

NOTE

Change in body mass associated with long-term fasting in a marine reptile: the case of green turtles (*Chelonia mydas*) at Ascension Island

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Abstract: Female green sea turtles (*Chelonia mydas*) nesting at Ascension Island (7°57'S, 14°22'W) in the middle of the Atlantic Ocean had a mean body mass (post oviposition) of 166.3 kg (range 107.5–243.5 kg, $n = 119$). Individuals lost mass slowly during the nesting season (mean mass loss 0.22 kg·d⁻¹, $n = 14$ individuals weighed more than once). Gut-content analysis and behavioural observations indicated a lack of feeding. Females of equivalent-sized pinniped species that also do not feed while reproducing (nursing pups) on islands lose mass about 17 times faster. This comparatively low rate of mass loss by green turtles probably reflects their ectothermic nature and, consequently, their low metabolic rate. We estimate that a female turtle would lose only 19% of her body mass during the 143-day, 4400-km round trip from Brazil if she did not eat, laid 3 clutches of eggs, and lost 0.22 kg·d⁻¹.

Résumé : La masse moyenne, après la ponte, des tortues marines *Chelonia mydas* femelles qui nichent dans l'île de l'Ascension (7°57'S, 14°22'O), au milieu de l'Atlantique, est de 166,3 kg ($n = 119$, étendue 107,5–243,5 kg). Les tortues subissent une perte de masse graduelle au cours de la saison de nidification ($n = 14$ individus pesés plus d'une fois, perte de masse moyenne de 0,22 kg/jour). L'analyse des contenus stomacaux et des observations du comportement ont révélé un arrêt de l'alimentation. Des pinnipèdes femelles de taille équivalente, qui cessent également de s'alimenter pendant la saison de la reproduction (allaitement) dans les îles, subissent des pertes de masse 17 fois plus rapides. Le taux relativement faible de perte de masse chez ces tortues marines reflète probablement leur ectothermie et, conséquemment, leur taux de métabolisme faible. Nous estimons qu'une tortue femelle qui ne mange pas, qui pond trois masses d'oeufs et qui perd 0,22 kg/jour, ne perdrait que 19 % de sa masse totale au cours de sa migration aller-retour du Brésil, un parcours de 4400 km, d'une durée de 143 jours.

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Introduction

During the breeding season, some animals do not feed at all, or feed at a reduced level, so their ability to endure periods of fasting may have important implications for their reproductive success. It has been predicted that owing to the different allometric scalings of body reserves and metabolic rate, all other things being equal, fasting endurance will be greater in larger animals (Lindstedt and Boyce 1985). While the use of this model to compare species that differ in their life histories has been criticized (Dunbrack and Ramsay 1993), for some groups the model holds true. For example, among breeding male pinnipeds, fasting endurance is greater in larger species; for example, male northern elephant seals (*Mirounga angustirostris*), which weigh around 1500 kg, are able to fast

for about 60 days, while smaller harbour seals (*Phoca vitulina*) (males weigh about 100 kg) are only able to fast for about 19 days (Coltman et al. 1998). Interestingly, the fasting endurance of even the largest mammals is dwarfed by that of some amphibians and reptiles. For example, van Beurden (1980) has estimated that the fasting endurance of the desert frog *Cyclorana platycephala* may be more than 5 years, while Wikelski and Trillmich (1997) have shown that some marine iguanas in the Galápagos Islands may survive long periods (many months) of very low food availability associated with extreme El Niño events. Such examples of survival through long periods of low food availability can largely be explained by the very low metabolic rate of ectotherms compared with endotherms, and illustrative examples of this energetic dichotomy are widespread. For example, Peterson (1996) calculated that the energy expended in 1 year by a 3-kg desert tortoise would support an equivalent-sized mammal for only 3.5 days.

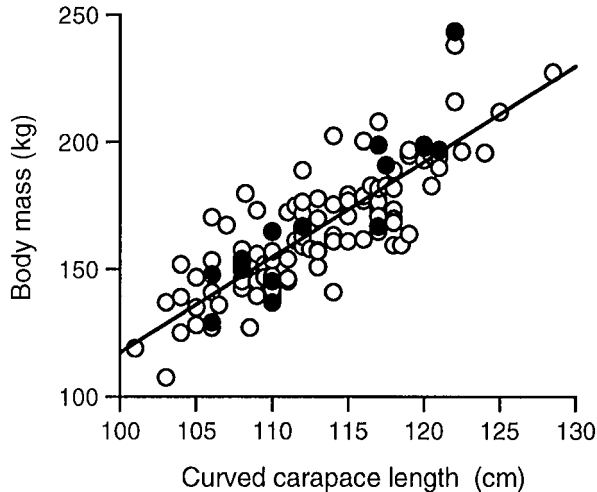
Low rates of energy utilization associated with ectothermy may be a key feature of the life history of sea turtles, since long-term fasting associated with migration to nesting areas is thought to be widespread in this group. To date, however, there are no estimates of the field metabolic rates (FMR) of adult sea turtles (Nagy et al. 1999), hence energy budgets for

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Fig. 1. Relationship between the body mass of green turtles (*Chelonia mydas*) and their curved carapace length (CCL). Solid circles represent the first measurement for individuals that were subsequently reweighed. For the entire dataset ($n = 119$ measurements of post-oviposition turtles): mass (kg) = $3.75 \text{ CCL} - 258$ ($r^2 = 0.69$, $F_{[1,117]} = 265$, $P < 0.001$).



this group are tentative (Prange 1976; Bjørndal 1995). As a corollary to their predicted low metabolic rates, it would be expected that the rate of mass loss for naturally fasting turtles would be much lower than for equivalent-sized endotherms. Since it is much easier, and cheaper, to measure the body mass of large vertebrates rather than their FMR, as a first step in testing the prediction that low rates of energy utilization occur in breeding turtles, we set out to measure rates of mass loss in fasting individuals.

Material and methods

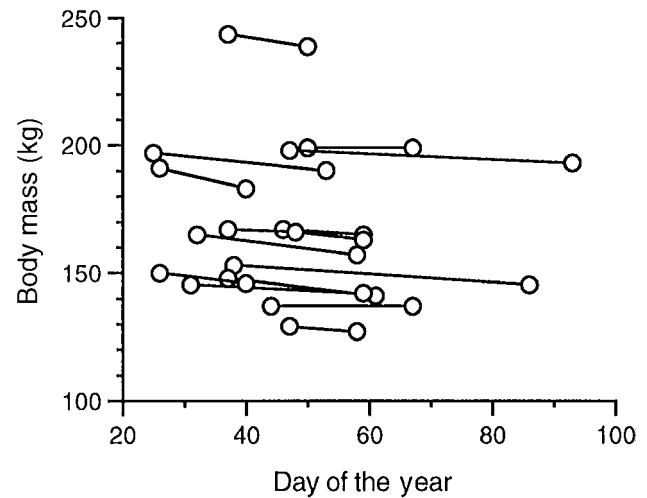
Green turtles at Ascension Island

The green turtles that nest at Ascension Island, a remote island in the middle of the Atlantic Ocean ($7^{\circ}57'S$, $14^{\circ}22'W$), migrate from feeding grounds along the South American coast at least 2200 km distant (Mortimer and Carr 1987). Based on the scarcity of macroalgae and seagrasses at Ascension Island and on direct observations that have failed to show turtles feeding, it is thought that the turtles generally do not feed while at this island (Carr et al. 1974). Hence, this nesting population is potentially suitable for examining rates of mass loss in fasting turtles. We set out to (i) measure the mass change of females and (ii) examine the gut contents of individuals at the island to establish whether or not they feed.

Body mass of turtles

During the 1999–2000 nesting season at Ascension Island, Long Beach, one of the major nesting beaches on the island, was patrolled at night to locate nesting turtles. Post oviposition, turtles were tagged with titanium flipper tags and their curved carapace length (CCL) was measured with a flexible tape. Individuals were then weighed to the nearest 0.5 kg using a spring balance (Salter model 233) before being allowed to return to the sea. The beach was patrolled on some nights throughout the nesting season and if marked individuals were

Fig. 2. The mass of female green turtles weighed more than once during the season. Each line joins masses for the same individual.



encountered, after oviposition was again completed they were reweighed. We used a range of known lead weights to confirm that the calibration of the scales did not alter during the season.

Gut-content analysis

During the 1998–1999 and 1999–2000 nesting seasons we dissected and examined the viscera of turtles that had died ashore from heat stress after becoming trapped amongst rocks on their return to the sea following nesting.

Results

The mean mass was 166.3 kg (range 107.5–243.5 kg, $n = 119$ measurements of 104 post-oviposition females), with mass increasing with CCL (Fig. 1). The individuals whose mass change was measured spanned much of the observed range in size recorded within the population as a whole, i.e., we measured mass change in a representative sample of different-sized animals. We weighed 14 turtles more than once (13 individuals were weighed twice and 1 was weighed 3 times), the interval between the first and last measurements ranging from 11 to 49 days, i.e., in some cases individuals were reweighed after laying their next clutch, but in other cases some nesting events were missed (Fig. 2). The mean rate of mass loss was $0.22 \text{ kg} \cdot \text{d}^{-1}$ (range 0.00–0.57 $\text{kg} \cdot \text{d}^{-1}$, $\text{SD} = 0.15 \text{ kg} \cdot \text{d}^{-1}$, $n = 14$ individuals). Four turtles were dissected after dying ashore and in all cases the gut contained no ingesta.

Discussion

A lack of feeding during the nesting season certainly does not apply universally to sea turtles. For example, during the internesting period leatherback turtles (*Dermochelys coriacea*), which are pelagic feeders on gelatinous zooplankton, dive deeply and their mass changes little, suggesting that they do feed at this time (Eckert et al. 1989), while gut-content analysis has shown that green turtles feed on seagrasses during the internesting interval in Cyprus (Hochscheid et al. 1999). However, there is strong evidence to support the suggestion

(Carr et al. 1974) that green turtles rarely feed at Ascension Island. First, green turtles are herbivorous and there is very little macroalgae or seagrass around the island. Second, while green turtles are frequently observed by SCUBA divers, they are almost never observed feeding except when artificially provided with food (Carr et al. 1974; personal observation). Third, data from time–depth recorders have suggested that individuals spend long periods quiescent on the seabed during the internesting interval (Hays et al. 2000). Fourth, autopsied animals have an empty gut.

We recorded mass change in a range of different-sized individuals and hence we probably obtained a fairly accurate representation of the mean rate of mass change for this population. The modal internesting interval at Ascension Island is 13 days, over which time the mean mass loss would be 2.9 kg. Much of this mass loss is probably accounted for by the production of eggs. Since much of the clutch mass is water taken on board by the female during egg production, the mass of the clutch will not equal the mass lost by the female. We therefore estimated the cost of egg production to the female in terms of energy investment. With a mean clutch size of 127.5 eggs (Hays et al. 1993) and a predicted energy content per egg of 279.5 kJ (Hays et al. 2000), the mean total structural investment in a clutch of eggs by green turtles at Ascension Island is 35.6 MJ, which equates to an energetic content of about 1 kg of fat.

To put our measured rates of mass loss into the context of the expected ectotherm/endotherm dichotomy, we can consider values for fasting marine mammals during lactation, i.e., an analogous situation in that individuals are making a structural investment in their offspring while not feeding. Rates of mass loss in pinnipeds increase in larger species. For example, female Antarctic and Galápagos fur seals (*Arctocephalus gazella* and *Arctocephalus galapagoensis*) are relatively small (around 40 kg) and lose about 1 kg·d⁻¹ during the perinatal fast (Costa and Trillmich 1988), while northern elephant seals (*Mirounga angustirostris*) are much larger (around 425 kg) and lose about 7.5 kg·d⁻¹ during lactation (Costa et al. 1986). Female green turtles at Ascension Island are of about the same mass as grey seals (*Halichoerus grypus*), which during their fast associated with lactation lose about 3.6 kg·d⁻¹ (Fedak and Anderson 1982), i.e., the rate of mass loss in green turtles (mean 0.22 kg·d⁻¹) is around 6% of that for an equivalent-sized pinniped. Therefore, in common with those obtained from other ectotherms, these results suggest that long-term fasting in green turtles is facilitated by their low rate of energy expenditure.

The round-trip migration of green turtles from Brazil to Ascension Island may necessitate a long fast if, as is suspected (e.g., Prange 1976), turtles indeed do not feed during the ocean crossing in addition to while they are at the island. We can estimate the length of this round trip by summing the times taken on each leg of the journey. (i) Previously, females have been satellite-tracked migrating from Ascension Island to Brazil at the end of the nesting season (Luschi et al. 1998). With a mean travel speed of 2.6 km·h⁻¹, a straight-line crossing distance of about 2200 km, and a typical straightness index (the beeline distance divided by the total distance covered) of 0.96, this crossing takes, on average, about 37 days to complete. (ii) While at Ascension Island each female is thought to lay, on average, about 3 clutches with a modal

interesting interval of 13 days (Mortimer and Carr 1987), i.e., the modal length of time to lay clutches is about $3 \times 13 = 39$ days. (iii) Prior to the first clutch being laid, mating takes place, with an interval of 30 days between mating and first oviposition (Booth and Peters 1972; Comuzzie and Owens 1990). If we assume that the Brazil – Ascension Island trip takes the same length of time as the reverse journey, then we obtain a mean round-trip duration of 143 days. On average, a female turtle would only lose about 19% of her body mass during this 143-day, 4400-km round trip from Brazil if she did not eat, laid 3 clutches of eggs, and lost 0.22 kg·d⁻¹. In short, a low rate of utilizing body reserves is probably crucial in facilitating such a prolonged fast.

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