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Telemetry as a tool for improving estimates of marine turtle abundance

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ABSTRACT

Accurate estimates of abundance are fundamental to the conservation of threatened species, but are often difficult to obtain directly. Population size assessments of marine turtles are often based on counts of nests, which are then related to abundance using the mean number of clutches laid by individuals within a season. Due to low re-encounter probabilities, clutch frequency has proven difficult to estimate reliably, particularly for large populations that make a major contribution to global stock assessments. We use a combination of VHF radio-telemetry and Argos-linked Fastloc™ GPS devices to improve clutch frequency estimates for one of the world's largest green turtle rookeries at Ascension Island. Females fitted with VHF tags at the start of the season ($n = 40$) were re-encountered with a probability of 85% and laid a minimum average of 5.8 clutches. Three of these turtles were fitted with VHF and GPS devices and using the data collected by the latter, were found to lay an average of 6.3 clutches. GPS-telemetry detected emergences observed using radio-telemetry, and confirmed that some radio-tagged turtles laid again after their last observed emergence. Correcting for missed nesting events yielded a mean clutch frequency of 6.3, more than doubling the previous estimate of 3.0 for this population. Applying this revised assessment to annual nest counts reduces the estimated size of this population by 52%. Conventional tagging approaches may considerably underestimate annual fecundity of turtles, resulting in inflated population size estimates. We call for urgent reassessment of baseline abundance values for regionally important populations.

1. Introduction

Reliable estimates of population size are essential in many biological fields and particularly for the conservation and management of threatened species (e.g. Flather et al., 2011; Hare et al., 2011). To be able to monitor and predict population trends it is first necessary to establish a reliable baseline of distribution and abundance. Unfortunately, however, for the vast majority of species it is not possible to directly census the number of individuals in a population, placing reliance on sampling-based approaches (e.g. distance transects and capture-mark-recapture) or indirect indices of abundance (Williams et al., 2002). Such indices can include camera-trapping (e.g. Garrote et al., 2011), scat sampling (e.g. Kindberg et al., 2011) or track counts (e.g. Balme et al., 2010). Although these methods are useful for assessing trends, for many applications absolute estimates of population size are needed (e.g. when setting harvesting limits and assessing extinction risk). Indirect approaches also assume that the scaling factors that relate them to absolute population size are well defined and remain constant over time, which may not be the case. Evaluations of the reliability of indirect survey methods with cross-validation studies are therefore necessary as technologies advance in order that more accurate population size estimates can be derived.

Due to the inherent difficulties of quantifying wide-ranging, marine species, global assessments of marine turtle abundance are generally based on studies of the annual nesting activity and egg production of adult females at nesting aggregations (Gerrodette and Taylor, 1999; Witt et al., 2009; National Research Council, 2010). Marine turtles are of global conservation concern following centuries of overexploitation that has seen many stocks reduced to a fraction of their former size (e.g. McClenachan et al., 2006; Tomillo et al., 2008; Dethmers and Baxter, 2011). Incidental capture in fisheries, habitat loss and marine pollution also continue to threaten the survival of many stocks (Seminoff, 2004). However, while some marine turtle populations are in rapid decline, others are stabilizing or increasing following sustained conservation

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efforts (reviewed in Wallace et al., 2011). Accurate estimates of abundance are therefore necessary to inform relevant conservation action. For most populations, such estimates are obtained indirectly from annual counts of the number of tracks and/or successful nests at nesting beaches (e.g. Gerrodette and Taylor, 1999; Bjorndal et al., 1999; Broderick et al., 2006; Witt et al., 2009; Witherington et al., 2009). Since all species of marine turtles nest more than once within a nesting season (Miller, 1997), this value must then be divided by the mean number of clutches laid per female per season ('clutch frequency') to estimate the annual number of nesters (Gerodette and Taylor, 1999; National Research Council, 2010). Small changes in average clutch frequency therefore have large effects on estimated population size, making it one of the most important demographic parameters in marine turtle biology and conservation (National Research Council, 2010). However, for most populations, it is also one of the least well defined.

For the vast majority of marine turtle populations, clutch frequency has been estimated using a standard mark-recapture design, whereby nesting females are tagged with uniquely numbered flipper tags or PIT (Personal Integrated Transponder) tags and relocated during nocturnal beach patrols as they come ashore to lay additional clutches (e.g. Frazer and Richardson, 1985; Johnson and Ehrhart, 1996; Broderick et al., 2002; Tomás et al., 2010). However, as this method relies on directly observing individual females, there is a tendency to underestimate the average clutch frequency value and hence overestimate population size (Schroeder et al., 2003; Rivalan et al., 2006; Briane et al., 2007; Tucker, 2010). Inaccuracies in the observed clutch frequency (OCF) arise when tagged females are either missed due to incomplete survey coverage or move to different beaches for some or all of their subsequent clutches. The measure of estimated clutch frequency (ECF) goes some way to remedying this by using the length of the intervals between observed clutches to infer whether any nesting events were missed (Frazer and Richardson, 1985; Johnson and Ehrhart, 1996). Since the time taken to produce a clutch of eggs (the 'inter-clutch interval') is physiologically constrained by water temperature (Weber et al., 2011), dividing the time elapsed between observed clutches by the known inter-clutch interval yields a reasonable estimate of the number of missed nesting events. However, inaccuracies are still introduced when a turtle is not observed for her first and/or last clutch(es), or when she is observed only once on the study beach (Rivalan et al., 2006; Girondot et al., 2007). Due to difficulties in re-identification and often more temporally extensive breeding seasons, these errors are likely to be exacerbated in large, high-density populations which make the greatest contributions to global stock assessments.

In response to these limitations, several recent studies have explored the use of alternative technologies and statistical models to improve clutch frequency estimates, and have found significant discrepancies with ECF values obtained from conventional tag-recapture (Rivalan et al., 2006; Rees et al., 2008; Tucker, 2010; Blanco et al., 2011). For example, Tucker (2010) deployed satellite-telemetry tags on loggerhead turtles (*Caretta caretta*) nesting in Florida and derived an average clutch frequency of 5.4 nests per female in comparison to the 2.2 nests that was previously detected by monitoring patrols. Similarly, using ultrasonography of females' ovaries to supplement beach patrols, Blanco et al. (2011) estimated a clutch frequency of 5.1 ± 1.3 (mean ± SD) for green turtles (*Chelonia mydas*) in Costa Rica, compared to the value of 3.7 ± 1.8 obtained from beach patrols alone. As an alternative approach, Rivalan et al. (2006) used capture-mark-recapture models to extract more reliable estimates of clutch frequency from conventional tagging records of leatherback turtles in French Guiana, and concluded that true clutch frequency is considerably higher than the ECF for this population. If replicated across all regionally important populations, these findings have significant implications for marine turtle stock assessments. Unfortunately, however, the high cost of technologies such as satellite-telemetry limits their widespread use and restricts sample sizes, calling for cheaper and more accessible alternatives for accurately assessing clutch frequency (National Research Council, 2010). Doubts have also been expressed as to whether the spatial resolution of the Argos system that is most commonly used in satellite tracking of marine turtles is sufficient to allow detection of individual nesting events (National Research Council, 2010).

In this study we trial a combination of low-cost VHF transmitters and recently-developed, high acquisition, Argos-linked Fastloc™ GPS tags as a method for assessing clutch frequency, using the globally important green turtle nesting population at Ascension Island as a test case (Broderick et al., 2006). This population has been the subject of a long-term monitoring programme spanning more than 30 years (Mortimer and Carr, 1987; Broderick et al., 2006), and is showing promising signs of recovery following a period of heavy exploitation during the 19th and early 20th centuries (Broderick et al., 2006). It is also one of 34 index sites used by the IUCN to assess the global status of the green turtle (Seminoff, 2004), but the high density of nesting makes assessment of clutch frequency by conventional mark-recapture difficult. Indeed, the current estimate of 3 clutches per female based on flipper-tagging is likely to be an underestimate (as acknowledged by the authors; Mortimer and Carr, 1987), suggesting that the Ascension Island green turtle colony may be considerably smaller than currently thought.

2. Materials and methods

2.1. Study site and tagging methodology

Ascension Island is an isolated volcanic peak on the mid-Atlantic ridge (14°20′W, 7°55′S), which, between December and June, hosts the second largest nesting aggregation of green turtles in the Atlantic Ocean (Broderick et al., 2006). Between 29th December 2011 and 12th January 2012 we deployed 40 VHF transmitters (Biotrack, Dorset, UK) and 3 Fastloc™ Argos-linked GPS tags (Wildlife Computers, Redmond, WA, USA) onto a randomly selected sample of females nesting on Long Beach ,which currently supports the highest density and numbers of nesting turtles on the island (Godley et al., 2001).

To allow cross-validation between methods, all turtles carrying a GPS tag were also fitted with a VHF transmitter. Telemetry devices were attached to the carapace using a two-part marine epoxy resin (Powers Fasteners, Brewster, NY, USA), and a metal flipper tag was applied to each female as a secondary means of identification. To reduce the chance of including an individual that had nested previously, the few females that were observed nesting on Long Beach for the 3 weeks prior to the start of the study were also fitted with metal flipper tags. This measure combined with the fact that <1% of nesting activity on Long Beach occurred prior to 29th December during the 2011–2012 nesting season (authors' unpublished data) gives a very high probability that VHF and Argos-linked GPS devices were fitted to females while they were depositing their first clutch. The mean curved carapace length (CCL) of study females was not significantly different than the mean of a random sample of $n = 40$ females measured during the peak of nesting between 20th February and 28th March (t-test, $t = 0.29$, $p = 0.77$; mean CCL ± SE, study females: 110.9 ± 1.0 cm; peak season females: 111.3 ± 0.8 cm), indicating that our clutch frequency estimates are unlikely to have been biased by seasonal variation in female size.

2.2. Radio-telemetry

Nightly patrols of Long Beach to detect returning VHF-tagged females were carried out from 21:00 to 03:00 using an R1000

receiver (Sirtrack Ltd., Havelock, NZ) and a directional Yagi antenna (Biotrack, Dorset, UK). Patrols began 10 days after the first tag deployment (i.e. <1 inter-nesting interval; Weber et al., 2011) and continued until 21 days (i.e. >1 inter-nesting interval; Weber et al., 2011) after the last observed clutch of a VHF tagged turtle (30th April 2012). Once located, study females were observed from a distance to allow nest excavation and were then approached to confirm whether eggs were present. The locations of all observed nests for satellite-tagged turtles were recorded using a handheld Garmin™ GPS (±10 m) for comparison with positional data obtained from Fastloc™ GPS devices. The duration separating consecutive clutches of individual turtles at Ascension Island ranges from 11 to 17 days and is physiologically constrained by water temperature (Weber et al., 2011). Thus, where intervals between observed clutches exceeded 22 days, we assumed one or more missed nesting events had occurred and divided by the mean inter-clutch interval (14 days) to derive an ECF (Frazer and Richardson, 1985). In practice, the high recapture probabilities afforded by VHF tags meant that in cases where nesting events were missed, this equated to only 1 (intervals of 22–32 days; $n = 10$) or at most 2 missed clutches (intervals of 33–44 days; $n = 5$).

As VHF-telemetry relies on directly observing females and was found to be ineffective at distances >1 km, there is the possibility that VHF-tagged females laid additional clutches after their last observed nesting event (indeed this was confirmed by Fastloc™ GPS data; see Section 3). To account for this, we followed Rivalan et al. (2006) and applied a local survival analysis to estimate the mean 'total clutch frequency' (TCF) of VHF-tagged turtles, including clutches deposited after the last sighting. Unlike ECF, which essentially 'fills in the gaps' between observed clutches, TCF is based on statistical extrapolation from individual encounter histories to estimate the time spent before the first capture (not necessary in our study; see above) and after the last capture, as well as the re-sighting probability (Rivalan et al., 2006). Encounter histories for VHF-tagged turtles were analyzed using a Cormack–Jolly–Seber (CJS) model in Program MARK v6.1 to select the most parsimonious local survival (φ) and re-encounter probability (p) model for the data. Model selection used the Akaike's Information Criterion corrected for small samples size (AICc) from a model set that included all combinations of time-dependence and constancy for φ and p (White and Burnham, 1999). Unlike Rivalan et al. (2006), we did not include a parameter for transient individuals as all turtles were found to nest more than once within the study area. The model with the lowest AICc score was then specified in SODA software (Schaub et al., 2001) to estimate TCF (see Rivalan et al., 2006 for further details), and confidence intervals were obtained using non-parametric boot-strapping (500 iterations) on individual encounter histories (Schaub et al., 2001).

2.3. Satellite telemetry

The Argos-linked Fastloc™ GPS tags used in this study are capable of recording and transmitting both Argos and GPS-quality positional data. Fastloc™ GPS geolocation differs from traditional GPS positioning in that much of the computational demand needed to derive a position occurs at a later point in time and hence the time required to acquire a position can be achieved in several milliseconds. This makes the technology useful in marine systems where animals that surface to breathe may only spend short times at the surface (e.g. Hazel, 2009; Witt et al., 2010; Costa et al., 2010; Schofield et al., 2010). The devices were also programmed to record periods of prolonged dryness (i.e. when an instrumented turtle was hauled out on the nesting beach for 20 consecutive minutes or more). For each haul out event, the total duration was recorded and up to 4 GPS "snap shots" were acquired at 2 min intervals starting on the turn of each hour. These data were stored onboard the tag for up to 7 days from acquisition and subsequently transmitted via the Argos System. Where Fastloc™ GPS-data suggested haul outs occurred over several consecutive nights, those activities occurring on the final night were assumed to have been associated with a successful nesting event, with the previous attempts failing for any one of a number of reasons that include disturbance to the female and the inability to find a suitable nesting site.

3. Results

VHF-tagged females had a mean observed clutch frequency of 5.1 ± 0.3 clutches per female (range = 2–8) and a mean estimated clutch frequency of 5.9 ± 0.2 clutches female^{-1} (range = 2–8); considerably higher than the previous estimate of 3 clutches female^{-1} obtained from an earlier flipper tagging study (Mortimer and Carr, 1987; Fig. 1). All VHF-tagged females nested multiple times within a season and clutch frequency data fit an approximately normal distribution, which contrasts with the significant number of single-nesting females and heavily right-skewed distribution suggested by flipper tagging (Fig. 1).

Of the 11 observed clutches laid by turtles carrying both VHF and GPS tags, 10 (91%) were successfully resolved by Fastloc™ GPS tags, with a high degree of temporal and spatial correlation between observed nesting events and those inferred from GPS data (Fig. 2). Indeed, mean geographic distance between Fastloc™ GPS positions associated with putative nesting events and actual clutch locations observed using radio-telemetry was just 48.8 ± 41.9 m ($n = 11$ clutches from $n = 3$ turtles; range: 19.3–171.5 m), falling to 36.6 ± 10.5 m (19.3–53.2 m) if a single clutch where the turtle crawled a significant distance before nesting was excluded (Fig. 2, Clutch 8). In contrast, Argos locations used to estimate clutch frequency previously (Tucker, 2010) were unable to definitively resolve individual nesting events in this population as the spatial order of movements was well within the spatial extents of Argos variance (see Supplementary material). Based on Fastloc™ GPS data, satellite-tagged turtles laid an average of 6.3 ± 0.9 clutches female^{-1}, with significant variation in nesting behavior among individuals. Female 1 deposited 8 clutches on Long Beach (the tag attachment site), all of which were verified by radio-telemetry (Figs. 2 and 3a). In contrast, females 2 and 3 both made

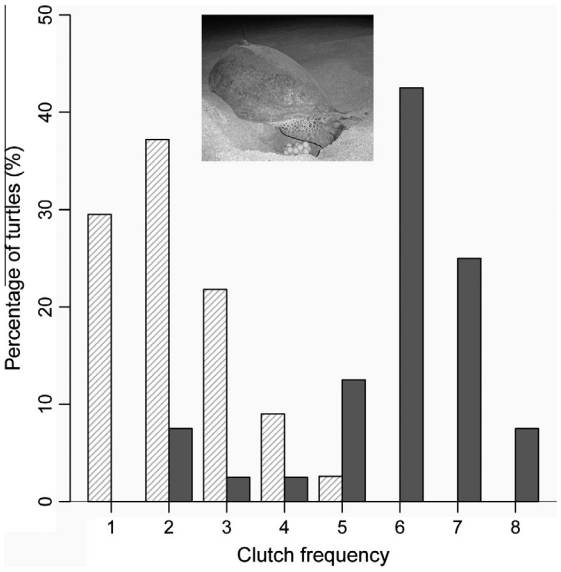

Fig. 1. Clutch frequency values for Ascension Island green turtles. Striped columns are OCF values from a flipper-tagging CMR study by Mortimer and Carr (1987); solid columns are ECF values obtained using radio-telemetry in this study. Inset: photograph of green turtle with VHF-transmitter laying eggs.

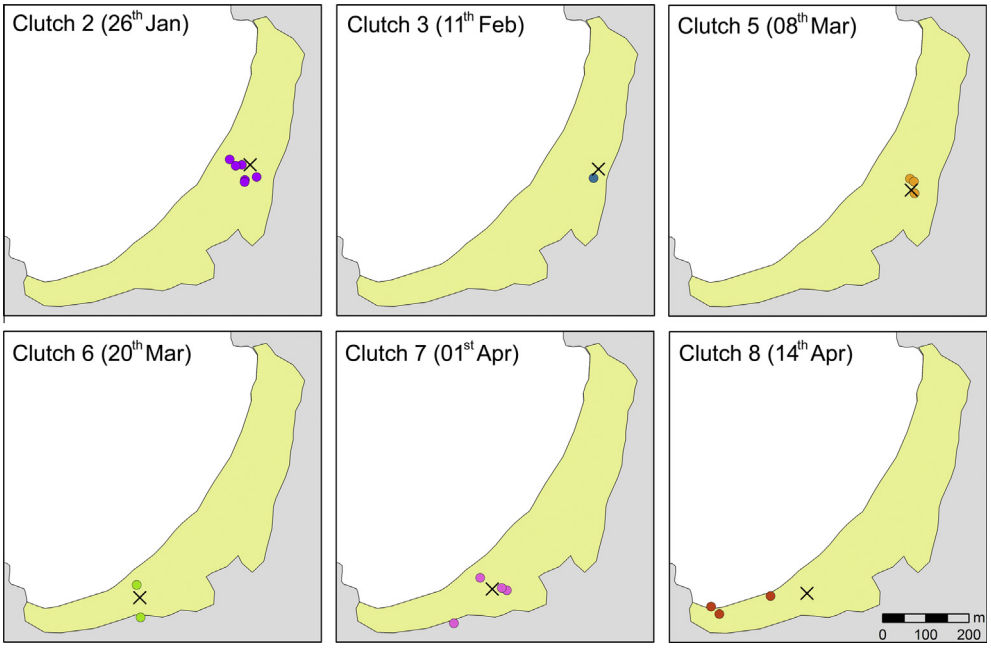

Fig. 2. Comparison of observed nest locations recorded by hand held GPS (crosses) and Fastloc™ GPS positions acquired during the detected haul out event (colored circles) for six clutches of the same female green turtle. GPS data for clutch 1 (tag attachment) and clutch 4 (not detected) are not available (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

excursions from Long Beach that were not detected by radio-telemetry (Fig. 3b and c). After laying her first four clutches on Long Beach, female 2 laid a fifth at beach approximately 1 km to the south (Deadman's Beach; Fig. 3b). Female 3 nested only twice on Long Beach with her final 4 clutches distributed among several beaches along the west coast of the island (Fig. 3c). Similar behavior may explain the small peak in VHF-tagged females observed nesting only twice during surveys of Long Beach (Fig. 1). Thus, of

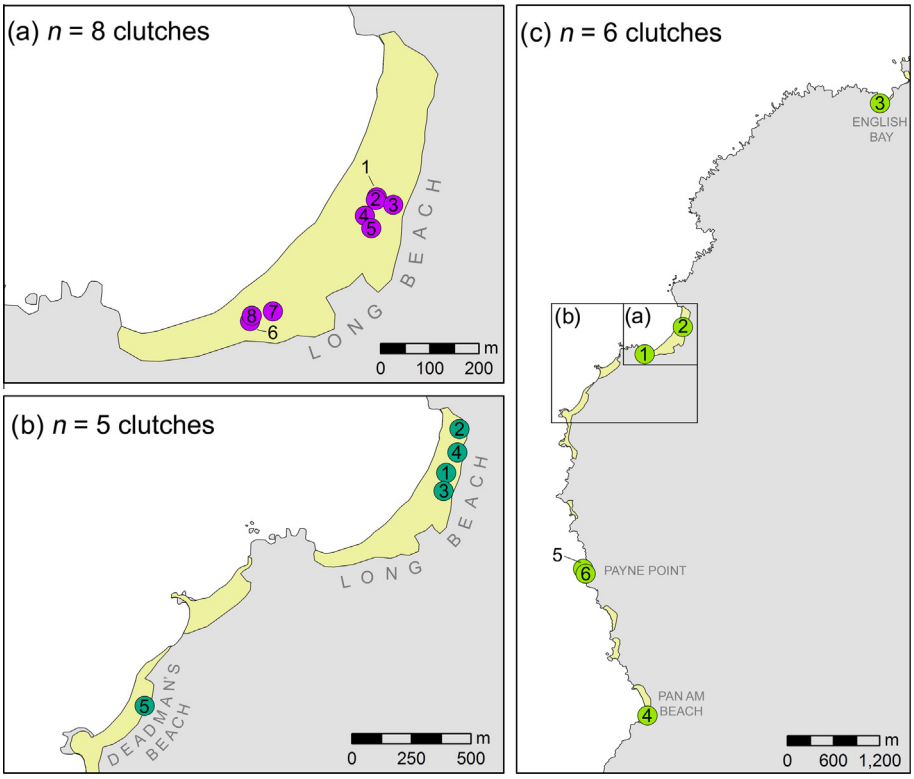

Fig. 3. Clutch frequencies and nest locations for 3 female green turtles fitted with Fastloc™ GPS tags. Nests on Long Beach (a and b) are observed locations (GPS quality), where turtles were initially identified from radio-telemetry, whereas those on other beaches are located at the geographic mean centre of GPS positions associated with putative nesting events (see Fig. 2). Numbering indicates the chronological order of clutches (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

19 clutches laid by GPS-tagged turtles, 14 (74%) were deposited on Long Beach and detected by radio-telemetry.

For estimating TCF, the most parsimonious CJS model describing the data (Akaike weight = 0.98) had a constant recapture probability of $p = 0.85$ (95% CI: 0.79–0.90), and a time-dependent local survival probability. Specifying this model in SODA yielded an estimated mean TCF of 6.3 clutches female^{-1} (95% CI: 6.2–6.4), identical to that obtained for GPS-tagged females. If this revised value is applied to annual nesting data collected at Ascension Island between 1999 and 2012 (Godley et al., 2001; Broderick et al., 2006; authors unpublished data) in place of the previous clutch frequency estimate of 3 (Mortimer and Carr, 1987), the estimated number of female green turtles breeding annually at Ascension Island is reduced from 1580–8400 to 740–4015, an effective reduction in population size of over 52%.

4. Discussion

Clutch frequency is considered to be one of the most important demographic parameters in marine turtle biology because of its relevance to population models and abundance estimation (National Research Council, 2010). In some smaller, low-density populations where saturation tagging and high survey coverage is possible, conventional mark-recapture approaches may yield robust clutch frequency estimates (e.g. Broderick et al., 2002). However, the results of our reassessment of clutch frequency for the South Atlantic's largest green turtle rookery show that such approaches may significantly underestimate the annual fecundity of marine turtles at larger rookeries, resulting in inflated population size estimates. Both satellite-telemetry and radio-telemetry (after statistical correction) yielded identical mean clutch frequency estimates of 6.3 clutches female^{-1}, more than doubling the estimate of 3 obtained by an earlier flipper tagging study (Mortimer and Carr, 1987; Figs. 1 and 3). When applied to long-term nest monitoring data (Godley et al., 2001; Broderick et al., 2006) this revised value more than halves the number of females thought to nest annually at Ascension Island, and thus has significant implications for regional green turtle stock assessments.

Caution is required when extrapolating clutch frequency assessments from a single nesting season across years as fecundity in marine turtles is known to vary inter-annually (Frazer and Richardson, 1985; Broderick et al., 2003; National Research Council, 2010), and as a function of female body size and age in some populations (e.g. Hawkes et al., 2005; but not others e.g. Broderick et al., 2003). In this case, however, the magnitude of the difference suggests that our revised assessment is unlikely to be an anomaly caused by an unusually productive year. Ascension Island is also experiencing a long-term reduction in the average size of nesting turtles linked to rapid population growth (authors' unpublished data), so the higher clutch frequency we report compared to earlier flipper-tagging studies (Mortimer and Carr, 1987) is in the opposite direction than might be expected from demographic trends. Indeed, our results are consistent with the few other studies to have reassessed fecundity in marine turtles using alternative technologies and statistical approaches where clutch frequency was found to be approximately double that estimated by conventional tagging alone (Rees et al., 2008; Tucker, 2010; Blanco et al., 2011). Taken together, these studies suggest that marine turtle population sizes may have been frequently over-estimated by standard mark-recapture protocols, calling for the widespread adoption of alternative methods.

Currently, satellite- and radio-telemetry remain the most practical methods for reliably estimating clutch frequency in marine turtle populations, with the major trade-off being one of sample size and cost vs. labor intensity (this study; National Research Council, 2010). Satellite telemetry has long been discussed as a potential tool for passively assessing clutch frequency in marine turtles (e.g. Hays, 1992), but until recently the spatial resolution offered by these devices has limited their use (National Research Council, 2010). Indeed, the Argos system used by Tucker (2010) to estimate clutch frequency in loggerhead turtles in our case was unable to confidently resolve individual nesting events for Ascension Island green turtles. This is likely to be because the area where they reside between nesting events is so close to the nesting beach that the locations cannot confidently be teased apart as being either indicative of nesting or indicative of resting during inter-nesting periods (i.e. the spatial order of movements was within the spatial error of Argos positions; Supplementary material). As shown here, with the advent of high-precision GPS platforms these constraints have now largely been removed. Putative nesting events inferred from Fastloc™ GPS tags showed exceptional spatial and temporal correlation with observed clutch locations from radio-telemetry (Fig. 2), and offer a powerful tool for studying the nesting behavior and annual fecundity of individual females (Fig. 3). However, the high cost of Argos-linked GPS devices currently limits their widespread use and the sample sizes that can typically be achieved.

In this regard, low-cost VHF transmitters offer a more affordable alternative for assessing clutch frequency in a large number of individuals, but have been used little for this purpose. Although this method is considerably more labor intensive than satellite telemetry, it is no more so than routine beach patrols to locate conventionally tagged turtles on beaches where saturation tagging is possible, and greatly increases recapture probabilities. This is particularly true of large populations such as that at Ascension Island where there may be several hundred turtles per night on the main study beach during peak nesting (authors, unpublished data). Assuming that observer effort is consistent across the season, the probability of relocating a tagged turtle depositing a given clutch is the product of two different probabilities: (1) the probability that the turtle is available to be re-sighted in the study area rather than nesting elsewhere, and (2) the probability that, conditional on being available, the turtle is actually re-sighted. Our finding that radio-telemetry carried out on a single, focal beach doubled previous clutch frequency estimates suggests that missed nesting of available females may often be the largest source of error in studies of this type, particularly at large, high-density nesting beaches. Unlike satellite-telemetry, however, radio-telemetry is unable to account for errors in clutch frequency arising from nesting events that occur away from the survey site (Fig. 3). Capture-mark-recapture analyses can help to correct for such errors (this study; Rivalan et al., 2006), but confidence in the estimates produced still relies heavily on the detection rates achieved. Thus, radio-telemetry is likely to be most useful in species and populations that are spatially constrained and/or where females show a high level of site fidelity. As demonstrated in this study, the complementary use of both radio- and satellite-telemetry with cross-validation between methods may provide one practical solution for simultaneously achieving accurate clutch frequency estimates and large sample sizes. Handheld Argos PTT locators with the same accuracy as radio telemetry are also a promising new tool and offer an affordable middle ground for combining improved clutch frequency estimation with remote tracking capabilities.

As many marine turtle populations are of conservation concern, their population trends and abundance are closely monitored. Although the results of this study do not alter the long-term trends reported for many populations, they do call for an urgent reassessment of baseline abundance values for regionally important populations. For example, of the 34 index sites used in the *IUCN Red List* assessment of the green turtle (Seminoff, 2004), only 17 (50%) have a published clutch frequency value, all of which (with the

exception of the Ascension Island population) were derived from conventional tagging (see Supplementary material). Even allowing for some inter-population variation in fecundity, the mean clutch frequency of 3.5 clutches female^{-1} (range = 1.5–5; see Supplementary material) for these populations is considerably lower than our revised assessment for the Ascension Island rookery, suggesting that many are likely to be underestimates. The heavily right-skewed clutch frequency distributions reported for many of these populations also tend to support this view (e.g. Johnson and Ehrhart, 1996; Tomás et al., 2010), as in reassessments using radio- and satellite-telemetry clutch frequency has been found to be approximately normally distributed (this study, Fig. 1; Tucker, 2010). If clutch frequency has indeed been consistently underestimated by conventional tagging methodology, many marine stocks are likely to be considerably smaller than is currently thought. The higher than expected annual fecundity of individual breeding females may also help to explain why marine turtle stocks are so vulnerable to factors that reduce the survival of this demographic group (Broderick et al., 2006); and, conversely, why populations are able to recover surprisingly quickly when these threats are addressed (e.g. Balazs and Chaloupka, 2004). As this study and other recent work has shown (Tucker, 2010; Blanco et al., 2011), the technology necessary to obtain more reliable estimates of female fecundity and abundance for marine turtles is now readily available where investment is possible. However, cheaper methods that can be rapidly applied across all major nesting populations are still needed.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.07.030.

References

Balazs, G.H., Chaloupka, M., 2004. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. Biol. Conserv. 117, 491–498.
Balme, G.A., Hunter, L.T.B., Slotow, R., 2010. Evaluating methods for counting cryptic carnivores. J. Wildlife Manage. 73, 433–441.
Bjorndal, K.A., Wetherall, J.A., Bolten, A.B., Mortimer, J.A., 1999. Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: an encouraging trend. Conserv. Biol. 13, 126–134.
Blanco, G.S., Morreale, S.J., Vélez, E., Piedra, R., Montes, W.M., Paladino, F.V., Spotila, J.R., 2011. Reproductive output and ultrasonography of an endangered population of East Pacific green turtles. J. Wildlife Manage. 76, 841–846.
Briane, J.-P., Rivalan, P., Girondot, M., 2007. The inverse problem applied to the observed clutch frequency of leatherback turtles from Yalimapo Beach, French Guiana. Chelonian Conserv. Biol. 6, 63–69.
Broderick, A.C., Glen, F., Godley, B.J., Hays, G.C., 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. Oryx 36, 227–235.
Broderick, A.C., Glen, F., Godley, B.J., Hays, G.C., 2003. Variation in reproductive output of marine turtles. J. Exp. Mar. Biol. Ecol. 288, 95–109.
Broderick, A.C., Frauenstein, R., Glen, F., Hays, G.C., Jackson, A.L., Pelembe, T., Ruxton, G.D., Godley, B.J., 2006. Are green turtles globally endangered? Glob. Ecol. Biogeog. 15, 21–26.
Costa, D.P., Robinson, P.W., Arnould, J.P.Y., Harrison, A.-L., Simmons, S.E., Hassrick, J.L., Hoskins, A.J., Kirkman, S.P., Oosthuizen, H., Villegas-Amtmann, S., Crocker, D.E., 2010. Accuracy of ARGOS locations of Pinnipeds at-Sea estimated using Fastloc GPS. PLoS One 5, e8677.
Dethmers, K.E.M., Baxter, P.W.J., 2011. Extinction risk analysis of exploited green turtle stocks in the Indo-Pacific. Anim. Conserv. 14, 140–150.
Flather, C.H., Hayward, G.D., Bessinger, S.R., Stephens, P.A., 2011. Minimum viable populations: is there a 'magic number' for conservation practitioners? Trends Ecol Evol. 26, 307–316.
Frazer, N.B., Richardson, J.I., 1985. Annual variation in clutch size and frequency for loggerhead turtles, *Caretta caretta*, nesting at Little Cumberland Island, Georgia, USA. Herpetologica 41, 246–251.
Garrote, G., Perez de Ayala, R., Pereira, P., 2011. Estimation of the Iberian lynx (*Lynx pardinus*) population in the Doñana area, SW Spain, using capture-recapture analysis of camera-trapping data. Eur. J. Wildlife Res. 57, 355–362.
Gerrodette, T., Taylor, B.L., 1999. Estimating population size. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group, Publication No. 4.
Girondot, M., Godfrey, M.H., Ponge, L., Rivalan, P., 2007. Modelling approaches to quantify Leatherback nesting trends in French Guiana and Suriname. Chelonian Conserv. Biol. 6, 37–46.
Godley, B.J., Broderick, A.C., Hays, G.C., 2001. Nesting of green turtles (*Chelonia mydas*) at Ascension Island, South Atlantic. Biol. Conserv. 97, 151–158.
Hare, M.P., Nunney, L., Schwartz, M.K., Ruzzante, D.E., Burford, M., Waples, R.S., Ruegg, K., Palstra, F., 2011. Understanding and estimating effective population size for practical application in marine species management. Conserv. Biol. 25, 438–449.
Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2005. Status of nesting loggerhead turtles *Caretta caretta* at Bald Head Island (North Carolina, USA) after 24 years of intensive monitoring and conservation. Oryx 39, 65–72.
Hays, G.C., 1992. Assessing the nesting beach fidelity and clutch frequency for sea turtles by satellite tracking. In: Priede, I.G., Swift, S.M. (Eds.), Wildlife Telemetry: Remote Monitoring and Tracking of Animals. Ellis Horwood, New York, pp. 203–213.
Hazel, J., 2009. Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. J. Exp. Mar. Biol. Ecol. 374, 58–68.
Johnson, S.A., Ehrhart, L.M., 1996. Reproductive ecology of the Florida green turtle: clutch frequency. J. Herpetol. 30, 407–410.
Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C., Taberlet, P., 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* populations. Wildlife Biol. 17, 114–123.
McClenachan, L., Jackson, J.B.C., Newman, M.J.H., 2006. Conservation implications of historic sea turtle nesting beach loss. Front. Ecol. Evol. 4, 290–296.
Miller, J.D., 1997. Reproduction in sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 51–81.
Mortimer, J.A., Carr, A., 1987. Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). Copeia 1, 103–113.
National Research Council; Committee on Sea Turtle Population Methods, 2010. Assessment of sea-turtle status and trends: integrating demography and abundance. The National Academies Press, Washington, USA.
Rees, A.F., Saadi, S.A., Coyne, M.S., Godley, B.J., 2008. Internesting habitat and nest frequency at a globally significant loggerhead nesting population described using Argos tracking. NOAA Tech Mem. NMFS-SEFSC-569, pp. 55.
Rivalan, P., Pradel, R., Choquet, R., Girondot, M., Prévot-Julliard, A.C., 2006. Estimating clutch frequency in the sea turtle *Dermochelys coriacea* using stopover duration. Mar. Ecol. Prog. Ser. 317, 285–295.
Schaub, M., Pradel, R., Jenni, L., Lebreton, J.D., 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. Ecology 82, 852–859.
Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2010. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers. Distrib. 16, 840–853.
Schroeder, B.A., Foley, A.M., Bagley, D.A., 2003. Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Books, Washington, DC, pp. 114–124.
Seminoff, J.A., 2004. IUCN Red List Global Status Assessment: Green turtle (*Chelonia mydas*).
Tomás, J., Godley, B.J., Castroviejo, J., Raga, J.A., 2010. Bioko: critically important nesting habitat for sea turtles of West Africa. Biodivers. Conserv. 19, 2699–2714.
Tomillo, P.S., Saba, V.S., Piedra, R., Paladino, F.V., Spotila, J.R., 2008. Effects of illegal harvest of eggs on the population decline of leatherback turtles in Las Baulas Marine National Park, Costa Rica. Conserv. Biol. 22, 1216–1224.
Tucker, A.D., 2010. Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock assessment. J. Exp. Mar. Biol. Ecol. 383, 48–55.
Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., et al., 2011. Global conservation priorities for marine turtles. PLoS One 6, e24510.
Weber, S.B., Blount, J.D., Godley, B.J., Witt, M.J., Broderick, A.C., 2011. Rate of egg maturation in marine turtles exhibits 'universal temperature dependence'. J. Anim. Ecol. 80, 1034–1041.
White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement), 120–138.
Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press, San Diego.

Witherington, B., Kubilis, P., Brost, B., Meylan, A., 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. Ecol. Appl. 19, 30–54.
Witt, M.J., Baert, B., Broderick, A.C., Formia, A., Fretey, J., et al., 2009. Aerial surveying of the world's largest leatherback turtle rookery: a more effective methodology for large-scale monitoring. Biol. Conserv. 142, 1719–1727.
Witt, M.J., Åkesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S., Godley, B.J., 2010. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim. Behav. 80, 571–581.