

Trophic status drives interannual variability in nesting numbers of marine turtles

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Large annual fluctuations are seen in breeding numbers in many populations of non-annual breeders. We examined the interannual variation in nesting numbers of populations of green (*Chelonia mydas*) ($n=16$ populations), loggerhead (*Caretta caretta*) ($n=10$ populations), leatherback (*Dermochelys coriacea*) ($n=9$ populations) and hawksbill turtles (*Eretmochelys imbricata*) ($n=10$ populations). Interannual variation was greatest in the green turtle. When comparing green and loggerhead turtles nesting in Cyprus we found that green turtles were more likely to change the interval between laying seasons and showed greater variation in the number of clutches laid in a season. We suggest that these differences are driven by the varying trophic statuses of the different species. Green turtles are herbivorous, feeding on sea grasses and macro-algae, and this primary production will be more tightly coupled with prevailing environmental conditions than the carnivorous diet of the loggerhead turtle.

Keywords: marine turtle; trophic status; interannual variation; population; remigration

1. INTRODUCTION

In many species, in particular large air-breathing marine vertebrates, it is only possible to attempt to quantify their population size during short periods of their life cycle, for example when individuals breed (e.g. penguins (Guinard *et al.* 1998), sea lions (Reyes *et al.* 1999) and sea turtles (Meylan 1982)). Where annual breeding is the norm in a population, variation in environmental conditions may affect the breeding performance of an individual (Sæther 1997; Post & Stenseth 1999; Coulson *et al.* 2000; Grant *et al.* 2000). In species which do not breed annually such factors may determine whether or not an individual breeds at all in a given year, thus leading to interannual variation in the numbers of individuals breeding (Baker 1938; Limpus & Nicholls 1988). This variation may mask changes in population size. Understanding the processes driving interannual variation in breeding numbers of animal species will lead to more efficient monitoring and management (Gerodette & Taylor 1999).

There are many reasons why an individual may fail to attempt to breed in a given year. The prevailing environmental conditions at the time of breeding may determine the likelihood of offspring survival and, thus, play a role in subsequent breeding or postponement to a future year (Murray 1979). For animals that do not breed every year, breeding may be dependent upon reaching a threshold body condition. Thus, in a good breeding year we might expect an increased likelihood of a breeding attempt. This threshold may not be fixed but may vary in response to environmental factors influencing body condition (Madsen & Shine 1999) and affecting the magnitude of any reproductive output, for example the number of offspring/broods produced (Grant *et al.* 2000; Wikelski & Thom 2000).

Feeding conditions might be expected to play a crucial role in influencing body condition between breeding years. Hence, we would expect the processes that drive variation in feeding conditions to be closely related to the breeding

biology of a population. Availability of nutrients, particularly in the marine environment, has been shown to be affected by climatic oscillations such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Aebischer *et al.* 1990; Ainley *et al.* 1995; Hayward 1997). For animals feeding on items, the abundance of which is closely linked to prevailing weather patterns, a tight coupling between weather and body condition would be expected. This effect has been shown to be greater in individuals feeding lower down the food chain (Post & Stenseth 1999; Coulson *et al.* 2000). Thus, we would expect herbivores feeding preferentially on new plant growth to be greatly affected by weather conditions and, thus, exhibit large interannual variation in breeding levels. In comparison, animals whose food abundance is less influenced by weather conditions in any individual year, e.g. those higher up the food chain, might be expected to show less variation in body condition and, hence, less interannual variation in breeding numbers (Ainley *et al.* 1995; Jaksic *et al.* 1997; Harrington *et al.* 1999).

In order to test this hypothesis we examined the interannual variation in nesting numbers of marine turtles. Marine turtles are iteroparous breeders that, upon reaching adulthood, undertake cyclical migrations from feeding grounds to nesting sites at variable intervals, most commonly 2–3 years (Miller 1997). Marine turtles are an excellent group on which to base such a study as they show marked similarity in many aspects of their life history, although they occupy very different trophic niches in the adult phase (reviewed by Bjørndal 1997). Adult green turtles (*Chelonia mydas*) are predominantly herbivorous, feeding on sea grasses and macro-algae, whilst the loggerhead turtle (*Caretta caretta*) has a diet of benthic molluscs, crustaceans and coelenterates. The leatherback turtle (*Dermochelys coriacea*) feeds on pelagic jellyfish, salps and other gelatinous organisms and hawksbill turtles (*Eretmochelys imbricata*) most commonly forage over coral reefs and rock outcroppings for sponges and, to a lesser extent, marine plants and tunicates.

Previous studies have noted the large interannual variation seen in the nesting numbers of marine turtles

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(Hughes 1982; Limpus 1996) and it has been suggested that this variation is driven by remigration intervals where non-annual breeding occurs (Carr & Carr 1970; Hays 2000). The ability to vary the interval between successive breeding seasons, e.g. from 2 to 3 years (Carr & Carr 1970), is likely to reflect changes in the conditions at the feeding grounds and produce greater variability in nesting numbers.

Here we examine long-term trends in the nesting numbers of populations of marine turtles in relation to their trophic status. We also examine the variation in nesting levels of the green and loggerhead turtles in relation to the remigration interval (i.e. number of years between laying seasons) and clutch frequency of individuals at the same nesting site.

2. METHODOLOGY

(a) Study site

We collected information on green and loggerhead turtles nesting on Alagadi Beach, northern Cyprus (35°33' N, 33°47' E) between 1992 and 2000. The beach consists of two small coves of 0.8 and 1.2 km length.

(b) Data collection

The beach was monitored from 21.00 to 06.00 local time (GMT + 3 h) each night throughout the nesting season by three to five groups of two observers. In 1992 only a portion of the nesting season was monitored and for this reason we do not include nesting numbers for this year. However, we do include the remigration data of females tagged in this initial year. Females were externally tagged with plastic flipper tags from 1992 to 1998 and titanium tags from 1998. In addition, since 1997 females have been injected with passive integrated transponder tags in order to increase the chances of reidentification of females in future years (Godley *et al.* 1999). Through mark and recapture of females within and between years we were able to estimate the number of clutches laid by an individual in a season and calculate the remigration interval of the female (number of years between breeding seasons). Where a missed nesting was apparent (e.g. when an interesting interval of more than 18 days was recorded) (Broderick 1997) we corrected the number of clutches laid accordingly and used these corrected numbers in these analyses.

(c) Data from other studies

Population data sets were obtained from the literature for comparison of the interannual variation in the numbers of nests for four species of marine turtle: green turtles ($n=16$ populations), loggerhead turtles ($n=10$ populations), leatherback turtles ($n=9$ populations) and hawksbill turtles ($n=10$ populations). For two of the green turtle populations examined here the number of females was used because data on the number of nests were not available. Where data sets were presented graphically in the literature we digitized the data in order to obtain nesting numbers. We selected data sets of at least 5 years for our analysis. The coefficient of variation (CV) for each population was calculated from the mean number and standard deviation (s.d.) of nests/females per year ($CV = s.d./mean$). Where a significant trend was found in the annual nesting numbers of a population, we fitted the most appropriate model (linear or curvilinear) and then examined the standard deviation of the residuals with the mean of the original data set in order to

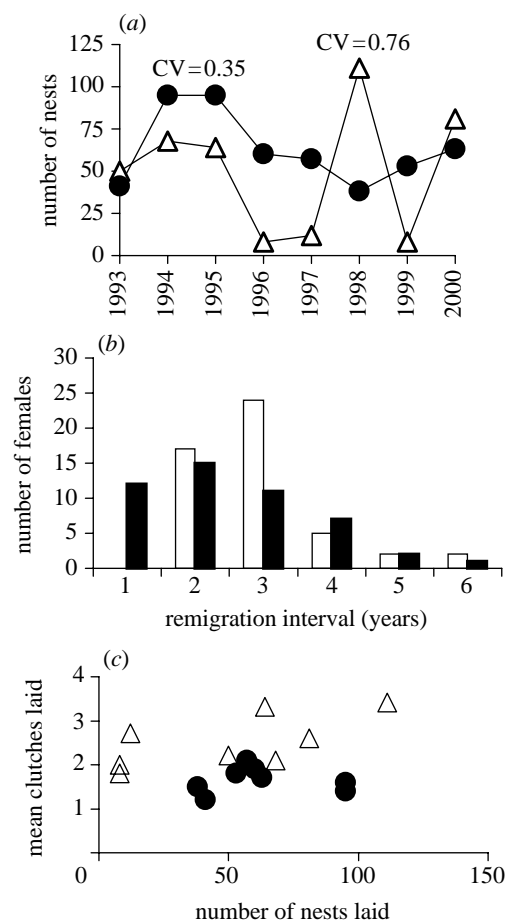


Figure 1. (a) Variation in nesting numbers at Alagadi beach for both green turtles (open triangles) and loggerhead turtles (filled circles). (b) Remigration intervals recorded for both species (open boxes are green turtles and filled boxes are loggerhead turtles) at Alagadi Beach 1994–2000. (c) Relationship between the number of nests laid in a given year and the mean number of clutches laid by nesting females in the same year for green turtles (open triangles) and loggerhead turtles (filled circles).

calculate the CV. This procedure removed the effect of an increasing or decreasing population size.

3. RESULTS

The interannual variation in the total number of clutches laid in each study year at our field site (Alagadi 1993–2000) was much higher in the green turtle, with between eight and 111 clutches laid in any one season ($CV = 0.76$) (figure 1a). Loggerhead turtle nesting ranged between 38 and 95 clutches ($CV = 0.35$) (figure 1a). The intensive monitoring at Alagadi enabled us to attribute 83% of all green turtle nests and 67% of all loggerhead turtle nests laid at this site (1993–2000) to individual females. By 2000 the percentage of green turtles nesting that were remigrants was 57% and for loggerhead turtles 39% were remigrants, having been tagged in a previous season. Most commonly, green turtles returned to nest after an interval of 2 (35%) or 3 (49%) years with loggerhead turtles predominantly returning after 1 (26%), 2 (32%) or 3 (23%) years (figure 1b). No green turtles were recorded nesting in consecutive years

although this did commonly occur in loggerhead turtles. Remigration intervals of 4, 5 and 6 years were recorded in both species (figure 1b).

In order to investigate whether variation in the remigration intervals of individual turtles was higher in green turtles than loggerhead turtles we examined the difference in the consecutive remigration intervals of the same individuals. A χ^2 -contingency test with Yates correction (Zar 1999) was used for comparing the frequency of repeat and differing remigration intervals. In green turtles, of the 20 females for which two remigration intervals were recorded, six returned after the same interval and 14 shifted to another interval (e.g. from 2 to 3 years). For loggerheads 10 females remigrated after the same interval and 4 shifted to another interval ($\chi^2=6.77$, d.f.=1 and $p < 0.01$), illustrating a greater variation in the remigration intervals of green turtles.

We examined the number of clutches laid by individual females in each study year (Kruskal–Wallis test with non-parametric multiple comparisons test for unequal sizes) and found that green turtles nesting in 1998 laid significantly more clutches than those nesting in 1994 (1993–2000, $H=21.89$, d.f.=7 and $p < 0.01$). No such relationship was found in loggerhead turtles (1993–2000, $H=9.13$, d.f.=7 and $p > 0.05$). No significant relationship was recorded between the total number of nests laid in a given year and the mean clutch frequency of nesting individuals in that year for either green turtles ($F_{1,7}=4.51$, $r^2=0.43$ and $p=0.078$) or loggerhead turtles ($F_{1,7}=0$, $r^2=0$ and $p=0.96$). Although not significant this relationship was positive in green turtles (figure 1c).

The typical interannual variations in nesting within individual populations of the four study species are illustrated in figure 2a–d. Comparison of the means and CVs of the four species (figure 3) using a one-way ANOVA and a post hoc Tukey test for unequal samples (Zar 1999) revealed that green turtles differed significantly from the other three species ($F_{3,46}=9.41$ and $p < 0.001$), exhibiting greater interannual variation in the number of nests laid. In addition, interannual variation was greater in leatherback turtle populations than hawksbill turtles and, in turn, loggerhead turtles, although not at a significant level.

4. DISCUSSION

In this paper we have shown that the large interannual variability in the number of green turtles nesting is common globally but that this variation is less in other non-herbivorous species. We chose not to include the remaining three species of marine turtles in this study for the following reasons: the flatback turtle (*Natator depressus*) is only found in Australasian waters and both the olive ridley (*Lepidochelys olivacea*) and Kemp's ridley (*Lepidochelys kempi*) turtles are often social nesters, nesting in arribadas, and the influence of these factors may affect the variation in the numbers found nesting. In addition, there is currently only one major nesting site of the Kemp's ridley turtle (Pritchard 1997).

The tagging data collected at our intensive study site in Cyprus suggest that variable remigration intervals may drive interannual variation in nesting numbers as previously modelled by Hays (2000). In turn, environ-

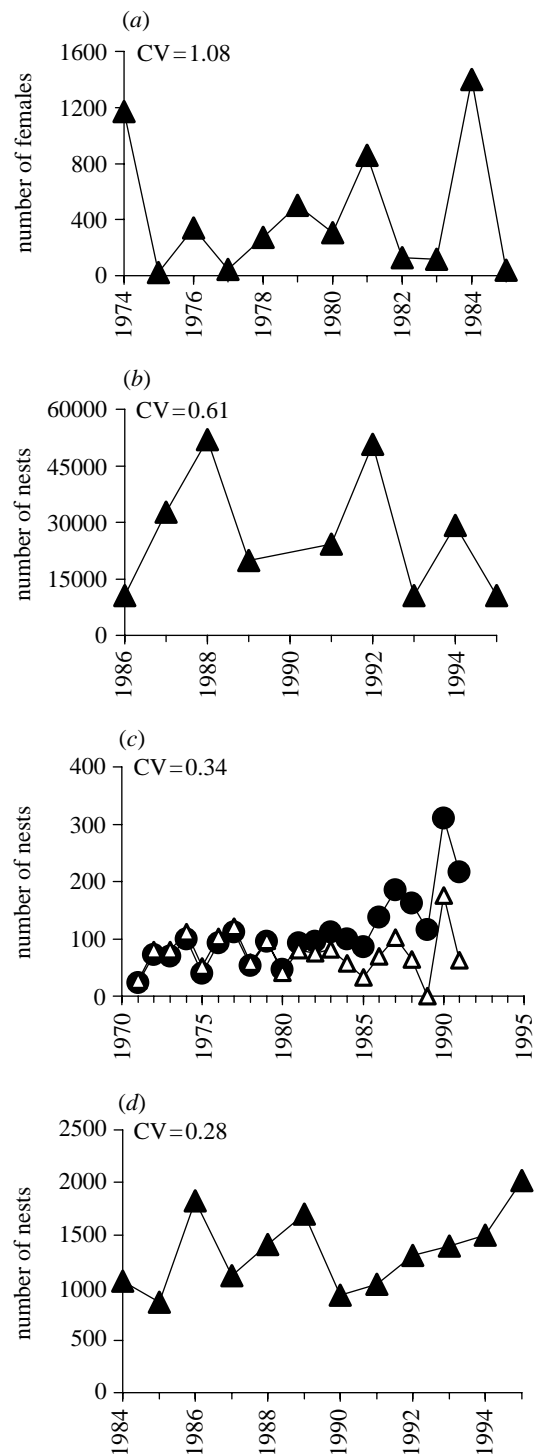


Figure 2. Illustrations of the variations found in populations of (a) green turtle, Heron Island, Australia (Limpus & Nicholls 1988), (b) leatherback turtle, French Guiana (Girondot & Fretey 1996), (c) hawksbill turtle, Cousin Island, Seychelles (open triangles represent detrended data) (Mortimer & Bresson 1994) and (d) loggerhead turtle, Zakynthos, Greece (Margaritoulis & Dimopoulos 1995; Dimopoulos & Margaritoulis 1997)

mental conditions are likely to be the forces driving such variations in remigration intervals. As we have shown, variation in remigration intervals is higher in green turtles and this is likely to be a result of variation in foraging opportunities, for example new sea grass growth

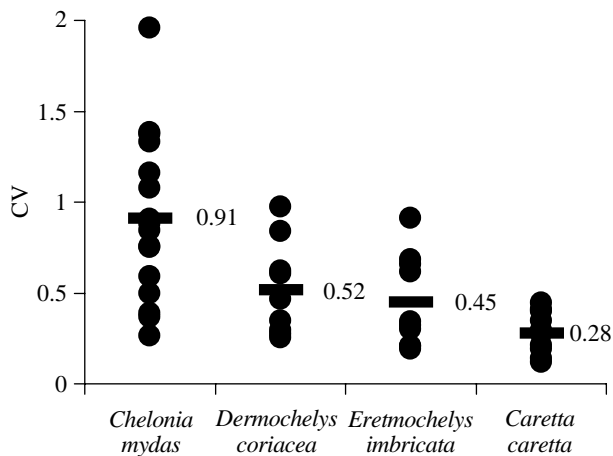


Figure 3. CVs recorded for 16 green (C.m), nine leatherback (D.c), ten hawksbill (E.i) and ten loggerhead (C.c) populations. The values given at bars are means for the species. The data for green turtles are from study sites in Australia (Limpus & Nicholls 1988), Brazil (Marcovaldi & Laurent 1996), Cyprus (this study), Hawaii (Balazs 1996), Indonesia (Arinal 1997), Israel (Kuller 1999), Mexico (Zurita *et al.* 1994), Pakistan (Asrar 1999), Surinam (Schulz 1982), Turkey (Gerosa *et al.* 1998) and the USA (Cantwell 1993; Atencio 1994; Bagley *et al.* 1996; Ehrhart *et al.* 1996; Woodson *et al.* 1998). The data for leatherback turtles are from study sites in Costa Rica (Spotila *et al.* 1996, 2000), French Guiana (Girondot & Fretey 1996), Indonesia (Arinal 1997), Malaysia (Chan & Liew (1996) in Spotila *et al.* (1996)), Mexico (Eckert & Sarti 1997), South Africa (Hughes 1996), Surinam (Schulz 1982), the USA (Cantwell 1993) and the US Virgin Islands (Boulon *et al.* 1996). The data for hawksbill turtles are from study sites in Antigua (Richardson *et al.* 1999), Australia (Dobbs *et al.* 1999), Brazil (Marcovaldi & Laurent 1996), Indonesia (Arinal 1997), Malaysia (Chan & Liew 1999), Mexico (Garduno-Andrade 1999), Puerto Rico (Meylan 1999), Tortuguero (Meylan 1999), Seychelles (Mortimer & Bresson 1994) and the US Virgin Islands (Hillis 1994; Meylan 1999). The data for loggerhead turtles are from study sites in Brazil (Santos *et al.* 2000), Cyprus (this study), Greece (Margaritoulis & Dimopoulos 1995; Dimopoulos & Margaritoulis 1997; Houghton *et al.* 1998), Israel (Kuller 1999), Japan (Sato *et al.* 1997) and the USA (Cantwell 1993; Atencio 1994; Ehrhart *et al.* 1996; Uong *et al.* 1998).

upon which green turtles feed preferentially (Bjorndal 1997). Such new growth will be strongly correlated with weather conditions at the foraging grounds during preparation for breeding. Limpus & Nicholls (1988) found that nesting of the green turtle at Raine Island and Heron Island, Australia, could be predicted from ENSO indices two years previously. Levels of variation in nesting numbers among green turtle populations are relatively high and may be indicative of differing levels of interannual variability in weather between foraging sites in addition to varying diet (Bjorndal 1997).

The higher trophic status of the loggerhead turtle with its diet of molluscs and crustaceans may account for the lower interannual variation in nesting numbers commonly recorded in this species. Whilst links between climate and productivity have been shown at many trophic levels (Aebischer *et al.* 1990; Jaksic *et al.* 1997), the availability of molluscs and crustaceans is more likely to

reflect an integration of weather patterns over several years. Thus, there is likely to be less variation in the abundance of the dietary components of the loggerhead turtle, which might account for the lower interannual variation in the breeding numbers of this species. However, variation between populations may reflect differing diets or environmental conditions at the foraging grounds.

In a study of the trophic status of marine turtles as defined by stable isotope signatures, Godley *et al.* (1998) found that loggerhead turtles fed at two to three trophic levels above green turtles, with leatherback turtles feeding at an intermediate level. In our present study, the interannual variation in leatherback, hawksbill and loggerhead turtles has been shown to be lower than that of green turtles, but no demonstrable differences were present among these three species. With an extended data set, our *a priori* prediction would be that leatherback and hawksbill turtles would demonstrate intermediate levels of interannual variability. The pelagic feeding environment of the leatherback turtle is one with few trophic steps and hawksbill turtles, feeding on encrusting reef organisms, are close to the base of the coral reef food web. Production in both of these systems is likely to be more prone to environmental influences than the benthic system, on which the loggerhead turtle is one of the top predators.

There will also be physiological constraints governing the interval between nesting seasons. For example, none of the green turtles at our study site have nested in successive years. All required at least a 2-year interval between nesting seasons. In addition, the number of green turtles nesting in a given year will be defined in part by the numbers nesting in the preceding years, for example a season with high nesting numbers involving most of the breeding population cannot be followed immediately by a similar season. The distance of the migration from feeding to nesting ground may also be a major factor in determining the frequency at which a female nests. Green turtles nesting in Cyprus overwinter and feed on the coast of North Africa and Turkey (our unpublished satellite tracking results), a relatively short migration in comparison, for example, to the 2000 km from Ascension Island to Brazil (Carr & Carr 1970). A long migration may require a longer remigration interval between nesting seasons and, thus, account for differences between populations (Limpus *et al.* 1994). From a review of the literature it appears that the 1-year remigration intervals commonly recorded in loggerhead females nesting in Cyprus are rare in this species (for a review see Ehrhart 1982; Miller 1997). Possibly this is indicative of a short migration. We do not know where females of this population forage between breeding seasons.

In addition to the more variable nesting numbers and remigration intervals of green turtles, there is greater interannual variation in clutch frequency in this species in comparison to loggerhead turtles at the same site (figure 1c). This might be indicative of a varying threshold in body condition triggering breeding in the green turtle. Indeed Madsen & Shine (1999) found that, in a 'bad' feeding year, the clutch size of female water pythons (*Liasis fuscus*) was reduced and the condition of breeding females was poorer than that of non-breeding females in a 'good' year. In this study, the variation in clutch

frequency of green turtles does have some effect on the interannual variation in nesting numbers. However, the magnitude of this change, e.g. a twofold increase from an annual mean of 1.8 to 3.4 clutches, is not the major driving force of the tenfold variation in the number of nests laid in a year (from eight to 111 nests).

Many stages of the life cycle of marine turtles are still poorly understood owing to the slower maturation, longevity and at-sea habitat of the species. Indeed, the only stage of the life cycle that is relatively easy to monitor is that of the nesting female and this provides us with an opportunity for monitoring the status of the population. This study has illustrated the importance of the duration over which monitoring of marine turtles is carried out and the need for a wider understanding of the biology of a population in order to gain a true indication of its status. In addition, given the differences in interannual variability among species, the time-frame necessary for adequate population size assessment will not be the same in every case.

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