. This model was not used for the adult female data because the RPs did not vary in duration. From these sets of models, the "best approximating model" for each set was identified by Program MARK (White and Burnham, 1999) using Akaike's Information Criterion, AIC (Akaike, 1985; Burnham and Anderson, 1998). This type of model selection identifies the most parsimonious model, and using a small sample size correction term yields AIC_c (Hurvich and Tsai, 1989). A Bootstrap goodness-of-fit (GOF, Program MARK, White and Burnham, 1999) test was conducted on each global model to ensure that each data set did not severely violate the assumptions of the model, then each group of models was adjusted for over-dispersion using a quasi-likelihood parameter, ĉ, (thus a quasi-likelihood AIC_c ($QAIC_c$), see Burnham and Anderson, 1998; Lebreton et al., 1992). There were insufficient data to use other means to evaluate model fit and estimate ĉ. The estimate of ĉ was based on the observed deviance (of the global model)/mean expected deviance (generated from the Bootstrap GOF test in Program MARK).

For the mixed large juvenile/adult group tagged on the Nicaragua foraging ground, MPs were not restricted to a particular time of year because animals can be found on the foraging grounds in Nicaragua year around, but rather were restricted primarily by weather conditions. All capture-mark-release locations were assumed to have the same recovery probabilities and therefore data from all locations were combined. In some instances, two MPs were combined into a single MP because of their temporal proximity; e.g., if the number of animals captured during a MP was low due to poor weather conditions, we conducted another MP as soon as possible and combined the two MPs into one. The RPs were variable in duration and were based on the time intervals between the midpoints of successive MPs. Because the RP intervals were less than one year, the proportion of a year that each RP represented was determined (i.e., RP duration/365 days) and used in the recovery model, resulting in an annual survival rate estimate.

For adult females tagged on the nesting beach in Costa Rica, the majority of tagging occurred between July and September of each year. The mid-point chosen for all MPs was 15 August; therefore, all tag recoveries could be assigned to an appropriate RP, and the duration of each RP was approximately one year. Recovery dates were sometimes not specific, often either because the fisher did not remember when the turtle with the tags was caught or because the fisher was unavailable to provide the information at the time the tag(s) was obtained. This variability resulted in 4 types of recovery dates: (1) the exact date, which included day, month and year, (2) a partial date which included only the month and year, (3) a year only date, and (4) a cut-off date, where the recovery date was not known, and thus the turtle had been recovered no later than the date the tag(s) was received. Recoveries with a cut-off date that was greater than a year after the turtle was marked were excluded from the analysis to avoid potential bias in estimates as a result of delayed band reporting (Anderson and Burnham, 1980). In addition, we established criteria to assign tag recoveries that lacked the exact recovery dates to a RP. For recoveries where the year and only the month of August was known, we assigned the recovery to the RP after 15 August for that year to avoid underestimating the time to tag recovery; all other months could be assigned to a RP either before or after the month of August. For recoveries when only the year of recovery was known ($n = 6$), we

TABLE 1.—Mark-release and recovery histories for the mixed large juvenile/adult group of green turtles tagged on the Nicaragua foraging ground between March 1999 and May 2002 and recovered by 14 September 2002. Marking period (MP) is a period when animals are captured, marked, and released. Recovery period (RP) is the interval between releases of newly marked animals when recoveries occur.

MP (duration in days)	MP mid-point	No. marked/released	Number of tag recoveries of dead marked turtles in each RP (duration in months)															
			1 (1.6)	2 (1.8)	3 (3)	4 (0.4)	5 (4.1)	6 (2.1)	7 (1.1)	8 (4.2)	9 (6)	10 (1)	11 (1.3)	12 (7.9)	13 (0.6)	14 (1.5)	15 (1.9)	16 (3.9)
1 (5)	5 Mar 99	14	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 (17)	22 Apr 99	24	—	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0
3 (11)	16 Jun 99	12	—	—	1	0	0	0	0	0	0	0	0	0	0	0	0	0
4 (2)	15 Sep 99	9	—	—	—	0	2	0	0	0	0	0	0	0	0	0	0	0
5 (11)	27 Sep 99	13	—	—	—	—	1	0	1	0	1	0	2	0	0	1	0	0
6 (3)	31 Jan 00	9	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0
7 (11)	3 Apr 00	20	—	—	—	—	—	—	1	1	4	0	1	3	0	0	1	0
8 (20)	5 May 00	25	—	—	—	—	—	—	—	1	3	0	1	1	0	0	1	0
9 (24)	11 Sep 00	14	—	—	—	—	—	—	—	—	1	0	1	1	0	1	0	0
10 (4)	12 Mar 01	15	—	—	—	—	—	—	—	—	—	0	1	1	0	0	0	0
11 (5)	10 Apr 01	13	—	—	—	—	—	—	—	—	—	—	0	2	0	0	0	0
12 (14)	20 May 01	21	—	—	—	—	—	—	—	—	—	—	—	0	0	1	0	2
13 (4)	17 Jan 02	11	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0
14 (12)	4 Feb 02	19	—	—	—	—	—	—	—	—	—	—	—	—	—	0	1	0
15 (6)	23 Mar 02	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
16 (3)	19 May 02	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1

assigned the RP depending on whether or not the turtle was tagged in the same year. If the turtle was tagged in the same year, then the RP following the RP when the turtle was tagged was used; however, if the turtle was recovered more than a year after being tagged, then we assumed it was captured before 15 August of that year. This classification was used because there are more months available for fishing prior to 15 August than after, and more fishing occurs in these first 7.5 mo of the year (Lagueux, 1998); thus the probability that the turtle was captured prior to 15 August of that year would be greater.

Comparison of Survival Rate Estimates Between Sites

To determine if the survival estimates for the two groups were homogeneous, a comparison was made using a chi-square test. The chi-square test was implemented using Program CONTRAST (Hines and Sauer, 1989).

RESULTS

Mixed Large Juvenile/Adult Group (Tagged on Nicaragua Foraging Ground)

Between March 1999 and May 2002, we marked and released turtles on 16 occasions, or marking periods (MP), ranging from 2 to 24 d in duration. Recovery periods (RPs) ranged

from 0.4 to 7.9 mo and included recoveries through 14 September 2002 (Table 1).

During the MPs, 250 green turtles were captured, marked, and released (Table 1). Turtles ranged in size from 67.4 to 102.0 cm SCL ($\bar{x} = 84.8$ cm, 1 SE = 0.43, $n = 250$) (Fig. 3). Turtles captured in the study area included large juveniles and adults of both sexes. The sex ratio for turtles where sex could be determined using external characteristics was strongly male biased with a male to female ratio of 3.4:1, which differs significantly from a 1:1 ratio (One-sample Proportion Test, Z = 7.9, $P < 0.0001$). Sex was not determined for 39 animals. If all 39 turtles of unknown sex were females the sex ratio would be 1.9 M: 1 F, still significantly male biased (One-sample Proportion Test, Z = 4.8, $P < 0.0001$).

During the RPs, 46 tagged green turtles (18.4%) were reported harvested (i.e., recovered) by turtle fishers (Table 1). The average duration between tagging and recovery was 303 d and ranged from 13 to 1003 d (1 SE = 37.5, $n = 45$, includes approximate capture dates). The duration could not be determined for one recovery, but, it was less than 260 days based on the day the tags were received by our program personnel. Most recoveries occurred at turtle fishing sites where turtles were released ($n = 21$) or at nearby fishing sites (up to a distance of approximately 14 km from
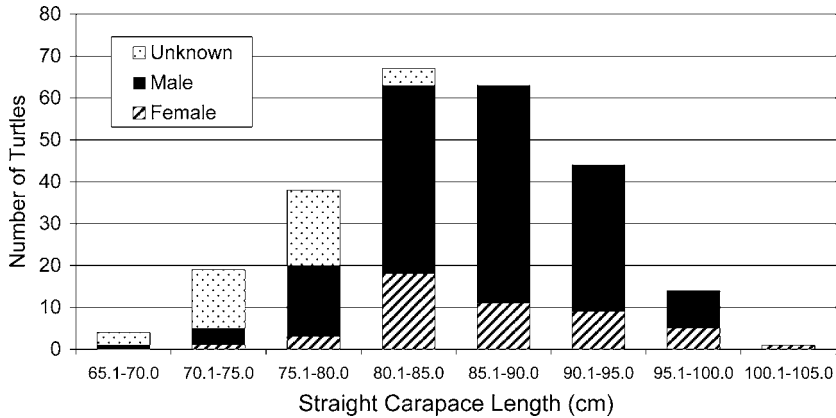
FIG. 3.—Size distribution according to sex of green turtles captured and tagged on the foraging grounds in Nicaragua between March 1999 and May 2002. Straight carapace length was measured along the mid-line from the nuchal notch to the longest posterior marginal tip ($\bar{x}$ = 84.8 cm, range = 67.4 to 102.0, 1 SE = 0.43, n = 250).

the release site, n = 18); when combined these recoveries represent 84.8% of all recoveries. Six recoveries occurred away from the original release site, but on the Nicaragua foraging grounds. The straight-line distances between these six release and recovery sites varied from 32 to 230 km. Only one recovery occurred outside the Nicaragua foraging grounds; a male turtle was harvested in Panama in June 2000 (A. Meylan, personal communication), two to three months after being tagged in Nicaragua. The straight-line distance from the release site in Nicaragua to the recovery site in Panama was approximately 380 km.

The mean annual survival probability estimate based on the most parsimonious model (Sr) was 0.554, 95% confidence interval (CI) = 0.332–0.756, 1 SE = 0.115. The reporting rate (r) based on this model was 0.284, CI = 0.180–0.418, 1 SE = 0.062. Model Sr (constant survival and recovery probabilities) was more than 2.5 times better supported by the data than the next "best" model, Sr(d), using the QAIC$_c$ weights (Table 2). The mean annual survival probability estimate from the second "best" model Sr(d), however, were nearly identical to model Sr, S = 0.559 and CI = 0.334–0.762, 1 SE = 0.117. It should be noted that we did not attempt to estimate survival rates separately for males and females tagged on the feeding ground due to the small sample size of tagged females (n = 48).

These results indicate that there was an estimated 55% probability that a turtle

tagged at the turtle fishing sites sampled in Nicaragua was alive and available for sampling the next year. It was not possible to separate mortality (hunting and natural) from permanent emigration out of the sampling area.

Adult Female Group (Tagged on Nesting Beach at Tortuguero, Costa Rica)

From the 1995 through 2000 nesting seasons, 8025 green turtles were tagged and re-

TABLE 2.—Model comparisons from band recovery data for green turtles tagged and released on the foraging grounds in Nicaragua, from March 1999 through May 2002. S = survival probability, r = recovery probability, t = time dependence, and d indicates that r is a function of the duration of the interval until the next release period. Adjusted ĉ = 1.063, QAIC$_c$ = corrected quasi-likelihood Akaike's Information Criterion value, Delta QAIC$_c$ = the difference in the current model QAIC$_c$ and the model with the lowest QAIC$_c$ value, QAIC$_c$ weight = the likelihood of the current model relative to the other models considered, # Parameters = the number of estimable parameters, QDeviance = difference between the −2log(Likelihood) for the current model and the −2log(Likelihood) of the saturated model (the model with the number of parameters equal to the sample size) (Cooch and White, 2001; White and Burnham, 1999).

Model	QAIC$_c$	Delta QAIC$_c$	QAIC$_c$ weight	# Parameters	QDeviance
Sr	373.62	0.00	0.684	2	96.63
Sr(d)	375.53	1.92	0.262	3	96.50
S$_t$r$_t$	378.80	5.19	0.051	19	64.56
S$_t$r	386.62	13.00	0.001	17	77.04
Sr$_t$	386.95	13.34	0.0009	17	77.37

TABLE 3.—Mark-release and recovery histories for adult female green turtles tagged on the Tortuguero, Costa Rica, nesting beach from 1995 to 2000 and recovered by 15 August 2001. Marking period (MP) is a period when animals are captured, marked, and released. Recovery period (RP) is the interval between releases of newly marked animals when recoveries occur. The mid-point for all MPs was 15 August and the duration of all RPs was 1 yr.

MP	No. marked/released	Number of tag recoveries of dead marked turtles in each RP					
		1	2	3	4	5	6
1 (1995)	1156	18	5	26	11	17	17
2 (1996)	1395	—	10	34	18	12	11
3 (1997)	1922	—	—	72	56	19	30
4 (1998)	1225	—	—	—	41	18	14
5 (1999)	1041	—	—	—	—	16	17
6 (2000)	1286	—	—	—	—	—	31

leased by the CCC field staff (Table 3). Of these, tags from 556 turtles were recovered (6.9%) up to 15 August of the 2001 nesting season. Only 493 of these recoveries, however, were included in the analyses due to imprecise recovery dates associated with the data. Approximately 95% of all tag recoveries were on the foraging grounds in Nicaragua.

The mean annual survival probability estimate for the adult female group based on the model Sr_t was 0.821, CI = 0.727–0.887, 1 SE = 0.041. This model was more than six times better supported by the data than the other models (Table 4). The mean reporting rate ($\hat{r}$) was 0.1174 based on the six reporting rate estimates. Based on these results there was an 82% chance that females marked for the first time at Tortuguero were alive and available for sampling the next year.

Comparison Between Tagging Sites

The hypothesis of homogeneous survival probabilities (i.e., mixed juvenile/adult group = adult females) was rejected at the $\alpha = 0.05$ level (Chi-SQ = 4.793, df = 1, $P = 0.029$). The survival rate estimate for the mixed group is more than 30% lower than the estimate for adult females tagged on the nesting beach at Tortuguero.

DISCUSSION

Comparison of Survival Rate Estimates Between Sites

The large difference in survival rate estimates between the adult female group and the mixed group may seem somewhat sur-

TABLE 4.—Model comparisons from band recovery data for green turtles tagged on the Tortuguero, Costa Rica, nesting beach from 1995 to 2000. Adjusted ĉ = 1.7. Abbreviations are the same as in Table 2.

Model	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight	# Parameters	Q Deviance
Sr_t	2867.1	0.00	0.7959	7	15.74
$S_t r_t$	2870.9	3.80	0.1192	11	11.51
$S_t r$	2871.6	4.47	0.0850	7	20.21
Sr	2900.9	33.79	0.0000	2	59.54

prising given that the principal feeding grounds for the Costa Rica rookery are in Nicaragua, and that one would expect large juveniles to have only a slightly lower natural survival rate than adults (less than 10% lower for studies of greens and loggerheads (*Caretta caretta*) in Australia; Chaloupka and Limpus, 2002, in press). However, for the survival rate estimates of the two groups to be more similar, the following would need to be true: (1) adult females would have to be equally susceptible to turtle fishing as those turtles that were marked and released at the established fishing sites sampled in Nicaragua, and/or (2) adult females that use foraging areas other than Nicaragua would have to be subjected to threats similar to those experienced by turtles using Nicaragua foraging sites. Neither of these requirements appears to be true.

For the first to be true, there would have to be little or no segregation between adult females and either large juveniles or adult males, indicating that they use the same habitats and thus would have a similar probability of being captured by turtle fishers. However, there is some evidence to suggest that sexual segregation on the Nicaragua foraging ground does occur.

Lagueux (1998) reported that the overall sex ratio for turtles captured in the turtle fishery in the northern region of Nicaragua was 1 male : 1.7 females. In this study, which was located at the very southern end of the foraging ground, the sex ratio was strongly male biased at 3.4 males : 1 female. In addition, adult females ($n = 9$) tracked by satellite from the Tortuguero nesting beach migrated to foraging areas either in the northern region of the Nicaragua foraging ground ($n = 7$) or farther north to foraging areas in Honduras and Belize (Caribbean Conservation Corporation, unpublished

data). These patterns provide strong evidence that there is some degree of sexual segregation on the Nicaragua foraging ground, with an apparent preference by adult females for the more northern foraging areas. This evidence combined with a lower proportion of the feeding grounds subjected to turtle fishing in the north (based on the position of the 20 m bathymetric lines as an indication of seagrass distribution), and that the majority of turtles captured are large juveniles suggests that adult females may have a reduced probability of being captured in the turtle fishery.

The second point, that adult females residing in other feeding areas in the Caribbean are subjected to the same threats as those in Nicaragua is also unlikely to be true. The Nicaragua turtle fishery is the largest and most intensive in the Caribbean, and since the majority of the adult female population occurs in this region (Carr et al., 1978), it is unlikely that they face a greater threat elsewhere.

Further evidence that adult females may be less affected by the turtle fishery in Nicaragua than the mixed group is found in inferences about fishing mortality and its relative importance in the two groups of turtles (adult female and mixed foraging groups). These inferences emerge from consideration of the survival and reporting rate estimates from the two data sets and are based on the assumption that the probability of a marked animal being reported if captured in the fishery is similar for the two groups. An assessment of the relative fishing mortality (RFM), calculated as

$$\hat{RFM} = \frac{(1 - \hat{S})\hat{r} \text{ for mixed group}}{(1 - \hat{S})\hat{r} \text{ for adult group}} = 6.06,$$

suggests that a turtle from the mixed large juvenile/adult group is about 6 times more likely to die in the turtle fishery than a turtle from the adult female group. Further, the relative fraction of total mortality attributed to fishing, estimated as 0.284 (r for mixed group)/ 0.117 (mean r for adult female group) = 2.43, suggests that about two and one half times more of the total mortality of the mixed group, relative to the adult female group, is attributed to fishing.

Precision and Potential Bias of Survival Rate Estimates

Delayed reporting of tag recoveries, when the recovery date reported is later than the actual recovery date, can cause a positive bias in survival rate estimates (Anderson and Burnham, 1980). Delayed reporting is not likely to be a problem for the mixed group tagged on the foraging ground because of the presence of a turtle conservation program in the area where most of the tags are recovered and frequent reminders to fishers to turn in any tags they obtain. Delayed reporting is more likely to occur with tag recoveries for the adult female group tagged in Costa Rica, since many of the animals are not captured for several years after being tagged and usually are captured some distance from the marking site. However, it has been shown that band recovery models are generally robust to this potential bias (Anderson and Burnham, 1980) and thus, in this case, would likely have a negligible effect on survival rate estimates.

Contrary to delayed reporting, tag loss could cause a negative bias in survival rate estimates (Nelson et al., 1980). Tag loss is probably minimal for the mixed group at the Nicaragua site because tag loss on foraging grounds (using similar tagging methods) has been shown to be low for relatively short time periods (Bellini et al., 2001; Limpus, 1992). Because turtles are double tagged, the probability of losing both tags is much lower and, thus, is not likely a significant source of bias for our foraging ground survival rate estimate. Tag loss for the adult female group may be higher because nesting females use their flippers extensively on land during the nesting process and are exposed to aggressive behavior during mating (Limpus, 1992). However, the probability of a turtle losing a single tag within a nesting season at Tortuguero was only 0.031 in 2000 and 0.033 in 2001 (Caribbean Conservation Corporation, unpublished data). An earlier study on tag loss at Tortuguero (Bjorndal et al., 1996) showed more variable within season tag loss during the 1987 to 1989 seasons (0.02 to 0.11), and probabilities for between season tag loss ranged from 0.226 to 0.333 for 2 to 4 yr recovery intervals. However, primarily monel flipper tags were used during the 1987 to

1989 nesting seasons. Monel metal tags vary in quality (Bjorndal et al., 1996), are highly corrosive (Limpus, 1992), are more prone to corrosion than inconel tags (Bellini et al., 2001), and have a different locking mechanism than the inconel tags used primarily at Tortuguero from 1995 to 2000 (this study). Nevertheless, because turtles included in this study were double tagged, the probability of losing both tags within a season is much lower, i.e., 0.0009 for 2000 and 0.001 for 2001 (calculated as single tag loss squared), although annual tag loss for adults has not been estimated. Furthermore, tag loss would have to be severe or mortality rates low to significantly bias survival rate estimates (Nelson et al., 1980).

Another possible source of bias is permanent emigration (or dispersal). Permanent emigration is thought to be minimal in the mixed group tagged on the foraging ground because of the large number of marked animals that were recovered in or near the banks where they were released, suggesting that at least some turtles are resident in the area. Satellite or radio telemetry studies of green turtles should help elucidate the extent of emigration from the Nicaragua feeding grounds.

Precision in the survival rate estimates for the two groups is much higher for the adult females than for the mixed group; this difference is reflected in the confidence intervals for each mean (CI = 0.73–0.89 for the adult female group, and CI = 0.33–0.76 for the mixed large juvenile/adult group). The CI for the adult female estimate is comparable to those of other studies on sea turtles using similar methods (e.g., Chaloupka and Limpus, 2002, in press; Seminoff et al., 2003). The wide CI for the mixed group estimate is at least in part due to the relatively small sample size of turtles marked and released ($n = 250$ turtles), but is similar to results from another feeding ground study with a similar sample size (Seminoff et al., 2003). Additional years of tagging and recovery of turtles on the foraging ground should reduce the confidence intervals for this estimate considerably.

Conservation Implications

The use of capture-mark-recapture (CMR) and band recovery (a special case of CMR) models has increased considerably in recent years as a tool to estimate survival rates of many

species (Lebreton et al., 1992). These methods are considered more robust than others such as enumeration, life tables, and catch curves, in part, because of the ability to estimate sampling fractions, such as capture, recapture, and band recovery probabilities (Nichols, 1994). Limitations of these earlier methods for estimation of survival probabilities are reported in Anderson et al. (1981), Martin et al. (1995), Nichols and Pollock (1983), and Seber (1982). Only recently have the more robust CMR models been applied to estimating survival rates of marine turtle species (e.g., Chaloupka and Limpus, 2002, in press; Heppell et al., 1996; Kendall and Bjorkland, 2001).

Survival probability estimates for marine turtles based on the more robust CMR methods indicate that large juvenile and adult marine turtles have naturally high survival rates, and attests to the natural longevity of marine turtles shown in studies on growth (Bjorndal et al., 2000; Limpus and Chaloupka, 1997; Seminoff et al., 2002). Survival rate estimates for adult green turtles in Australia were very high (0.948) and lower for subadults and juveniles, 0.847 and 0.880, respectively (Chaloupka and Limpus, in press). A study of loggerheads in Australia estimated annual survival rate at 0.91 for adults and 0.83 to 0.88 for immatures in a stable population (Heppell et al., 1996). Seminoff et al. (2003) reported an annual adult survival rate for green turtles in the east Pacific at 0.97, and similarly, Kendall and Bjorkland (2001) reported 0.95 for annual adult female hawksbill survival in Antigua. Natural survival rates for some of these populations would likely be even higher because at least some of them are subjected to varying degrees of human induced mortality, particularly the Australian loggerheads that are taken incidentally in various fisheries (Slater et al., 1998). Thus, the mean estimates of survival probabilities for green turtles generated in this study (0.55 for the mixed large juvenile/adult group and 0.82 for the adult female group) are very low for marine turtles in these life stages and have serious conservation implications for green turtles in the western Caribbean.

The annual survival probability estimates derived in this study are not too surprising when one considers the magnitude of the marine turtle fishery on the principal foraging ground for this population. A minimum of

11,000 adult and large juvenile green turtles are harvested each year on the foraging grounds off the Caribbean coast of Nicaragua (Lagueux, 1998), which is greater than estimates of annual harvest levels just prior to a decline in nesting observed at Tortuguero in the 1960's and 1970's. As shown by tag recoveries (Carr et al., 1978; Caribbean Conservation Corporation, unpublished data), fisheries in other parts of the Caribbean (e.g., Costa Rica, Cuba, Honduras, Panama) take an additional unknown number of green turtles from the Tortuguero population.

Two parameters, mean life span and half-life, calculated from the Tortuguero survival rate estimate, provide a better understanding of the implications of the low survival probabilities for adult females. The estimated mean life span (MLS) for nesting green turtles with an annual survival rate of 0.821 is only 5.1 years, calculated as $1/{-}\ln(S)$ (Brownie et al., 1985; Seber, 1982). The estimated "half-life," the time period from banding until half the animals are expected to be dead, is 3.5 years, calculated as MLS(0.69) (Brownie et al., 1985). Thus, about one-half of the adult females are able to produce young during only two nesting seasons, since 3 years is the mean inter-nesting interval for green turtles at Tortuguero (Carr et al., 1978).

The survival rate estimate for green turtles exposed to the turtle fishery on the Nicaragua foraging ground (0.55), including both males and females, is extremely low for a "long-lived" species. It is widely accepted that marine turtles exhibit life-history characteristics that are consistent with other long-lived organisms, such as taking a long time to mature and low mortality of adults. Iverson (1991) suggested that in general turtle species exhibit a Type III survivorship curve (high initial mortality and low mortality in later stages), and Shine and Iverson (1995) found that age at maturation is positively linked to adult survival in turtles (i.e., high adult survival is correlated with late age to maturity). In light of this relationship, Congdon et al. (1993, 1994) suggested that the life-history traits that co-evolve with longevity result in a limited ability of those species to withstand chronic increases in mortality, especially of the later life stages.

Based on the relatively low survival probability estimates derived in this study for the later life stages of the Tortuguero green turtle population, it is likely that the population as a whole, and possibly other green turtle populations that share the Nicaragua foraging ground, are declining. Of further consideration, however, is that the proportion of large juveniles from the Tortuguero population that are exposed to the Nicaragua turtle fishery is not well known, although no other major feeding area for large juvenile green turtles has been identified in the Caribbean. A quantitative assessment of the Tortuguero green turtle population is needed to determine its status and to identify and implement appropriate management actions needed to ensure the conservation of this important remaining population of green turtles.

Resumen

La mayor población remanente de tortuga verde (*Chelonia mydas*) en el Atlántico se encuentra potencialmente amenazada por el resurgimiento de la pesquería comercial artesanal de tortugas en Nicaragua. Nicaragua es el sitio de la principal área de alimentación para los adultos de la colonia de Tortuguero, Costa Rica. Se conoce poco acerca de los parámetros de la historia de vida de esta población fuera de la playa de anidación. Para comprender mejor el impacto potencial de la captura en Nicaragua de individuos de la población de Tortuguero, estimamos las tasas de sobrevivencia de hembras adultas marcadas en la playa de Tortuguero, y de un grupo mixto de juveniles grandes y adultos marcados en las localidades de pesca en Nicaragua. Con base en un análisis de recuperación de bandas, los juveniles grandes y adultos de tortuga verde marcados en las localidades de pesca en Nicaragua tienen una probabilidad de sobrevivencia anual muy baja, 0.55. Las hembras adultas marcadas en la playa de anidación, las cuales pueden alimentarse en un rango amplio de zonas de forrajeo en el Caribe, tienen una probabilidad anual de sobrevivencia de 0.82. Estos valores estimados para tasas de sobrevivencia son probablemente demasiado bajos para sostener la población y tienen importantes implicaciones para el futuro de la colonia de Tortuguero.

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