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OBSERVATIONS ON THE ECOLOGY AND SURVIVAL OUTLOOK OF THE HAWKSBILL TURTLE

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ABSTRACT

The hawksbill turtle (Eretmochelys imbricata) has declined to endangered status before its ecology has been adequately investigated. A limited amount of data on the species has accumulated at the Green Turtle Station at Tortuguero, on the Caribbean coast of Costa Rica. Stomach contents of 29 mature turtles (11 males, 13 females and 5 unsexed), killed by shell hunters on Tortuguero Bank, are listed. Tag returns that have been recorded add to knowledge of remigratory and renesting intervals, multiple nesting, philopatry and post-breeding movements. The bearing of the reproductive isolation of separate island colonies on the survival position of the genus is briefly discussed.

INTRODUCTION

Like other endangered species, the Atlantic hawksbill or carey (Eretmochelys imbricata) has reached low population levels before its ecology has been adequately investigated. The dearth of life history data hinders effective protection and management, and it therefore seems appropriate to present the information that has accumulated at Tortuguero, Costa Rica, since Carr et al. summarised findings there in 1966.

Tortuguero is the most heavily used green turtle beach in American waters. It is not a major hawksbill nesting ground, however, even for the Caribbean Sea, where the nesting of the species is generally diffuse. Throughout the Caribbean, wherever hawksbill nesting has been heavy the shell-hunters have concentrated their efforts, and an accurate reconstruction of the original ecological geography of the species is not possible. Today the carey comes ashore to nest on most wild sections of mainland and island beach. Somewhat heightened nesting density, amounting to

Biol. Conserv. (8) (1975)—© Applied Science Publishers Ltd, England, 1975 Printed in Great Britain incipient aggregation, occurs in a few places—the San Blas Islands and Bastimento region of Panama (unpublished data, and Tovar, 1973); islets off the coast of Nicaragua (Nietschmann and others, pers. comm.); Isla de Pinos, Cuba (Ubeda, 1973); perhaps Mona Island off Puerto Rico (T. Carr, 1974; Jean Thurston, pers. comm.); and the Grenadines (Melvin Goodwin and others, pers. comm.). Nowhere in the Caribbean, however, is there any such aggregation as Bustard (1972) recently found on Long Island in Torres Strait. At Tortuguero nests are somewhat less frequent than they are to the south in Costa Rica, between Puerto Limon and the Panamanian border. The Tortuguero nesting ground is nevertheless probably fairly typical of the Caribbean shore as a whole.

FEEDING HABITS

One of several conspicuous gaps in the natural history of Eretmochelys is the scarcity of information on its natural feeding habits. Most of what has been learned about hawksbill ecology has come from tagging projects, which involve only mature nesting females. The turtles are not killed by their taggers, and such projects have yielded few data on stomach contents. Designation of the hawksbill as an endangered species (IUCN Red Data Book, 1970) suggested the desirability of examining the contents of hawksbill stomachs made available by the existence of a small fishery that operated on Tortuguero Bank until 1973. Except for desultory poaching this fishery has now been stopped. It is unlikely that feeding data will henceforth be available there, or anywhere else in the Caribbean, and it seems appropriate to present what we have gathered.

The foraging habitat

There are two patches of rocky bottom off the northern end of Tortuguero Beach. One of these is known as Tortuguero Bank. This begins a few hundred metres off the mouth of the river, and appears to serve as a mobilising site for hawksbills during the breeding season. Courtship and mating are regularly seen there during July and August. Sea turtles are easily harpooned when courting and copulating, and for many years the Bank was the regular turtling ground of the local careyeros. Another, far larger area of rocky bottom, known as Fifteen Mile Bank, is located some 24 km off the mouth of Tortuguero River. This is too far away for the turtle canoes to reach, and no hunting has been done there. Although snapper fishermen have told us that hawksbills can be seen there regularly nothing is known of their density or seasonality.

Very little has been learned about the benthic ecology of Tortuguero Bank. Big rivers enter the sea along this section of the Caribbean shore. The water is discoloured during much of the year, and bull sharks (Carcharinus leucas) abound. Accordingly, no one dives there, and about all that can be said of the reef com-

munity is that the bottom is craggy volcanic or old coralline rock, where boat anchors are often lost and where snappers, grunts and grouper can sometimes be caught. During calm weather, from late August through October, hawksbills gather there in numbers greater than would be expected for a permanent resident population.

Throughout its circumtropical range Eretmochelys is known to inhabit reefs. It is thus generally regarded as carnivorous. Divers, and fishermen who search for grouper or fish traps with glass-bottom buckets, regularly report seeing hawksbills scraping and chewing at reef faces, evidently feeding on encrusting organisms. Little definite information on the diet has been published, however. The stomachs of two hawksbills from the Gulf of Fonseca, on the Pacific coast of Honduras, examined by Carr (1952), were 'crammed with two-inch sections of the cylindrical fruits (shoots) of the red mangrove; and another individual from the same place had eaten some two pounds of a mixture of mangrove leaves, bark and wood'. Unpublished information from divers at Ascension Island indicates that a recently discovered small, and possibly itinerant, hawksbill colony there feeds mainly on a species of rock-encrusting sponge. Several different divers have seen the turtles biting at sponges. The sponge chiefly involved is a rock-inhabiting species identified by Dr George Hechtel as Ircinia fasciculata. The sessile invertebrate fauna of Ascension waters appears to be extremely lean, and there is little submerged vegetation of any kind. This may account for the peculiarly scrawny look of Ascension hawksbills, and also may explain their observed tendency to group about any refuse that is dumped in shore waters.

Stomach contents

Table 1 shows the frequency of different food items found in the stomachs of 29 hawksbills—eleven males, thirteen females and five of unknown sex—taken on Tortuguero Bank. Twenty of the stomachs contained food; the others were empty. It was hoped that the food items found might shed light on the ecology of the bank itself, as well as on the feeding habits of the turtles. All that the samples reveal, however, is that (1) the invertebrate fauna in the area is diverse; and (2) encrusting sponges predominate in the diet, and perhaps on the rocks of Tortuguero Bank.

The most frequent food item was the sponge Geodia gibberosa, although the chi square test showed no significant difference between the numbers of samples with Geodia and those with the next most prevalent item, the ascidean, Styela. All but two of the stomachs with food contained Geodia; and all but six also contained Styela. Another noteworthy feature was the diversity but low frequency of molluses, which comprised two families of pelecypods and seven families of gastropods. All were of small size (2 cm or less) and infrequent occurrence, suggesting that they were casually ingested along with encrusting organisms or bottom material. The three kinds of trematodes listed were all alive when collected, and were obviously gut parasites rather than food items.

STOMACH CONTENTS OF HAWKSBILL TURILES AT TORTUGUERO, COSTA RICA, 1970-72, ALL SAMPLES WERE TAKEN BETWEEN MID-JULY AND EARLY OCTOBER.

	-	OCT OFFICE	-				The second second	
	Male	Males with	Fema	Females with	One	Unsexed	% of further	% of all
Food stem	. No.	%	No.	%	No.	%	gut (20)	
Rottom material	4	36-4	5	38.4	2	9	55.0	37.9
Terrestrial plant material	4	36-4	5	38-4		R	000	000
Plastic and manmade litter	2	18.2	7.	15.3	00	1	1000	0.9
Unidentifiable matter	1	16		100	00		18.0	10.3
Marine algae—Sargassum	2	18.5	-	1-1	,	1	0.51	17.5
Marine angiosperms	*	10.0		15.3	545	20	25-0	17.2
Trialassia sp. Surinendium sp.		16.	0	1	0	1	5.0	5.5
Porifera							95.0	65-5
Demospongia					•		6.0	5.2
Poecilosclerina		5	0.	100	00		20.5	1 60
Epipolasida	0 -	10		7-7	00	1.1	10.0	6-9
Hadromerma								
Chendeille necula	0	ļ	-	7.7	0	1	2.0	en e
other	-	9-1	0	1	0	1	000	65.5
Choristida				4.0	0		29	5.5
Craniella sp.	09	00.00	- 7	10-7	0.4	08	0-06	62-1
Ceodia gioverosa	5.4	36.4	-	7.7	0	1	25-0	17.2
Coelenterata								0.9
Octocorallia	- 0	1.6	0 -	15.3		202	150	10-3
Hydrozoa	0		4			1	35-0	24.1
Schingerelle sp.	-	9-1	0	1	0	1	2.0	50.0
Himmonoring SD.	-	1.6	0	i	0	15	0.00	3.5
other	2	18-2	-	1.1	7	40	35.0	24-1
Mollusca	7	26.4	-	7.7	0	I	250	17.2
Castronoda	1 79	18.2		7.7	-	8	20-0	13-8
Scaphopoda							6.0	2.5
Dentalium lagueatum	-	15	0	1	0	1	0.0	
Urochordata							70.0	48.3
Charle to	7	9-69	44	30-7	m	9	70.0	48.3
other	5	18-2	1	7.7	0	1	13-0	103
Platybelminthes								
Trematoda	4	36-4	en	23-1	0	1	350	24-1
Species 2	0	1		1:1	00	1	20	e e
Species 3	0	13		1.1	0-	18	45.0	310
Empty		1.	2	93.0	,	1		

Because of the lack of information on the ecology of the bank and of volumetric data on the stomach contents, it is impossible to judge the degree of selectivity exerted by the turtles in their foraging. The combined diversity and infrequency of the molluscan remains suggests indiscriminate, opportunistic feeding, and the frequency and quantity of amorphous bottom material and detritus ingested—including a compacted ball of well-chewed sheet plastic—would seem to support that idea. Next to Geodia and Styela, bottom material was both the most frequent and the most voluminous item in eleven of the 29 digestive tracts.

All samples were taken between the middle of July and early October. This period includes a part of the nesting season (Carr et al., 1966). A comparison of males with food in the gut (10 of 11 examined) and females with food (6 of 13 examined) showed no significant difference (z = 1.05 in Mann-Whitney U test). Nevertheless, the trend shown in the Table suggests that a larger sample would reveal that males feed more actively at this season, and also that they are more inclined to select the sponge Geodia in their foraging.

It seems fairly clear that the hawksbill is a relatively indiscriminate feeder whose food consists mainly of benthic invertebrates. Since large numbers of reef-inhabiting invertebrates, particularly sponges, are toxic (Halstead, 1965; Bakus & Green, 1974), such a diet would be consistent with the occasionally poisonous character of hawksbill flesh that has been noted in various parts of the circumtropical range.

RENESTING

Multiple nesting

The Tortuguero hawksbill probably nests at least twice during a given season. Whether more nestings occur is not clear from our data. Table 2 shows every return of a hawksbill recorded at Tortuguero during a single season. Taking the small sample at face value, one would be inclined to say that only one or two nestings occur. However, the existence of the fishery on the bank introduces the possibility that renesting records were reduced by attrition of the tagged sample. The longer the stay of a turtle at Tortuguero the greater the likelihood that she would be killed.

A noteworthy feature of the tag-return records is the curiously comparable numbers of renesters and remigrants. In work with green turtles, both at Tortuguero and at Ascension Island, renestings have been found to outnumber remigrations by at least ten to one. Since the beginning of the Tortuguero project, eleven renestings and six remigrations of hawksbills have been recorded. The correspondence suggests that the low observed number of renestings may really mean that Tortuguero careys nest only once or twice, and then return to foraging grounds on the Outer Bank or elsewhere.

TABLE 2

OBSERVED RENESTING RETURNS OF HAWKSBELL TURTLES AT TORTUGUERO BEACH, NUMBER \$385 LAID ON BOTH AUGUST EMERGENCIS, BUT EGG NUMBERS WERE NOT RECORDED. NUMBER 9009 LAID NO EGGS ON 6 SEPTEMBER

	First observed emergence		Inter- nesting	Return		
Tag no.	Date	Mile	period (days)	Date	Mile	
348	20 August 1956	0	20	8 September 1956	11	
1167	1 July 1960	22	20 32	1 August 1960	. 2	
2149	17 July 1962	14	19	4 August 1962	1	
3390	16 July 1965	1	19	3 August 1965	14	
6766	13 August 1970	18	17	29 August 1970	.1	
8385	31 July 1972	31	17	16 August 1972	31	
0505			2	18 August 1972	18	
9009	15 August 1972	17	23	6 September 1972	-1	
3007			24	7 September 1972	28	
H117	25 August 1972	48	2	27 August 1972	34	
10015	16 July 1974	+	50 20	3 September 1974	28	
10127	30 July 1974	31	20	18 August 1974	11 31	
10173	14 August 1974	31	3	17 August 1974	31	

Renesting interval

Records bearing on the length of the internesting period are ambiguous. Table 2 shows lengths of all recorded internesting intervals. The second return of turtle 9009 evidently followed a previous false crawl, as did the returns of H117 and 10173. The significance of the return of 8385 on 18 August 1972, after having nested two nights previously, is not known. When these aberrant periods are deleted from the list it includes nine intervals the lengths of which, in days, are as follows: 17, 17, 19, 19, 20, 20, 24, 32, 50. With the exception of the two longest intervals, each of these periods might qualify as either one or two consecutive internesting periods. The seven shorter periods have a mean and standard deviation of 19-43 ± 2-37 days. If one assumes that the 32- and 50-day intervals are actually made up of two internesting periods of 16 and 25 days, respectively, the mean and standard deviation for the eleven intervals (17, 17, 19, 19, 20, 20, 24, 16, 16, 25, 25) is 19.82 ± 3.43 days. Of course, the 32- and 50-day periods could represent three internesting intervals of 11 and 16 days, respectively; so the above figures could represent one, two or more periods of 8-16 days. Obviously this small sample does little to clarify the uncertainty concerning length of the internesting interval. At face value, the means indicate that the internesting interval approaches three weeks, which is somewhat longer than the 'about two weeks' usually said by local people to be the time between nestings, and is longer than the recorded internesting period of any other kind of sea turtle.

DISTANT TAG RECOVERIES

Information is still too limited to show whether at least a part of the Tortuguero

TABLE 3

LONG-RANGE RECOVERIES OF HAWKSBILL TURTLES TAGGED AT TORTUGUERO, COSTA RICA, 1956–1973

Tag no.	Date turtle lagged	Place of recovery	Date of recovery	Distance travelled km
330	18 August 1956	Miskito coast, near Awastara, 15 miles north of Puerto Cabezas, Nicaragua	Before 18 October 1956	385
903	17 June 1959	Mouth of Matina River, Costa Rica	6 September 1959	57
984	27 July 1959	Miskito Cays, Nicaragua, latitude 14°35' N., longitude 82°35' W.	25 July 1960	463
1627	16 July 1961	Barra del Colorado, Costa Rica	9 August 1961	28
4122	25 July 1966	8 km North of Barra del Colorado, Costa Rica	June-July 1970	36
8453 H140	3 August 1972 26 August 1972	Miskito Cays, Nicaragua Miskito Cays, Nicaragua	November 1973 10 January 1974	385 385

nesting colony may commute between Tortuguero and some distant resident feeding place. Of the 130 hawksbills tagged at Tortuguero there have been only seven recoveries away from Tortuguero Beach (Table 3). The most distant of these were recorded in the Miskito Cays, Nicaragua, in 1960, 1973 and 1974. Although these recoveries might suggest long range migration, it is also possible that a part of the nesting colony merely moves out to Fifteen Mile Bank after the breeding season and takes up residence there. Elsewhere, reports by divers, trap-fishermen and operators of glass-bottom reef-viewing boats suggest that hawksbills may take up definite refuges and feeding areas on particular sections of reefs (see also Carr, 1974, and Nietschmann, pers. comm.). In any case, tag recovery data are insufficient to justify conclusions concerning the movements of the Tortuguero turtles after leaving the nesting shore, and the recorded periods between tagging and recovery have all been too long to give any indication of travel speed.

All we can add to the brief list of long-range recoveries is the consensus of Tortuguero careyeros that between November and April, hawksbills disappear completely from the Inner Bank. Certainly the recovery data alone show nothing to negate the possibility of random wandering after the breeding season. However, no hawksbill tagged at Tortuguero has been recovered nesting on any other beach. A striking recovery of unknown significance, recorded by Nietschmann (pers. comm.), seems to support an assumption that some purposeful, long-range travel may occur. A female tagged by Nietschmann after being taken when feeding on a shoal off Big Miskito Cay, 64 km NE of Sandy Bay, Nicaragua, on 22 June 1972, was found nesting 496 km away, at Pedro Keys near Jamaica on 14 November 1972.

The question of the extent of post-breeding migration is obviously an open one of great importance for any effort to protect this endangered species.

PHILOPATRY AND SITE FIXITY

It has hitherto not been known whether Eretmochelys shows philopatry and site tenacity in its nesting. Recently Carr & Main (1973, and unpublished data) found that in Torres Strait nesting occurs on at least 40 islands of the Western and Central Groups, and that some of these colonies show evidence of rigid philopatry in their nesting. During visits to more than 100 small turtle farms operated by the islanders, Carr & Main saw thousands of young hawksbills of various ages that had been hatched artificially from eggs taken by the farmers from neighbouring islands. In most cases the eggs and young from each island had been segregated. There was a marked tendency for these lots to be homogeneous in pigmentation and pattern, and to differ trenchantly in these respects from island to island. Sets of 20 to 100 turtles from islands no more than 32 km apart could readily be distinguished; and according to Dr Robert Bustard and numerous informants among the islanders, this tendency is widespread in the region. Japanese shell buyers, who had been in the region shortly before, had recognised the phenomenon, and had urged the islanders to select and breed the strains from certain islands that produced the particular shell patterns prized by the Japanese tortoiseshell industry.

The existence of these Torres Strait demes must indicate that isolation occurs at breeding time. The colour distinctions among the colonies must be genetic, because the differences remain constant when the eggs are hatched and the young reared under identical conditions. The implications of this apparent microevolution are (1) that in the colonies in which it occurs the females return faithfully to nest on their natal islands, even though only a few km may separate these, and (2) that mating, as well as nesting, occurs only at those island nesting grounds.

Nesting-site records at Tortuguero (Tables 2 and 4) are too few to reveal a tendency to return to a particular short section of beach for successive nestings. An interesting feature of the data, however, is the frequency with which renesting turtles return with less precision than is shown by remigrants. In other words, the mean separation of the nest sites of a single season tends to be greater than the distance between the last nesting place of a given season and the first site of a return migration, two or more years later. Although the sample is limited, the reality of the trend may be enhanced by the fact that *Chelonia* appears to show the same tendency. The Tortuguero data have not yet been analysed in this respect, but Carr (in press) found the scatter of within-season renestings at Ascension Island to be clearly greater than that between interseason sites of returning migrants.

If this reversal of the expected difference in site fidelity in the two kinds of returns is real, this question arises: Why should a turtle show a more fine-scale discrimination after a period of two to six years than after periods of a few days or weeks? One answer that comes to mind is that the difference does not reflect differential site recognition at all, but is instead a behavioural adaptation by which the nests

of a given season are scattered to spread the risk of overcrowding, loss to concentrated predation or storm damage to the beach. In the initial emergence of a season, however, the operative response may be precise landfall recognition—and the remigrant turtle may be simply returning as closely as possible to a place of last emergence two or more years earlier.

REMIGRATION

Table 4 shows all recorded remigratory returns of hawksbills to the Tortuguero study beach. Although six is a small total, it is not an unreasonably low proportion of returns, as turtle-tagging projects go. The striking comparability of the figure with the low number of renestings within single seasons is noted in the preceding section. Periods of interseasonal absence were, in years: 3, 6, 3, 4, 3, 4. Even this short list offers strong evidence that the hawksbill, like the Tortuguero green turtle, never nests in consecutive years—the reasoning being that if an annual cycle did occur it ought to show up in the sample as the most frequent period.

TABLE 4
REMIGRATION OF HAWKSBILL TURTLES AT TORTUGUERO BEACH

Tag no.	Date tagged	Place tagged	Date retaken	Place retaken
306	15 August 1956	Mile 4	18 June 1959	Mile b
783	25 August 1958	Mile 1	6 August 1964	Mile 4
2149	17 July 1962	Mile 14	6 August 1965	Mile 14
3241	17 August 1964	Mile 1	5 September 1970	Mile 3
4617	9 October 1967	Mile #	7 September 1970	Mile #
5326	3 September 1968	Mile 17	31 August 1972	Mile 44

Further consonance with green turtle periodicity is to be seen in the three remigratory intervals of three years each. Because of the improbability that an annual period exists, these could not be attributed to missed intervening visits. It therefore seems evident that a three-year remigration cycle predominates. With regard to the periods of four and six years' duration, there is no way of knowing whether these represent actual periods of absence, or were composite terms in which an intervening visit was missed by the turtle patrols.

This evidence of a possible three-year nesting cycle is especially interesting because of the lack of any obvious physiological or ecological cause of either its existence or its predominance in both the Tortuguero and Ascension colonies of Chelonia. The agreement of two such divergent genera as Chelonia and Eretmochelys in such a peculiar and fundamental attribute ought to provide clues in the search for the cause of a non-annual breeding periodicity in sea turtles.

THE SURVIVAL OUTLOOK FOR Eretmochelys

Eretmochelys must be regarded as an endangered genus. Despite the recent discovery of important new nesting grounds in the Indo-Pacific (Hirth & Carr, 1970, Jabla Asiz Island; Bustard, 1972, Long Island) the hawksbill is clearly being extirpated from the Atlantic and Caribbean. The tagging record at Tortuguero furnishes what appears to be strong statistical evidence of the decline of the small hawksbill population there. In Table 5, the numbers of hawksbills tagged by the Tortuguero green-turtle patrol parties during two four-year periods, 1956-59, and 1970-73 are compared. The numbers of turtles tagged, per patrol-hour per patrol-mile, were 3-7 during the earlier four years and 0-97 during the later period. This contrast would be even greater if the comparison included such qualitative factors as the reinforced effort during the later period to accumulate data on a vanishing species, and the better understanding by recent beach patrols that when hawksbills are turned on their backs to be tagged at a later time they often right themselves and leave, and thus go untagged.

TABLE 5
HAWKSBILL TURTLES TAGGED WHILE NESTING ON TORTUGUERO BEACH DURING TWO FOUR-YEAR PERIODS

	Years	Miles patrolled nightly	Approx. period per night (hours)	No. tagged	No. tagged per patrol-kour per-mile
1956-59 1970-73	4	2 5	5 7	37 34	3-7 0-97

Exploitation of Eretmochelys is of several different kinds. The most intensive is that from the Japanese tortoiseshell trade, an atypically avid and discriminating market that concentrates on certain types of shell and pays inflated prices for it. Turtles and tortoiseshell have traditional ceremonial value in Japan. With the rise in prosperity there, the demand for shell has grown enormously. According to Smart (1973) prices paid for preferred shell in Japan are as high as \$41 Australian (\$76 US) per pound, and up to \$350 Australian (\$525 US) for a mature turtle. The Japanese market is the chief source of revenue for a whole district of Panama (Bastimentos), and was responsible for Panama's reluctance to agree to protect the species during the International Convention of Endangered Species in 1973. Outside Japan, and other Asian countries that share Japan's reverence for shell but little of its prosperity, tortoiseshell goes largely to the tourist trade. There is some traditional demand elsewhere, notably in Spain and Italy, but the main outlets for tortoiseshell jewellery and mounted juvenile hawksbills are local maritime novelty stores.

Another kind of drain, and one that has grown markedly with the spread of snorkelling and scuba diving, is imposed by spearfishermen. On many tropical seashores hawksbills are regularly speared, along with the grouper and snappers they live with on the reefs.

A serious obstacle to the effort to protect the hawksbill is the uncertainty as to the number of taxonomic entities that should be designated objects of concentrated concern. So long as the monospecific genus *Eretmochelys* is considered a single endangered interbreeding entity, protection in any part of the range is likely to be regarded as improving the survival position of the whole complex.

In discussing the survival prospects for Chelonia, Carr (in press) has called attention to the danger that comes from lumping genetically different, noninterbreeding populations. Green turtles breed where they nest. Each nesting colony is therefore a separate reproductive unit that does not demographically reinforce any other. Protection for the Tortuguero population, for example, has no beneficial effect whatever on that at Ascension Island, or on any other colony. The problem is, therefore, not merely that distinct demes (i.e. that 'genetic information') will be overlooked in a survival programme; but, rather, that by regarding a mosaic of isolated colonies as a single entity, protection for any of the separate components brings a sense of achievement and security that is wholly unjustified. This problem is brought into sharp focus in the Torres Strait colonies of Eretmochelys, and no doubt exists among many other isolated populations of the genus. The philopatry implied by the incipient speciation of island colonies makes each a separate reproductive enterprise whose fate is in no way linked with that of any other colony. If this concept is valid it has important bearing on any effort to establish a rational balance between taxonomic lumping and splitting as they bear on intervention procedures to prevent the loss of natural species.

ACKNOWLEDGEMENTS

The research on which this paper is based was supported by the National Science Foundation (Biological Oceanography Program, current grant GA 36638) and the Caribbean Conservation Corporation. For information on foraging habits of Ascension Island hawksbills we are indebted to Mr Marlin Simon of Mariculture, Ltd.

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