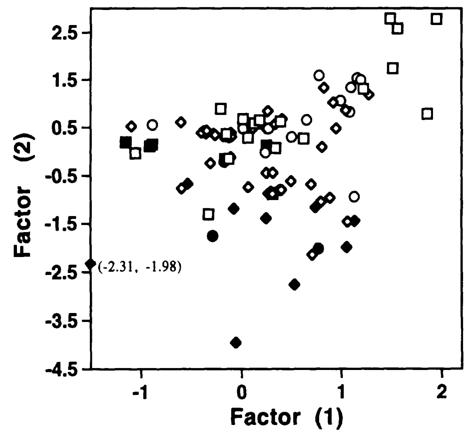

FIG. 2. Expanded view of Fig. 1 with only *C. grandis* and *C. helenae* shown. The discriminate scores used are identical to those in Fig. 1. Squares = summer; diamonds = autumn; circles = spring. No specimens were collected in winter. Open symbols are *C. grandis*, closed symbols are *C. helenae*.

greatest amounts of termites in autumn when environmental conditions are generally at their driest. Thus our study, and those of Pianka (1969) and James (1991a), suggest that while our three species of skinks display considerable niche overlap, they are able to coexist because of an abundant food supply (termites), and to a lesser extent, because they have the ability to include a variety of items in their diet and can, at least, partially partition their use of either space, time or their food supply.

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Probability of Tag Loss in Green Turtles Nesting at Tortuguero, Costa Rica

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The study of the life history of sea turtles has been limited by the relatively short retention time of external identification tags (Henwood, 1986; Limpus, 1992). Tagging marine turtles is a challenge because they are long lived, increase their body mass some 2000-fold during their life, and live in an environment in which metal tags may corrode and plastic tags become brittle.

The extent of tag loss has important implications for interpretation of the demography of sea turtles. Frazer (1983) found that estimates of survivorship of adult female loggerheads (*Caretta caretta*) increased significantly when corrected for tag loss. Hughes (1982) summarized data that indicated that at many nesting beaches only a low percentage of female sea turtles tagged while nesting are recorded again at the nesting beach in later years; the majority are never

TABLE 1. Probability of a turtle losing one tag within a nesting season. Tag year is the year in which the turtle was originally tagged; r_{di} is number of turtles recovered with two tags at interval i; r_{si} is the number of turtles recovered with only one tag at interval i; $1 - K_i$ is probability of tag loss during the recapture interval i; CL is confidence limit. Individual turtles are only included in the sample for the year in which they were originally tagged.

	Recovery interval					
	First-to-last sighting			First-to-third sighting		
Tag year	r_{di}	r_{si}	$1 - K_i \pm$ 95% CL	r_{di}	r_{si}	$1 - K_i \pm$ 95% CL
Monel tags						
1987	155	40	0.114 ± 0.036	40	10	0.111 ± 0.070
1988	616	30	0.024 ± 0.009	122	9	0.036 ± 0.024
1989	138	35	0.113 ± 0.038	56	14	0.111 ± 0.059
Total	909	105	0.055 ± 0.011	218	33	0.070 ± 0.024
Inconel tags						
1989	28	18	0.243 ± 0.111	9	7	0.280 ± 0.203

seen again. He suggested that a high percentage of female sea turtles may have only one breeding season, although, as he acknowledged, it is difficult to accept that a green turtle (*Chelonia mydas*) would take over 30 years to reach sexual maturity and then only reproduce in one breeding season. The possibility that tag loss accounted for this "missing majority" has been raised (Carr, 1980; Hughes, 1982; Mrosovsky and Shettleworth, 1982). To address issues such as these, accurate estimates of the probability of tag loss are required.

Presence of tag scars has been used to identify turtles that have lost tags, but the reliability of this technique has not been evaluated. In some cases, particularly if the tag has been lost soon after application, no scar will be evident (Bolten and Bjorndal, unpubl. data). Also, natural scars on the flippers can make interpretation of scars difficult.

We measured tag loss from 1987 through 1992 in adult female green turtles that were double tagged from 1987 through 1989 at the nesting beach at Tortuguero, Costa Rica (10°34′N 83°32′W). Probability of tag loss within and between nesting seasons and the variation among years were evaluated. We have also assessed the reliability of estimates of tag loss based on the presence of tag scars.

At Tortuguero, green turtles are tagged at night after they come ashore to deposit their eggs. Beginning in 1987, all green turtles have been double tagged, with one tag placed in the trailing edge of each front flipper, proximal to the first large scale. From 1987 through 1989, turtles were tagged by a team of about 8 to 10 idividuals who worked throughout the season. For the first few nights of the season, all taggers worked together and were instructed by an individual experienced in turtle tagging. The taggers were trained to inspect each turtle for scars from lost tags by looking and palpating for scar tissue; to place the tag so that approximately one-third of the tag extended beyond the posterior edge of the flipper; to check each tag for proper closure; and to ensure that the tag applicators were working properly.

In 1987 and 1988 all turtles were double tagged with style 49 Monel tags (Monel 400 alloy; National Band and Tag, Newport, Kentucky). In 1989, 1021 green turtles were double tagged with Monel tags and 246 were double tagged with style 681 Inconel tags (Inconel 625 alloy) from the same manufacturer. Turtles included in this study received either two Monel tags or two Inconel tags. In addition to the difference in metal alloys, Inconel tags are smaller than the Monel tags and have a different locking mechanism.

Green turtles at Tortuguero may nest several times within a nesting season, and their reproductive seasons are separated by intervals of two or more years (Bjorndal and Carr, 1989). Probabilities of tag loss were calculated for both within season and between seasons. For within season tag loss, individual turtles were only included in the sample for the year in which they were first tagged. For between season tag loss, an individual turtle was included in the sample for each year she was observed until she was recorded as having lost a tag; after that year she was not included in the study.

Probability of retaining a tag during the recapture interval i (K_i) was calculated by the equation

$$K_i = (2r_{di})/(r_{si} + 2r_{di}) \quad (1)$$

where r_{di} is the number of turtles recovered with two tags at interval i and r_{si} is the number of turtles recovered with only one tag at interval i (Wetherall, 1982). Probability of losing one tag is $1 - K_i$. Confidence intervals (95%) were calculated for probability of tag loss by the equation (Wetherall, 1982)

$$(1 - K_i) \pm 2\,[(K_i(1 - K_i)(2 - K_i)^2)/(2(r_{si} + r_{di}))]^{0.5} \quad (2)$$

Probabilities for within season tag loss were calculated for two samples each year. One sample ("first-to-last" sample) included all turtles for which the interval between first and last sighting was > 5 d. Six days is the shortest known interval between successive egg clutches for a green turtle at Tortuguero (Bjorndal and Carr, 1989). The other sample ("first-to-third" sample) was limited to those turtles that were recorded three times with both internesting intervals between 6 and 19 d-the normal internesting interval for Tortuguero green turtles (Bjorndal and Carr, 1989). Tag loss was assessed at the third sighting,

TABLE 2. Probability of a turtle losing one tag between nesting seasons for green turtles tagged from 1987 through 1989 and monitored from 1987 through 1992. Terms are defined in Table 1.

Tag year	Recovery interval: 2 Years r_{di}	r_{si}	$1 - K_i \pm$ 95% CL	3 Years r_{di}	r_{si}	$1 - K_i \pm$ 95% CL	4 Years r_{di}	r_{si}	$1 - K_i \pm$ 95% CL	5 Years r_{di}	r_{si}	$1 - K_i \pm$ 95% CL
Monel tags												
1987	12	7	0.226 ± 0.166	37	37	0.333 ± 0.103	14	13	0.317 ± 0.167	1	0	0 ± 0
1988	52	20	0.161 ± 0.071	223	80	0.152 ± 0.034	17	21	0.382 ± 0.154	—	—	—
1989	22	14	0.241 ± 0.125	26	27	0.342 ± 0.124	—	—	—	—	—	—
Total	86	41	0.192 ± 0.059	286	144	0.201 ± 0.033	31	34	0.354 ± 0.114	1	0	0 ± 0
Inconel tags												
1989	3	0	0 ± 0	15	5	0.143 ± 0.126	—	—	—	—	—	—

even if the turtle was seen more than three times. The first-to-third sample is a subset of the first-to-last sample.

Estimates of tag loss in the first-to-last samples can be used to correct for within season tag loss. Evaluation of tag loss in the first-to-last samples also provides an estimate of the proportion of turtles that were mistakenly counted as two turtles in earlier years at Tortuguero when only one tag was applied to each turtle. However, the intervals over which tag loss is measured varies widely in the first-to-last sample, from 6 d to about 3 mo. Tag loss in the first-to-third sample was measured over more uniform time intervals and levels of nesting activity, which can stress tags and/or flipper tissue. The latter sample provides a better basis for comparing within season tag loss among years.

Probability of a lost tag being recognized and reported as a tag scar i years after tag application (S_i) was calculated by the equation

$$S_i = r_{ti}/(r_{ti} + r_{vi}) \quad (3)$$

where r_{ti} is the number of double-tagged turtles recovered at interval i with only one tag and reported to have a tag scar on the other flipper, and r_{vi} is the number of double-tagged turtles recovered at interval i with only one tag and not reported to have a tag scar on the other flipper.

Two methods were used to compare probabilities statistically. First, counts of turtles (r_{di} and r_{si}; r_{ti} and r_{vi}) were analyzed with k-sample chi-square tests or, if cell sizes were less than five in 2 × 2 contingency tables, with Fisher's exact tests (Zar, 1984). Second, the confidence intervals for probabilities of tag loss were compared. Unless stated otherwise, alpha = 0.05.

Within Season Tag Loss.—Probability of a turtle losing one Monel tag within a season ranged from 0.02 to 0.11 (Table 1). If each year is given equal weighting, the mean probabilities are 0.08 for the first-to-last sample and 0.09 for the first-to-third sample. If values for all years are summed, the probabilities are 0.06 and 0.07, respectively (Table 1).

Probabilities of Monel tag loss within a nesting season varied significantly among years for both first-to-last samples and first-to-third samples (k-sample chi-square tests, df = 2, $P < 0.001$ and $P = 0.009$, respectively). Chi-square tests for pairs of years, as well as examination of the 95% confidence intervals (Table 1) indicate that, for both first-to-last and first-to-third samples, values for 1988 are significantly different from those for 1987 and 1989, which are not significantly different from each other.

Loss of Inconel tags was significantly greater than that of Monel tags within the 1989 nesting season (Table 1) for first-to-last samples (Fisher's exact test, $P = 0.008$). For the first-to-third samples, the difference in probabilities of loss for the two tag types approached significance (Fisher's exact test, $P = 0.052$).

Within tagging year and tag type, the tag loss probabilities are very similar between the first-to-last and the first-to-third samples (Table 1), despite the great differences in sample size and degree of variation within the two samples. The only exception is that in 1988, tag loss in the first-to-third sample is 50% higher than in the first-to-last sample.

Tag loss is generally a result of application error by the tagger, rejection of the tag by the turtle's tissue

TABLE 3. Probability of detecting a lost tag from presence of a tag scar. Tag year is the year in which the tag was applied; r_{ti} is the number of double tagged turtles recovered with one tag and reported to have a tag scar on the other flipper at interval i; r_{vi} is the number of double tagged turtles recovered with one tag and not reported to have a tag scar on the other flipper at interval i; and S_i is the probability of a lost tag being recognized as a tag scar i years after tag application.

Tag year	Recovery interval								
	2 Years			3 Years			4 Years		
	r_{ti}	r_{vi}	S_i	r_{ti}	r_{vi}	S_i	r_{ti}	r_{vi}	S_i
Monel tags									
1987	4	3	0.57	13	24	0.35	5	8	0.38
1988	3	17	0.15	21	59	0.26	10	11	0.48
1989	10	4	0.71	15	12	0.56	—	—	—
Total	17	24	0.41	49	95	0.34	15	19	0.44
Inconel tags									
1989	—	—	—	3	2	0.60	—	—	—

(e.g., tissue necrosis), tag failure (e.g., corrosion), or biting of the tag by other turtles during courtship. Because the last factor has not been reported at Tortuguero and because tag loss from tag failure or tissue rejection would normally not occur within an interval as short as a nesting season, most within season tag loss is probably attributable to poor application of the tag. The importance of, and variation in, within season tag loss—and thus application error—underscores the importance of selection and training of tagging personnel.

Between Season Tag Loss.—For green turtles tagged with Monel tags between 1987 and 1989, 127 turtles were seen again after 2 yr, 430 after 3 yr, 65 after 4 yr, and one after 5 yr between 1989 and 1992. For green turtles tagged with Inconel tags in 1989, three turtles were recorded after 2 yr, and 20 after 3 years.

Probabilities of a turtle losing one Monel tag after 2 and 4 yr intervals are not significantly different among tagging years (k-sample chi-square, $P = 0.457$, df = 2, and $P = 0.754$, df = 1, respectively). However, probability of tag loss after the 3 yr interval (the most commonly recorded interbreeding interval for Tortuguero green turtles) does vary significantly among tagging years (k-sample chi-square, $P < 0.001$, df = 2). Chi-square tests for pairs of years, as well as examination of the 95% confidence intervals (Table 2), indicate that for the 3 yr interval, the 1988 value is significantly different from those for 1987 and 1989, which are not significantly different from each other.

Because the probabilities of interseasonal tag loss vary significantly among tag years, probabilities of Monel tag loss after 2, 3, and 4 yr intervals (Table 2) must be compared separately for each year. For 1987, tag loss after 2, 3, and 4 yr intervals were not significantly different (k-sample chi-square, df = 2, $P = 0.590$); for 1989, tag loss for 2 and 3 yr intervals were not significantly different (k-sample chi-square, df = 1, $P = 0.366$). For 1988, however, tag loss after 2, 3, and 4 yr intervals were significantly different (k-sample chi-square, df = 2, $P = 0.001$). Chi-square tests for pairs of intervals, as well as examination of the 95% confidence intervals (Table 2), indicate that the value for the 4 yr interval is significantly different from those for the 2 and 3 yr intervals, which are not significantly different from each other. Whereas tag loss probabilities for tags applied in 1987 and 1989 were fairly constant from 0.23 to 0.34 for 2 to 4 yr after tagging, for tags applied in 1988, tag loss probabilities were significantly lower—about 0.15—for 2 and 3 yr after application. After 4 yr, tag loss probability for 1988 tags (0.38) equalled that of the other years.

Between season tag loss can only be compared between 1989 Monel and Inconel tags for the 3 yr interval because of the small sample sizes for Inconel tags after 2 yr. Probabilities of tag loss for the two types of tags were not significantly different (k-sample chi-square, $P = 0.084$, df = 1; overlap of 95% confidence intervals).

Old Tag Scars.—Probabilities of detecting a lost Monel tag from a tag scar (Table 3) varied significantly among tag years for the 2 yr intervals (Fishers exact tests for pairs of years) and for 3 yr intervals (k-sample chi-square, df = 2, $P = 0.021$). Values for 4 yr intervals were not significantly different between years (k-sample chi-square, df = 1, $P = 0.867$). Probabilities of detecting a lost Monel tag from a tag scar after 2, 3, or 4 yr intervals were analyzed for each year separately because of the significant variation among years. There was no significant variation among 2, 3, or 4 yr intervals for 1987 and 1988 or between 2 and 3 yr intervals for 1989 (k-sample chi-square tests). If values are combined for the 2, 3, and 4 yr intervals, there is an overall probability of only 0.37 that a lost tag will be detected by a tag scar. The small sample ($N = 5$) of turtles that lost one Inconel tag between breeding seasons precluded meaningful comparison of reliability of tag scars from Monel and Inconel tags.

Tag Loss in Tortuguero Green Turtles.—Particularly for studies in which only one tag is applied to each turtle, within season tag loss can result in overestimation of the numbers of turtles nesting each season (and therefore population size); overestimation of recruitment to the breeding population; and underestimation of the number of clutches deposited by individual turtles (and therefore individual reproductive output). Tag loss between seasons can result in overestimation of mortality of mature female turtles and overestimation of recruitment to the breeding population.

From 1955 to 1986, standard procedure was to apply only one tag to each green turtle at Tortuguero. Unfortunately, the significant variation among years in both within season tag loss and between season tag loss limits extrapolation of correction factors calculated for years in which turtles were double tagged after 1986 to the years when turtles were single tagged. In addition to the annual variation in tag loss, it is difficult to extrapolate correction factors because the quality of Monel tags varies considerably among batches of tags (Bolten and Bjorndal, unpubl. data), and people applying one tag per turtle may apply the tag more carefully because they are less rushed and know that just one tag identifies the animal.

Presence of tag scars has been used in an attempt to correct for tag loss in studies based on Tortuguero data collected in the years before double tagging was initiated (e.g., Bjorndal, 1980; Carr, 1980). However, based on the results of this study, presence of tag scars is not a reliable indicator of tag loss. Only about 37% of lost tags were detected by tag scars. Reliance on tag scars can result in significant underestimation of tag loss.

Based on a small sample size, Inconel tags were not retained by Tortuguero green turtles to a greater extent than were Monel tags. Retention of Inconel tags was poorer than retention of Monel tags within the 1989 season, and retention of Inconel tags was not significantly different from that of Monel tags between the 1989 and 1992 nesting seasons. The similar performance of the two tag types is not unexpected because corrosion of Monel tags does not appear to be a major problem in the Tortuguero population, so the superior corrosion resistance of the Inconel alloy would not be a significant advantage. Further evaluation, based on larger sample sizes, is needed before firm conclusions can be drawn concerning the relative performance of Monel and Inconel tags in the Tortuguero population.

All tag loss probabilities presented in this paper are expressed as the probability of a turtle losing one tag. The probability of a turtle losing both tags can be estimated by squaring the probability of losing one tag. For example, the probability of a turtle tagged in 1989 losing a Monel tag within 3 yr is 0.342 (Table 2), from which we estimate that the probability of a turtle tagged in 1989 losing two Monel tags within 3 yr is 0.117.

Comparison with Other Populations.—Several studies have calculated probabilities of tag loss in sea turtle populations based on double tagged turtles. Although equations are presented in different forms in these publications, probability of tag loss has been calculated in the same manner, so direct comparisons can be made. Within season tag loss has received less attention than between season tag loss. Alvarado et al. (1988) calculated within season probability of loss of Monel tags attached to the front flippers of the black turtle, *Chelonia mydas agassizi* (= *C. agassizi*), as 0.412 (N = 98) and 0.468 (N = 48) in two successive years. These estimates are far above the maximum upper confidence limit of 0.151 calculated for within season loss of Monel tags in the first-to-last samples (the appropriate comparison for the Alvarado et al. study) of the Tortuguero population (Table 1).

Limpus (1992) calculated the probabilities of tag loss for green turtles and loggerheads at foraging grounds and between seasons at nesting beaches in Australia. Several tag types and tag positions were included in the study. The sample that provides the best comparison for the Tortuguero data (C. Limpus, pers. comm.) is the nesting green turtles tagged with the same style of Monel tag in the proximal position (#3) in the front flipper (Limpus, 1992). For this group, the probability of tag loss after three years was 0.875 ± 0.229 95% confidence limit (N = 8), and after four years was 0.591 ± 0.205 (N = 22) (Limpus, 1992). Both of these values are substantially higher than those of the Tortuguero population. The minimum 95% confidence limit for the Australian green turtles for the 3 yr interval (0.646) is higher than the upper confidence limit calculated for the 3 yr interval for the Tortuguero population (0.234 for total sample). For the 4 yr interval, although the 95% confidence intervals overlap, the point estimates for both populations fall outside the confidence intervals of the other population.

Probabilities of loss of Inconel tags of the same style used at Tortuguero have been calculated for green turtles in Hawaii (Balazs, 1983). For a 3 yr interval, the probability of tag loss in Hawaiian turtles (0.23 ± 0.14 95% CL, N = 27) overlaps broadly with probability of Inconel tag loss measured at Tortuguero (0.14 ± 0.13 95% CL, N = 20).

Tag loss in sea turtles remains a serious problem. Studies that report values for population demographic parameters without appropriately correcting for tag loss should be interpreted with caution. Because of the variation in probabilities of tag loss within the same population and among different populations of the same species (as reviewed here for the green turtle), probabilities of tag loss calculated for one study should not be extrapolated to other studies. Significant annual variation in tag loss may preclude reliable extrapolation within a population. Differences in probabilities of tag loss are even greater among different tag types, turtle species, and size classes (Alvarado et al., 1988; Eckert and Eckert, 1989; Limpus, 1992; Parmenter, 1993). In demographic studies, at least two tags should be applied to each turtle to improve long-term recognition of individuals and to allow corrections for tag loss to be calculated.

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