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How numbers of nesting sea turtles can be over-estimated by nearly a factor of two

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Running title: Assessing numbers of nesting sea turtles

Estimating the absolute number of individuals in populations and their fecundity is central to understanding the ecosystem role of species and their population dynamics as well as allowing informed conservation management for endangered species. Estimates of abundance and fecundity are often difficult to obtain for rare or cryptic species. Yet, in addition, here we show for a charismatic group, sea turtles, that are neither cryptic nor rare and whose nesting is easy to observe, that the traditional approach of direct observations of nesting has likely led to a gross over-estimation of the number of individuals in populations and underestimation of their fecundity. We use high resolution GPS satellite tags to track female green turtles throughout their nesting season in the Chagos Archipelago (Indian Ocean) and assess when and where they nested. For individual turtles, nest locations were often spread over several 10s of km of coastline. Assessed by satellite observations, a mean of 6.0 clutches (range 2-9, SD=2.2) was laid by individuals, about twice as many as previously assumed, a finding also reported in other species and ocean basins.

Taken together, these findings suggest that the actual number of nesting turtles may be almost 50% less than previously assumed.

Subject Areas: ecology, population and community ecology

Keywords: Chagos, Chelonia, Argos, Fastloc GPS, clutch frequency, critically endangered

1. Introduction

Detailed census data for populations lies at the heart of conservation efforts striving to protect the world's biodiversity, but for some groups obtaining accurate estimates of their abundance can be very difficult. For example, evidence of the occurrence of very rare and/or cryptic species, such as via direct sightings, cameras traps or scat samples, may simply be obtained so rarely that abundance estimates are poor and even assessing whether such species are extinct or extant may be difficult [1-3]. However, surprisingly even for some groups that are both relatively easy to observe and abundant, estimating the number of individuals in populations remains a challenge [4]. One example is sea turtles, whose population size is typically assessed by counting tracks on nesting beaches and these data, collected over many years, have revealed trends in abundance and hence underpin species conservation status assessments [5-7]. Yet estimating the number of nesting turtles responsible for those observed nests is more problematic because while individual turtles may nest more than once in a single season, it is logistically challenging to identify and record them every time they nest [8,9]. While there have been efforts to correct individual clutch frequency estimates to account for nesting events where the individuals are not observed [10-13], these approaches have limitations. So for many years there has been a concern that the true numbers of clutches laid by females is poorly estimated [14,15].

More than 20 years ago it was suggested that transmitters attached to individuals would allow them to be tracked during the nesting season and hence reveal their true clutch frequency [16]. However, there have been only limited attempts to use animal-borne transmitters in this way, with this technology more typically being used to assess migration patterns at the end of the breeding season, foraging destinations and diving behavior [17-19]. This lack of focus on assessing movements within the nesting season has stemmed from two problems with tracking technology. First, while turtles are in shallow water close to shore, transmitters run the risk of being damaged, for example by turtles scraping against rocks [20]. Second, satellite transmitters typically use the Argos system which tends to provide fairly coarse quality locations, accurate to only a few km, which may be inadequate to identify when turtles nest [21]. We overcame these commonly encountered obstacles by using state-of-the-art robust satellite transmitters that provided high resolution Fastloc-GPS locations [22] allowing nesting events to be identified. In this way we assessed the true clutch frequency for sea turtles at an Indian Ocean breeding ground. By extending our observations to those made in other ocean basins and with other species, we re-evaluate the likely number of nesting turtles that exist around the world and discuss the implications of this fundamental shift in our knowledge of the life-history of this group.

2. Methods

Satellite tags were attached to nesting green turtles on the island of Diego Garcia (7.42°S, 72.45° E) within the Chagos Archipelago during October 2012 and July 2015. The study beach supports the highest numbers of nesting turtles in the archipelago [23,24]. Turtles were located while they were nesting ashore at night. After egg laying was completed, the midline curved carapace length (CCL) was measured to the nearest 0.5 cm using a flexible tape measure. Once turtles were returning to the sea they were restrained in a large open topped and bottomless wooden box. The carapace was first cleaned of biota with acetone and then lightly sandpapered to provide a better surface for transmitter attachment. Satellite tags were then attached with quick setting epoxy (Pure-2K, Powers Fastening Innovations and Pure 150-PRO, DeWalt), with the epoxy smoothed to provide a streamlined shape before the epoxy and transmitters were covered with anti-fouling paint (Trilux 33, International) to minimise epi-biont growth. The attachment process took around 2 h to complete and then the turtles were allowed to return to the sea.

In 2012 we used two models of satellite tag (SPLASH10-BF, Wildlife Computers, Seattle, Washington (*n* = 4) and model F4G 291A, Sirtrack, Havelock North, New Zealand (*n* = 4). In 2015 we deployed 10 SPLASH10-BF units (figure 1). Transmitters relayed data via the Argos system (http://www.argos-system.org/) that allowed Fastloc-GPS positions to be determined along with the standard Argos locations. In addition the tags transmitted information on haul-out events, defined by the salt-water switch on the transmitter staying continuously dry for 20 minutes. Due to intermittent satellite overpasses and the limited bandwidth of the Argos system, combined with the fact that we programmed tags to preferentially relay Fastloc-GPS data rather than haul-out data, information was not received on all haul-out events. Only Fastloc-GPS positions obtained with a minimum of 5 satellites and a residual error value of <35 were used, producing locations that were generally within a few 10s of metres of the true location [22]. This compares to the Argos locations that are typically only accurate to a few kms of the true location.

Data relayed from the satellite tags were used to record subsequent nesting events in two ways: (1) Using Fastloc-GPS positions close to the beach. Turtles spent the period between nesting emergences on the seaward side of the reef crest, which was typically 200 m from the beach. So the accuracy of Fastloc-GPS locations resolved movement onto the back reef (the region between the reef crest and beach) and the beach itself. (2) Using data on haul-out events. Sometimes sea turtles will emerge onto beaches multiple times (termed false crawls) in quick succession (on the same or subsequent nights) before they lay eggs, so we defined an egg laying event as occurring on the last night of these successive emergences. Residence at the breeding grounds was defined as the elapsed period in days between the transmitter attachment and departure from Diego Garcia to the foraging grounds. On departure from Diego Garcia, we interpolated the point of departure as the nearest landfall to the first point at sea.

To estimate the nesting seasonality, a 2.3 km section of nesting beach, which supports a high density of nesting on the island, was patrolled during the day at approximately bi-weekly intervals and the number of green turtle tracks counted.

Using available literature we compiled estimates of the mean clutch frequency for green turtles and loggerhead turtles measured around the world using beach patrols. Where there were multiple estimates for the same location we used the most recent value (see electronic supplementary material, table S2).

All work was approved by Swansea University Ethics Committee and the British Indian Ocean Territory (BIOT) Administration of the UK Foreign and Commonwealth Office.

3. Results

Counts of turtle tracks showed that the timing of satellite tag deployments in relation to the nesting season varied between 2012 and 2015 (figure 2). In July 2015, there were no tracks counted in the weeks preceding satellite tag deployment, suggesting that tagged individuals were most likely encountered on their first nesting event of that season. By contrast, in 2012 the satellite tags were deployed during October, well into the green turtle nesting season, with considerable nesting activity in the weeks before tag deployment. Hence some of these turtles equipped in 2012 are likely to have nested several times before tag deployment. For this reason we focus the analysis below on the 2015 data. All 18 turtles equipped with satellite tags during 2012 and 2015 were tracked until they departed on their post-nesting migration to their foraging grounds (figure 3*a*, see electronic supplementary material, figures S2-S11).

In 2015, a total of 2025 Fastloc-GPS locations were obtained prior to individuals departing from the breeding grounds. Sizes and tracking details of tagged turtles are given in electronic supplementary material, table S1. One of the 10 tags deployed in 2015 stopped transmitting Fastloc-GPS data after seven days, but post-breeding departure from Diego Garcia was still clearly evident (figure 3*a*). Whilst at the breeding grounds, individuals had fairly restricted movements offshore, never travelling far beyond the fringing reef and staying in water depths that nautical charts showed were <20 m. However, while individuals did not move far offshore, they did move longer distances along the coast with individual nesting events being recorded around most of the ocean side of the island (figure 4*b*).

The daily timing of 286 Fastloc-GPS locations on the back reef and nesting beaches was consistent with nocturnal emergences to nest (86.4% occurring between sunset and sunrise, with >99.9% occurring within 2 h before sunset and 2 h after sunrise (electronic supplementary figure

S1*a*). The timing of nesting inferred from these Fastloc-GPS locations or the haul-out data indicated a modal inter-nesting interval of 13 days (electronic supplementary material, figure S1*b*). In some cases, inter-nesting intervals were recorded that were multiples of this modal interval (*n* = 1 nesting event out of a total of 50 assessed by the locations and haul-outs). In these cases we assumed the individual had nested in the interim but neither a Fastloc-GPS location nor a haul-out event had been recorded because of the limited bandwidth of the Argos system. The lines of evidence used to determine each nesting event are reported in electronic supplementary table S1.

Across these ten individuals equipped in 2015 that supplied Fastloc-GPS and haul-out data, the length of time spent at the breeding grounds subsequent to tag attachment was very closely related to the number of subsequent clutches assessed by the Fastloc-GPS and haul-out data-sets. This relationship was further strengthened when we included data from individuals equipped in 2012 (figure 3*b*). For the one tag that largely only supplied Argos locations, we therefore assessed clutch frequency by the length of residency at the breeding grounds.

Including both the nesting event when they were equipped and those subsequently assessed by satellite, equipped individuals laid between 2 and 9 clutches before departing from the breeding grounds (mean = 6.0 clutches, SD = 2.2) (figure 5*a*). Previous studies conducted elsewhere comparing clutch frequency measured by foot patrols and inferred by tracking individuals equipped with transmitters highlight the broader generality of our findings. For both loggerhead turtles (*Caretta caretta*) nesting in Florida (North Atlantic) and green turtles nesting on Ascension Island (central Atlantic), the clutch frequency assessed by tracking individuals was approximately twice that measured by foot patrols (figure 5*b*,*c*).

Furthermore, the mean clutch frequency measured by foot patrols for populations around the world tended to be around 2 to 4 clutches (mean 3.5 clutches per female), significantly and appreciably less than those values reported by tracking (mean 5.9 clutches per female) (t_{43}=3.4, P< 0.001) (figure 6).

For our mid-nesting season satellite tag deployments in 2012 (n = 8), when some individuals had likely nested several times prior to tag attachment, the tracking data revealed that one individual departed immediately after tag attachment while others nested 6, 7 and 9 times subsequently, so possibly at least 7, 8 and 10 times in total for those individuals.

4. Discussion

Our results add further evidence to the long-standing suggestion [16] that foot patrols may often underestimate the true clutch frequency for sea turtles. For loggerhead turtles in Florida [25] and green turtles in Ascension Island [26], the clutch frequency measured by tracking was almost twice that measured by foot patrols, while our mean clutch frequency measured by tracking green turtles at Diego Garcia was again almost twice the mean value measured elsewhere in the world for this species by foot patrols. Several lines of evidence suggest the approach of using tracking data to assess nesting events is robust. The location accuracy of Fastloc-GPS is good enough to indicate when turtles come ashore and haul-out data provide an independent method to record nesting events since, at sea, turtles will very rarely be at the surface for long periods during the breeding season [27]. Furthermore the nocturnal timing of nesting events assessed by satellite is consistent with nocturnal nesting by green turtles, while the modal internesting interval we recorded is in line with previous reports of this interval typically being 10-14 days in tropical waters [28]. Moreover, our calculations of true clutch frequency from tracking individuals might still be a slight underestimate as turtles may have nested prior to the night of transmitter attachment, although this possibility is likely to be rare both in our study and others [25,26] given the absence of nesting tracks in the weeks prior to satellite tag attachment.

It is well known that in some taxa, including many birds, reproductive success varies between early and late breeders, generally declining later in the breeding season [29,30]. So it might be argued that the first turtles to nest at the start of the nesting season, i.e. those that were equipped by ourselves in 2015 and by others [25,26], might not represent a random sample of individuals from a population, with individuals that start nesting later in the season having a different clutch frequency. If this were the case then our use of tracking data might not reflect the clutch frequencies for individuals in the population as a whole. However, our 2012 deployments suggest that this scenario might not be the case, since we found that after the middle of the nesting season individuals could still lay up to 10 clutches. These individuals are presumably those that had arrived slightly later at the breeding grounds and had started nesting later in the season.

There is a need for further studies to establish if our key finding, that sea turtles lay substantially more clutches than inferred from beach patrols, is also valid for other sea turtle populations. While the conservation status of species is typically assessed by the trends in relative abundance (www.iucnredlist.org/), the absolute number of individuals in a population is important for a number of reasons. Absolute numbers impact the ability of populations to withstand exploitation or mortality associated with environmental perturbations and allow realistic population models to be developed that allow a better understanding of the roles of hatchling production, juvenile growth and survival, and adult mortality in driving population trends [31-33]. Our findings, that the clutches laid by sea turtles each year around the world are likely being laid by significantly fewer turtles than previously assumed, magnifies the importance of ongoing conservation efforts to protect the adult life history stage which is often the target for exploitation [34]. Knowing absolute numbers is also important for assessing the ecosystem role of sea turtles. For example, green turtles are important grazers of seagrass meadows and, in this role, may impact carbon sequestration and biogeochemical cycling [35] as well as habitat quality [36]. Similarly hawksbill turtles are important grazers of sponges, consequently influencing the relative abundance of corals versus sponges on tropical reefs and hence play a role in reef health [37]. Knowing the links between the total number of nests and the total number of females may also improve the comparability of data collected from different sea turtles populations around the world and hence help drive directed conservation efforts towards key populations (e.g. green turtle IUCN assessment [38]).

Given the demonstration that satellite tags now allow the assessment of the true clutch frequency for sea turtles, using high accuracy GPS locations, haul-out data and the length of residence at nesting sites, applications of this technology may start to reveal the drivers of clutch frequency which potentially includes factors such as migration distance, female age [39], size [40] and body condition [41]. Furthermore, our findings based on precise locality data collected with the relatively more expensive Fastloc-GPS units provide assurance that clutch frequency can also be reliably estimated using data provided by the less expensive and more commonly used Argos transmitters, simply by dividing the length of residency at the breeding area after the first clutch is laid by the known inter-nesting interval. Given the robustness of satellite tags and the demonstration that they can survive well during the breeding season, this approach can now potentially be used in the many sea turtle projects around the world that use Argos satellite tracking [42].

We also show how high resolution tracking can clearly reveal the extent of beach used by individuals for nesting. While DNA evidence has convincingly shown that sea turtles generally return to their natal area to breed [43], individuals can clearly nest in several different places within the same general area (our study and others [8,25]). This tendency to spread nests across multiple sites may improve the resilience of sea turtles to loss of a nesting beach, such as through erosion, beach development, or climate change.

Given that our work and that of others now convincingly show the utility of accurately assessing the clutch frequency of sea turtles by tracking, there is value in extending this approach to other sea turtle rookeries around the world. In this way the broader generality of our conclusions will become clear. While global conservation efforts have led to increases in nesting activity at many sea turtle breeding sites [5,7,44], there is a need for sober reflection of whether the absolute numbers of nesting turtles are likely much less than has been assumed previously, with individuals often laying more clutches than inferred from beach patrols.

Ethics. All work was approved by the Swansea University Ethics Committee.

Data accessibility. The data-set supporting this study is stored in the electronic supplementary material and the main text.

Authors' contributions. G.C.H. conceived the study. N.E. and G.C.H. completed the fieldwork in 2012 and 2015 and analysed the satellite tracking data. J.A.M. participated in the 2012 fieldwork and assembled the data on observed clutch frequencies around the world. G.C.H. and N.E. wrote the manuscript with input from J.A.M. All authors gave final approval for publication.

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Competing interests. The authors declare no conflict of interest.

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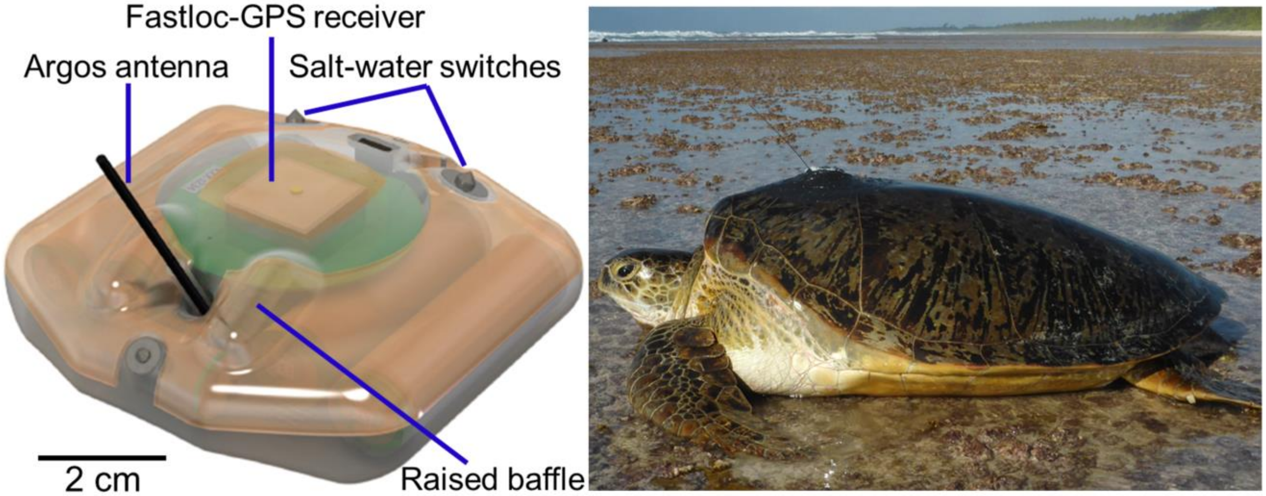

Figure 1. Fastloc-GPS Argos SPLASH tags attached to nesting green turtles in 2012 and 2015. (*a*) Schematic of the tag and (*b*) A photograph of an attached tag. Various features of the Fastloc-GPS Argos SPLASH tag enhance protection from impacts during inter-nesting activities: (i) The tag has a low profile, (ii) the tag has a flexible Argos antenna that is sited in a depression so that it can be repeatedly folded over to horizontal with no fatigue at the antenna base, (iii) the base of the antenna is protected by raised baffles that reduce the likelihood of direct impacts.

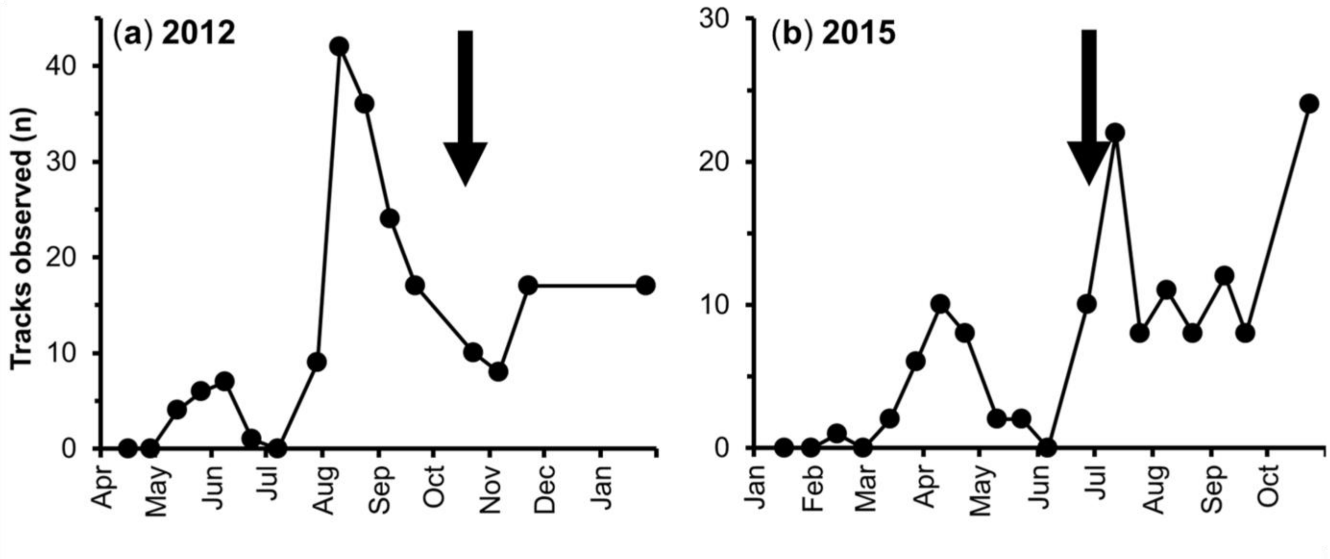

Figure 2. The number of green turtle tracks counted during approximately biweekly surveys on a 2.3 km section of nesting beach, encompassing where the satellite tags were deployed. The timing of satellite tag deployments is shown by the black arrow and listed in electronic supplementary material, table S1. (*a*) During 2012 the satellite tags were attached in the middle of the peak nesting season, so some of the equipped turtles had most probably nested previously. (*b*) In 2015 the satellite tags were attached at the start of the peak nesting season and so most turtles were likely encountered laying their first clutch of the season.

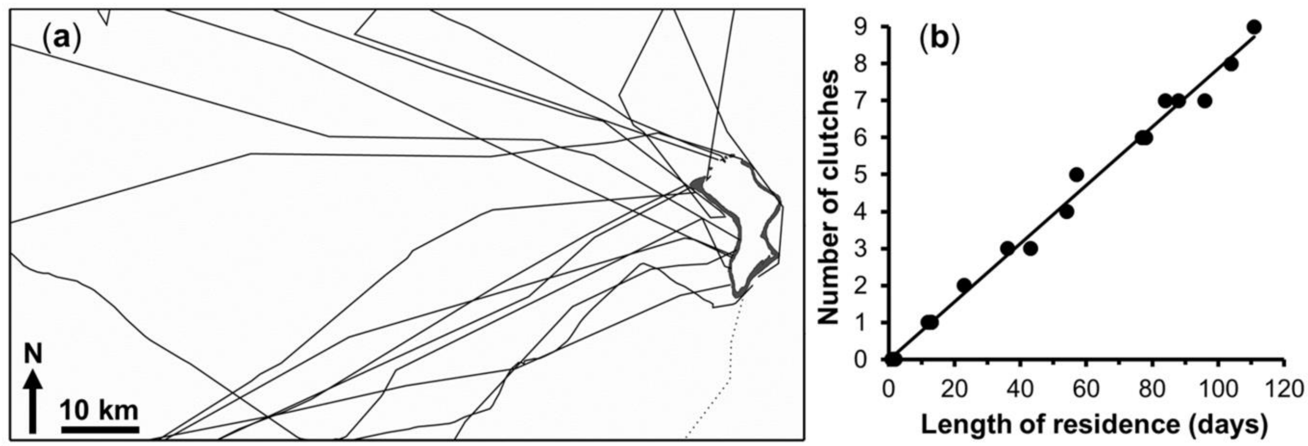

Figure 3. Relationship between number of clutches and length of residence. (*a*) The tracks of 18 green turtles equipped in 2012 and 2015 indicating their departure from Diego Garcia at the end of their breeding season. In all cases the time of departure was clearly evident, including one individual for which only Argos locations were relayed at this time (dotted line), (*b*) For 18 individuals equipped with satellite tags, the number of clutches assessed by the tracking data (Fastloc-GPS and haul-out data) versus the length of residence at the breeding grounds subsequent to tag deployment (black line indicates linear regression). The strong relationship shows that in the absence of Fastloc-GPS and haul-out data, the length of residence at the breeding grounds after turtles are observed nesting provides a very good indication of the number of clutches they lay subsequently.

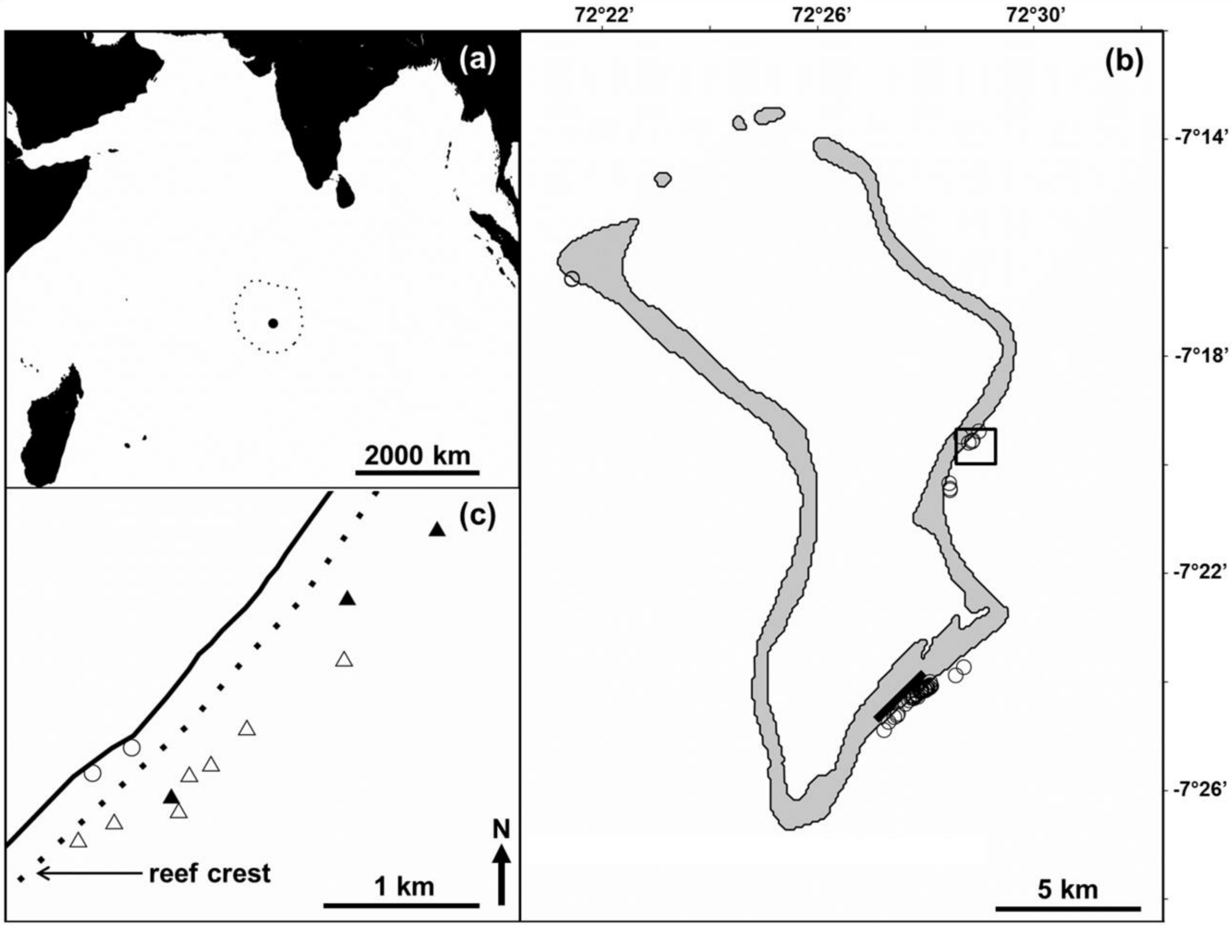

Figure 4. Estimated clutch locations on Diego Garcia (*a*) Location of Diego Garcia (black dot) in the Chagos Archipelago, Central Indian Ocean and the marine reserve boundary (dotted line), (*b*) Locations of 50 nesting events in 2015 (open circles) for satellite tagged green turtles on Diego Garcia derived from satellite tracking data. The beach section of tag attachment is shown by the solid black line, (c) An example of the series of Fastloc-GPS locations relayed via the Argos satellite transmitters for one individual (location shown as inset on figure 4*b*). The section of track covers 6 days during which time the turtle (ID 29358) shifted from an area close to the reef crest (black dotted line) during a night-time movement to the adjacent back reef and nesting beach (open circles). The locations on the back reef and on the beach at night and the interval between other nesting events derived from satellite tracking data all point to the turtle nesting at this time. Triangles indicate locations pre- (open) and post- (closed) nesting (2 nights prior to this night and 3 nights subsequent to this night).

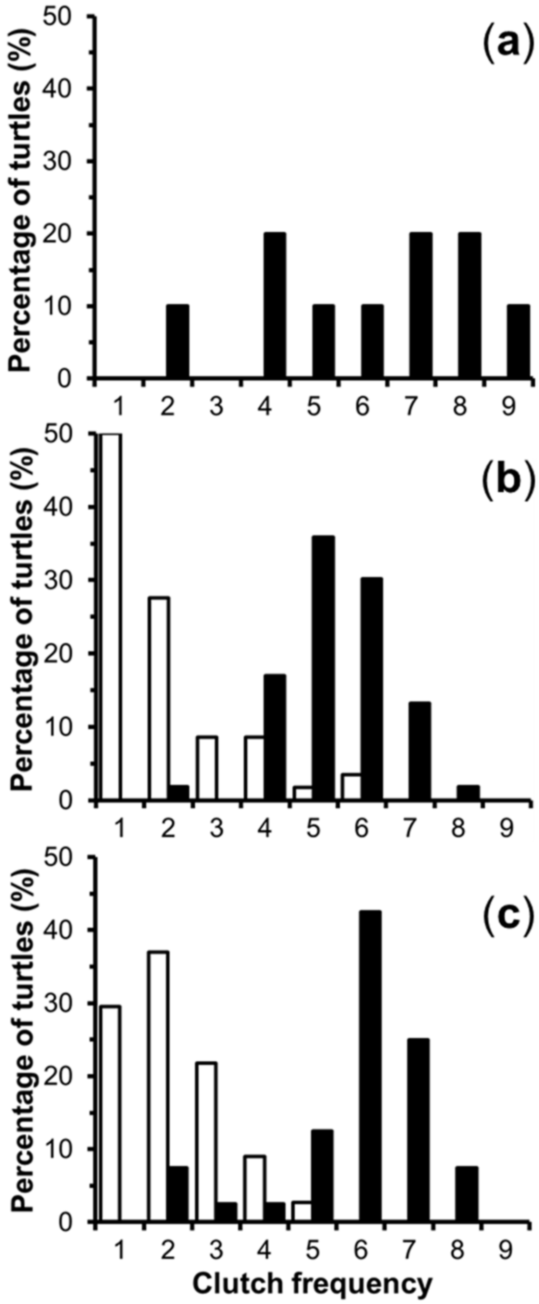

Figure 5. Comparison of the clutch frequency measured by foot patrols (open bars) and inferred by tracking individuals equipped with transmitters (solid bars). (*a*) Chagos green turtles (this study), (*b*) Loggerhead turtles in Florida [25] and (c) Ascension Island green turtles with tracking data from [26] and foot patrol data [45, Mortimer (unpublished data)]. Clutch frequency estimates assessed by tracking were 1.7x and 1.9x higher than by foot patrols in (*b*) and (*c*).

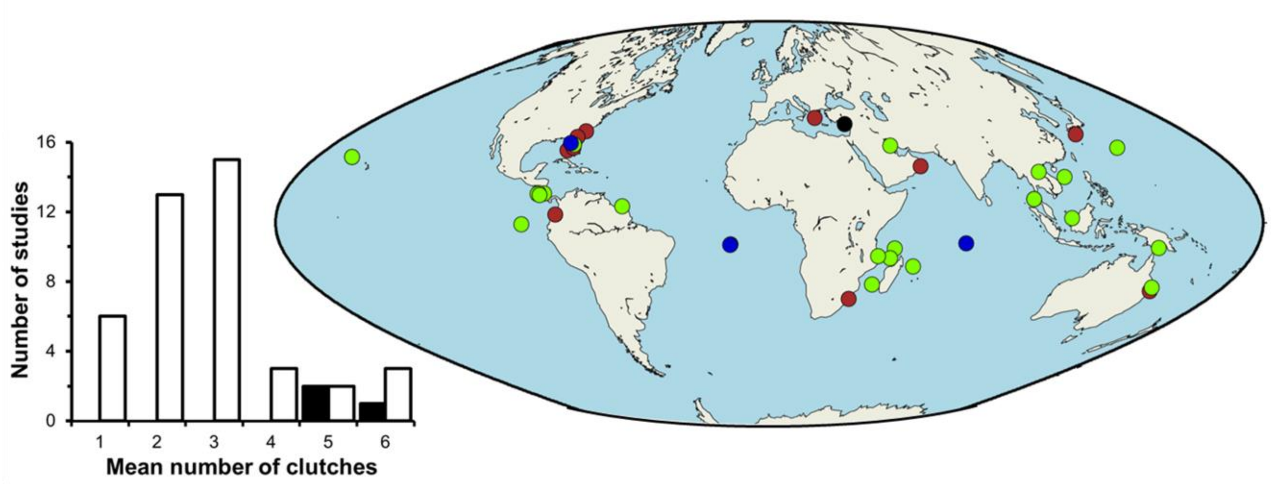

Figure 6. The locations of mean clutch frequency estimated by foot patrols at green turtle (green dots), loggerhead turtle (brown dots) or both species (black dots) rookeries around the world. Locations of estimates of clutch frequency from satellite tracking (our study, [25,26,45, Mortimer, unpublished data]) are shown by the blue dots. Inset: values for the mean clutch frequency measured by foot patrols (open bars) and by satellite tracking (closed bars), see electronic supplementary material, table S2 for source data.