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Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations

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Abstract We used time-depth recorders to measure depth utilisation in gravid green turtles (*Chelonia mydas*) during the internesting period at northern Cyprus (Mediterranean), a nesting area where individuals feed, and at Ascension Island (mid-Atlantic), a nesting area where individuals fast. There were contrasting patterns of depth utilisation between the two sites, illustrating that the behaviour of this species is shaped by local conditions. For example, the amount of time spent shallower than 4 m was 90% at Cyprus but only 31% at Ascension Island, and there was a clear difference between the mean depth at Cyprus (2.7 m, $n=9$ internesting intervals) versus Ascension Island (9.5 m, $n=6$ internesting intervals) ($t_5=5.92$, $P=0.002$). At Cyprus, turtles spent the greatest percentage of their time at very shallow depths, where surveys revealed a high abundance of seagrass on which this population feeds. In contrast, the deeper distribution at Ascension Island may reflect the preferred depth for resting on the seabed.

Introduction

A fundamental goal of behavioural ecology is to understand how life history traits are shaped by

spatio-temporal patterns in resource quality and availability. While our understanding of some animal groups is now extensive, some less tractable species remain enigmatic. Green turtles (*Chelonia mydas*) are a paradigmatic group of long-distance migrants, regularly moving between foraging grounds and nesting areas that may be separated by thousands of kilometres (e.g. Meylan 1995; Pough et al. 1998). The often cited reason for these migrations is that nesting beaches are generated by high wave action and that these conditions are not conducive to the growth of macroalgal and seagrass beds upon which green turtles feed (e.g. Carr 1967). Consequently, some populations, are believed to fast for several months while at the nesting grounds, due to the absence of food, with a classically cited example being the green turtles that nest at Ascension Island in the mid-Atlantic (Carr et al. 1974; Mortimer and Carr 1987). It would be predicted, however, that fasting during the nesting season should not be an invariant trait within green turtles. Rather, at nesting sites where food is available at sufficient densities, it might be expected that individuals supplement their energy stores by feeding, and, indeed, evidence of internesting foraging has been presented (Balazs 1980; Tucker and Read 2001).

Given this dichotomy between areas where green turtles fast and forage, we would expect their diving behaviour to be variant, i.e. modified to maximise net energy gain where food is available (i.e. turtles might feed and not just rest) and minimise energy loss where food is absent. To examine this possibility of behavioural plasticity we recorded the patterns of depth utilisation by individuals at two contrasting sites.

Materials and methods

Food availability and foraging

In northern Cyprus, to examine the distribution of seagrass beds with respect to depth, we swam 12 transects perpendicularly out

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to sea from Alagadi beach (35°33'N; 33°47'E) in July 2001. Estimated length of transects was 300–600 m, and transects were between 200 and 500 m apart. On each transect water depth was measured with a SCUBA diving computer (Aladin Pro, Uwatec, Switzerland). Between 1992 and 1998 we dissected and examined the viscera of green turtles washed ashore dead during the nesting season. Often these turtles had cranial traumas, suggesting they may have been killed by fisherman. At Ascension Island there is no available forage (neither beds of macroalgae nor of seagrass) for green turtles, and turtles are never observed feeding on natural forage (Carr et al. 1974, and personal communications with SCUBA divers on the island). To confirm the absence of any feeding at this site during the 1998/1999 and 1999/2000 nesting seasons, we dissected and examined the viscera of turtles that had died ashore after becoming trapped amongst rocks on their return to the sea following nesting.

Depth distribution

Fieldwork was conducted at Alagadi, northern Cyprus in June and July 2000. Turtles were located on the beach while they were nesting at night. Once egg laying was complete we attached a Lotek LTD 100 time-depth recorder (TDR) to the carapace using quick-setting epoxy (Foilfast, SFS components, Cheltenham, UK). To help prevent damage each TDR was secured in an open-ended Perspex casing which was embedded in the epoxy. Each TDR was programmed to record depth (range 0–100 m, resolution 0.06 m) every 5 s. We made a total of ten TDR deployments in Cyprus, and in nine cases (a total of eight different turtles) the units were successfully recovered when turtles were observed re-nesting with intervals of between 10 and 14 days.

For green turtles nesting at Ascension Island (7°57'S; 14°22'W) we used diving information collected in April 1998 ($n=6$ individuals) that has been partly described by Hays et al. (2000). In short, as at Cyprus, TDRs were again attached once turtles had completed laying and were recovered when they returned to lay a subsequent clutch. A variety of first generation TDRs were used (Wildlife Computers Mk 6, Vemco Minilog TX and CEFAS Mk 1), which, due to the limited memory of recorders at that time, sampled depth at 10, 60 or 120 s (for full details see Hays et al. 2000).

Results

At Cyprus, more than 30 green turtles (*Chelonia mydas*) were dissected, and in all cases guts were full of recently ingested seagrass. Although the amount of ingesta was not determined quantitatively, all the guts were visually packed with fresh seagrass, confirming recent feeding by these individuals. Four of these turtles were adults. Two were adult males and two were adult females with fully formed, shelled eggs ready for laying, i.e. these females had certainly died during the internesting period. By contrast, at Ascension Island, four adult female turtles were dissected, and in all cases the gut contained no ingesta. At Cyprus the abundance of seagrass was assessed in water depths ranging from 0 to 12.5 m. With the exception of very shallow (≤ 0.5 m) depths, seagrass beds were found over this entire depth range.

There was a very clear difference between the typical dive records for adult female green turtles at Cyprus versus Ascension Island. At Cyprus, much of the time was spent at relatively shallow depths (only a few metres), and there was a generally irregular pattern of

diving, in that consecutive dive profiles were rarely the same. By contrast, at Ascension Island, there was a tendency for much more regular bouts of deeper (> 10 m) U-dives, particularly at night, with repeated dives to the same depth separated by only brief periods of surfacing (Fig. 1a, b).

This general dichotomy in diving behaviour between Cyprus and Ascension Island is revealed in various objective analyses of the dive records. First there were differences between the two sites in the overall patterns of depth utilisation. For example, the amount of time spent shallower than 4 m was 90% at Cyprus but only 31% at Ascension Island, and there was a clear difference between the mean depth at Cyprus (2.7 m, $n=9$ internesting intervals) versus that at Ascension Island (9.5 m, $n=6$ internesting intervals) ($t_5=5.92$, $P=0.002$) (Figs. 2, 3). These differences in depth distribution tended to be maintained throughout the internesting period. For example, Fig. 4 shows how the mean depth recorded during each 12-h period of the internesting period was generally only around 2–3 m at Cyprus, but was typically around 10 m at Ascension. However, there were occasional excursions into deeper water by the turtles at Cyprus, as indicated by the maximum depth attained in each 12-h period (Fig. 4).

The true extent of the behavioural difference between turtles at Cyprus versus Ascension Island is perhaps best illustrated by examining the proportion of time spent conducting deep (> 5 m) U-dives. The percentage of

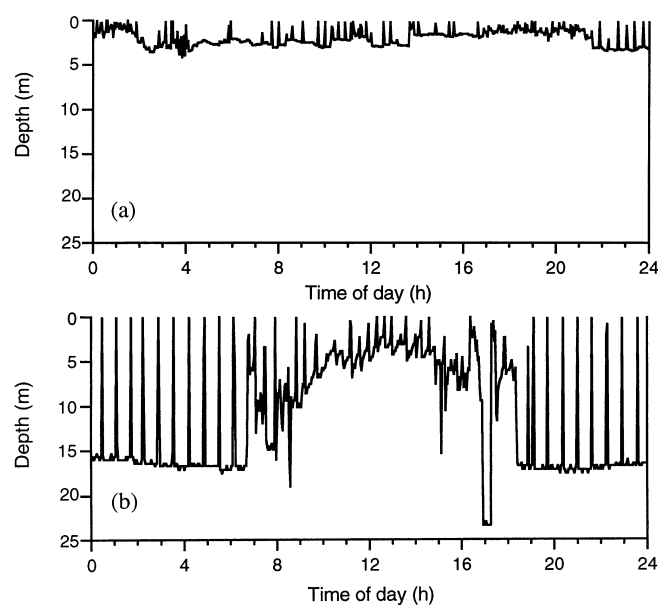
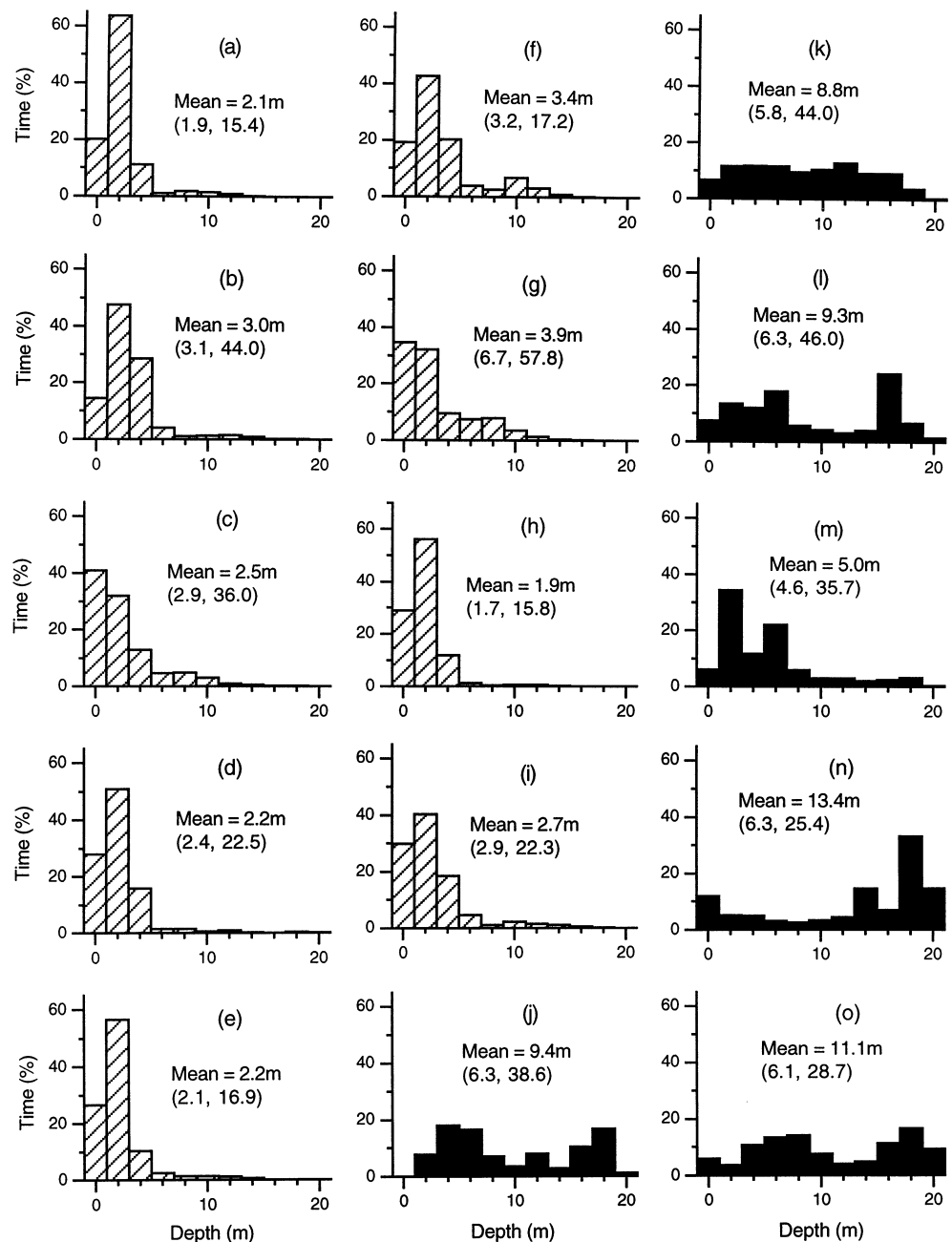


Fig. 1 *Chelonia mydas*. Typical examples of the dive traces recorded by individual female green turtles at: **a** Cyprus and **b** Ascension Island. At Cyprus, the pattern of diving was generally shallow and irregular, while at Ascension Island there were often bouts of regular U-dives to the seabed, particularly at night. Local times are shown. For clarity only one depth value per 2.5 min is plotted

Fig. 2 *Chelonia mydas*. Depth distribution recorded for green turtles during nine internesting intervals at Cyprus (a–i) and six internesting intervals at Ascension Island (j–o). Bars show the proportion of time spent within each 2 m depth interval. Mean depth (SD and maximum in parentheses) is shown for each record



time spent conducting such dives was very low at Cyprus (generally <10%) and relatively high at Ascension Island (always >40%) (Fig. 5).

Discussion

In contrast to studies of marine mammals and birds, the deployment of TDRs onto sea turtles has been far less extensive, but has still revealed many novel aspects of the free-living behaviour of this group. Resting dives to the seabed have been shown in both hawksbill (*Eretmochelys coriacea*) (van Dam and Diez 1996) and green

turtles (*Chelonia mydas*) (Hays et al. 2000), and have been confirmed by direct observation from divers of turtles “sleeping” on the seabed (Davis et al. 2000; J. Young, personal communication). However, in common with marine mammal studies, the function of many other dives by sea turtles is still obscure, and, again, will probably only be conclusively established through the use of multi-sensor logging units. For example, for gravid green turtles during the internesting period at Cyprus, Hochscheid et al. (1999) used simultaneous measurements of depth and activity to show that on many flat-bottomed “U-dives” there was activity during the bottom phase, which is thought to be associated with

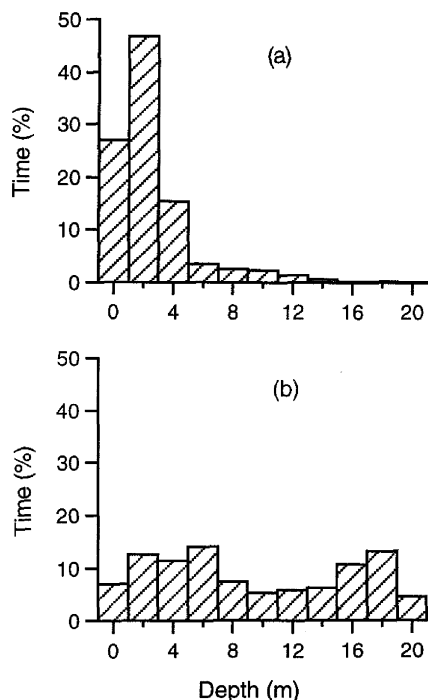


Fig. 3 *Chelonia mydas*. Mean depth distribution of turtles during the interesting periods at: **a** Cyprus and **b** Ascension Island. Values were calculated as the means from Fig. 1, giving equal weighting to data from each interesting interval

benthic foraging on seagrass. In other words, at sites where food is available, so that turtles may either forage or rest on the seabed, it may then be impossible to distinguish between these two behaviours from dive profiles alone.

Regardless of these problems with interpreting the details of behaviour from depth measurements alone, it is very clear that there was a major difference in depth utilisation between green turtles at Cyprus versus Ascension Island. In short, the diving behaviour of green turtles is clearly not invariant, but, instead, is shaped by local conditions in common with terrestrial herbivores (e.g. Hulbert and Andersen 2001). Although this difference in green turtle behaviour could conceivably be related to factors such as local tides, currents or wave heights, which we did not measure, presumably the difference is mainly linked to the fact that green turtles feed at Cyprus but fast at Ascension Island. Nevertheless, this hypothesis begs the question of why feeding and fasting depths should be so different. Certainly the difference in diving behaviour does not reflect any difference in the available range of depths at the two localities (Fig. 4). For example, occasional deeper excursions at Cyprus suggest that the shallow dives at other times were not simply a reflection of the bathymetry close to the nesting beaches. That deep water was readily available at both sites is confirmed by analysis of nautical charts, which show that within a few kilometres of the respective nesting beaches at Cyprus and

Ascension, the water was many tens or even hundreds of metres deep.

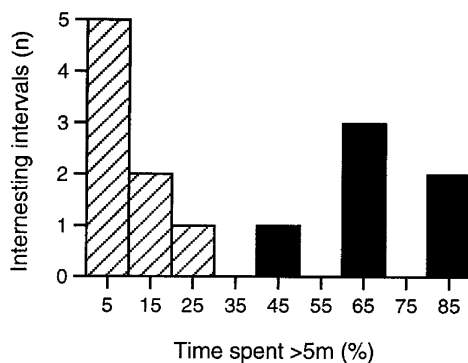
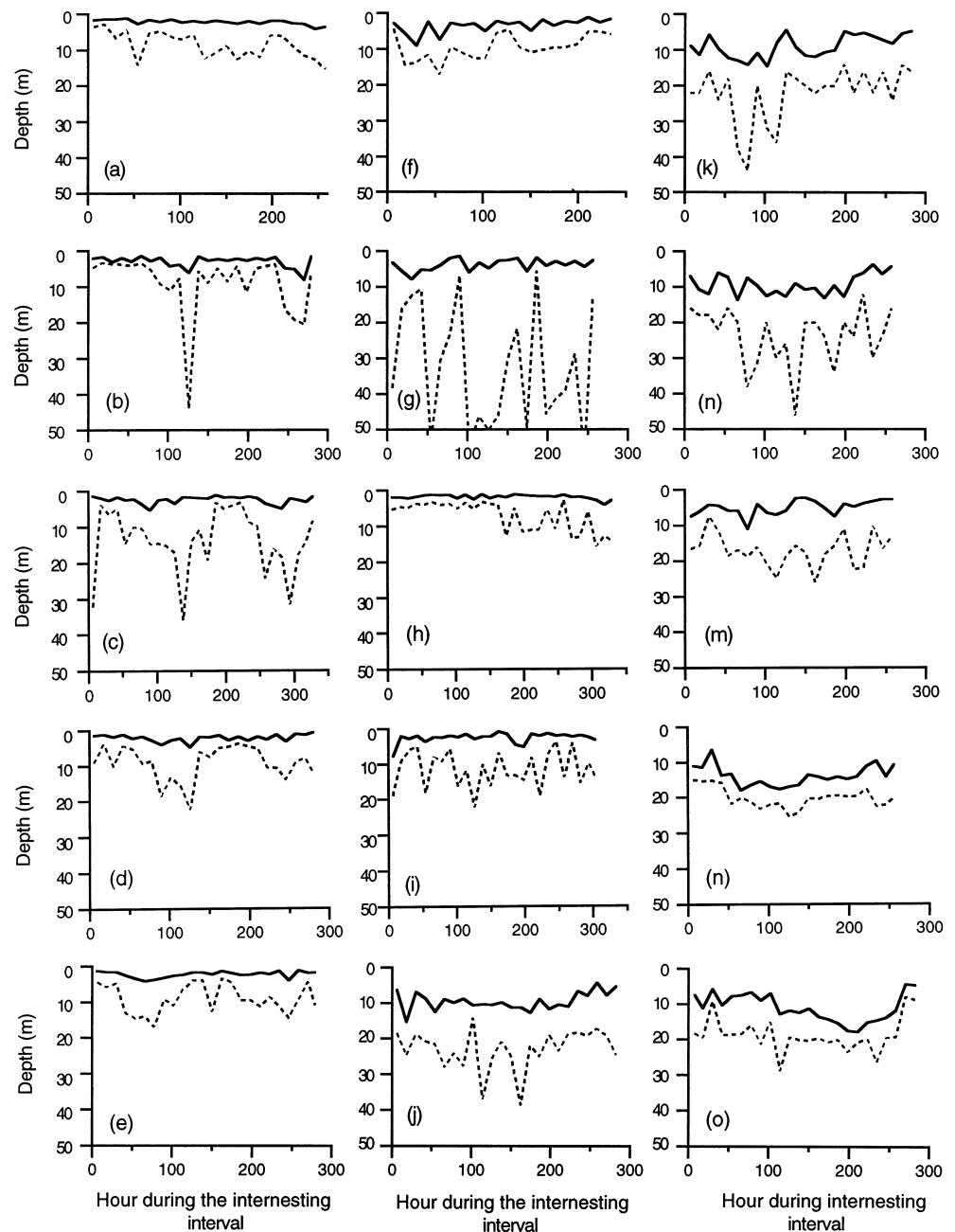
If we first consider the case of turtles fasting at Ascension Island, we have speculated that 19 m may represent the maximum depth at which individuals can still attain near-neutral buoyancy after diving with full lungs and that beyond this depth the increased lung compression leads to negative buoyancy (Hays et al. 2000). By resting at this depth, turtles may therefore be able to submerge with full lungs and, hence, a maximal oxygen store for the dive, while still attaining neutral buoyancy on the seabed. Thus, by resting at this depth, the maximal oxygen stores allow maximisation of dive duration and so minimisation of the daily costs of commuting to the seabed (Hays et al. 2000).

In contrast, when the key objective is foraging, then maximisation of energy intake may be more important than minimisation of energy expenditure. In this regard it is well known that, due to higher levels of solar radiation, the maximum primary productivity and shoot density of seagrass beds is found very close to the surface (Pirc 1986; Alcoverro et al. 2001). Furthermore our transects confirmed that seagrass, on which turtles at Cyprus feed, occurred at shallow depths adjacent to the nesting beach. We therefore suggest that improved forage is the primary reason for the generally very shallow depths occupied by green turtles in Cyprus. However, even if green turtles at Cyprus forage at shallow depths, they might still move to deeper water to rest, effectively commuting between foraging and resting sites as has been reported for green turtles elsewhere (Bjorndal 1980; Brill et al. 1995). On the other hand, the near-absence of deep diving suggests that, at Cyprus, turtles did not commute to deeper resting sites. While resting deeply may be profitable, at Cyprus this advantage may be outweighed by the costs of commuting away from foraging areas to deeper sites, and hence turtles simply remain in shallow water to both forage and rest.

In summary, it is clear that depth utilisation differed markedly between green turtles at Cyprus compared to Ascension Island, in line with the differing availability of food at these two rookeries. Interesting diving behaviour for this species is, therefore, not an invariant trait, and we would suggest that at sites where food is available diving behaviour is adapted to maximise energy gain through feeding, while at sites where food is absent diving behaviour is adapted to minimise energy loss.

Fig. 5 *Chelonia mydas*. Frequency distribution for the overall percentage of time spent conducting deep U-dives to > 5 m by each individual during the interesting period; $n=9$ interesting intervals at Cyprus (hatched bars), $n=6$ interesting intervals at Ascension Island (filled bars)

Fig. 4 *Chelonia mydas*. For each 12-h period of the interesting period the mean and maximum depth recorded during nine interesting intervals at Cyprus (a–i) and six interesting intervals at Ascension Island (j–o). Solid lines show mean depth, dashed lines show maximum depth



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