

# Using community-based monitoring to estimate demographic parameters for a remote nesting population of the Critically Endangered leatherback turtle

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**ABSTRACT:** Leatherback turtles are exposed to many anthropogenic hazards in the Pacific, but too little is known about their demography to reliably estimate abundance and develop hazard mitigation strategies. Most populations nest in remote locations, and leatherbacks do not generally breed annually, which results in biased demographic parameter estimates using traditional capture-mark-recapture (CMR) analysis. We estimated survival and breeding probabilities for a remote nesting population using a long-term community-based CMR study coupled with a multistate open robust design (MSORD) statistical modelling approach. This approach accounts for skipped breeding behaviour and the staggered seasonal arrival and departure of the nesters. The study comprised CMR histories for 178 nesting leatherbacks tagged at Lababia beach on the Huon Coast of Papua New Guinea over a 3 mo seasonal sampling period for 10 austral summer nesting seasons (2000–2009). The best-fit MSORD model comprised constant adult survival (accounting for transients), constant conditional breeding and time-dependent arrival, departure and detection probabilities. The annual survival probability was constant over the 10 yr at ca. 0.85, which is lower than estimated for other leatherback populations but likely reflects a lower probability of nest beach fidelity that has been inferred previously using satellite telemetry. The annual breeding probability for female leatherbacks that skipped the previous nesting season was 0.41. The probability of breeding in consecutive seasons was 0.06, indicative of a skipped breeding behaviour. These first estimates of annual survival and breeding probabilities for a Pacific leatherback stock provide a basis for developing an understanding of regional population dynamics and assessing risk of exposure to anthropogenic hazards such as coastal development and fisheries.

**KEY WORDS:** Leatherback turtle · *Dermochelys coriacea* · Community-based monitoring · Papua New Guinea · Population demography · Breeding probability · Survival

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## INTRODUCTION

The leatherback turtle *Dermochelys coriacea* is classified by IUCN as Critically Endangered, with many nesting populations in the Pacific in significant long-term decline (Spotila et al. 2000), although in the Atlantic some populations appear to be recovering (Dutton et al. 2005, Stewart et al. 2011, but see

Troëng et al. 2007). Population declines are attributed to egg poaching, predation of eggs by feral animals, coastal development and incidental capture in coastal or pelagic fisheries (Chan & Liew 1996, Lewison et al. 2004, Alfaro-Shigueto et al. 2007, Hitipeuw et al. 2007). However, diagnosing and modelling marine turtle abundance trends is difficult without information on demographic parameters such as

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survival, breeding and recruitment probabilities (National Research Council 2010). Demographic information derived from long-term in-water capture-mark-recapture (CMR) studies has been steadily accumulating over recent years for some marine turtle species such as loggerhead and green turtles in the Pacific (Chaloupka & Limpus 2002, 2005), but little is known of leatherback population demography (Dutton et al. 2005, Rivalan et al. 2005), especially in the western Pacific (Gaspar et al. 2012).

Establishing a long-term demographic study of leatherbacks faces at least 2 major challenges. The first challenge is ensuring sufficiently high encounter probabilities. Leatherbacks live in dispersed oceanic habitats (Wallace et al. 2006), with many Pacific populations nesting at remote beach locations (Spotila et al. 1996, Benson et al. 2007). Aerial and beach surveys have shown that the most significant leatherback nesting in the western Pacific occurs along the remote north coast of New Guinea (Dutton et al. 2007), especially in the northwest of West Papua, Indonesia (Hitipeuw et al. 2007) and along the Huon Coast of Papua New Guinea (Benson et al. 2007). Overcoming substantial logistical challenges, the Western Pacific Regional Fisheries Management Council and US National Marine Fisheries Service have supported several local community-based leatherback conservation and monitoring programmes on the Huon Coast since 2000 (Kinch 2006). One of these sites, the Kamiali Wildlife Management Area (WMA), was declared in 1996 to protect leatherback turtles that nest near the village of Lababia, which was considered one of the most important nesting areas on the Huon Coast (Benson et al. 2007). Local villagers have been employed since 1999 to monitor leatherback nesting at the Lababia beach over each austral summer season and to tag nesters encountered during nightly beach patrols as part of a community-based conservation and data collection programme (Kinch 2006), and this data set has enabled the current demographic analysis.

Secondly, because leatherbacks, like other marine turtles, do not generally breed annually due to the high energy demands of vitellogenesis and long-distance breeding migration (Miller 1997), there is a need for a modelling approach which accounts for the temporary emigration, which can lead to biased demographic parameter estimates derived when using a nesting population-based CMR study (Kendall & Bjorkland 2001). An open robust sampling design (ORD) modelling approach for CMR studies explicitly accounts for this temporary emigration due to skipped breeding behaviour (Schwarz & Stobo

1997, Kendall & Bjorkland 2001), and this approach has been used to derive survival and breeding probability estimates for hawksbill (Kendall & Bjorkland 2001), leatherback (Dutton et al. 2005) and green turtles (Troëng & Chaloupka 2007). Kendall (2004) developed a more comprehensive statistical modelling approach fitting the same ORD models for CMR studies but within a multistate modelling framework (Schaub et al. 2004). This multistate open robust design (MSORD) approach has been used more recently to model the demography of endangered marine species that skip annual breeding opportunities, such as albatrosses (Converse et al. 2009), whale sharks (Holmberg et al. 2009) and hawksbill sea turtles (Prince & Chaloupka 2012).

Another challenge for CMR nesting beach-based demographic studies is a requirement for an ongoing and sufficiently saturated level of monitoring to ensure high capture and recapture probabilities with a modelling approach to account for missed nesting events. The present analysis is based on continued daily monitoring of the beach at Lababia during 10 nesting seasons. This near-saturation monitoring provides us with the first long-term community-based data set for western Pacific leatherbacks upon which to determine population demographic parameters.

We estimated survival and breeding probabilities for a Pacific leatherback nesting population using the Lababia community-based CMR data coupled with the MSORD modelling approach. The community-based sampling programme enabled us to access an important but remote leatherback nesting beach in northeast Papua New Guinea, while the MSORD modelling approach enabled us to account for skipped breeding behaviour and staggered seasonal arrival and departure of the nesters. The demographic parameter estimates derived from this community-based CMR study will provide the basis for developing better insight into the regional population dynamics for this Critically Endangered marine species, and demonstrate the value of using community-gathered data to support robust statistical modelling.

## MATERIALS AND METHODS

### Study area and data set

The village of Lababia is located within the Kamiali WMA on the Huon Coast of Morobe Province in northeast Papua New Guinea (Fig. 1). Lababia is sited at the southern end of a 7 km sandy beach that

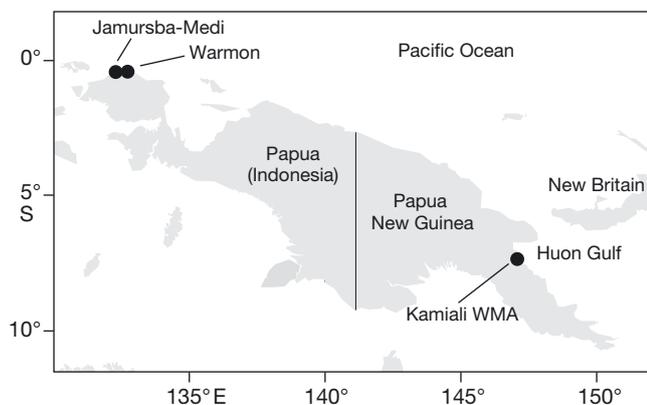


Fig. 1. Location of the community-based capture-mark-recapture study site at Lababia village in the Kamiali Wildlife Management Area (WMA) on the Huon Coast of northeast Papua New Guinea. The major leatherback nesting beaches at Jamursba-Medi and Warmon in Papua (Indonesia) are also shown

is one of the main leatherback nesting sites along the Huon Coast (Benson et al. 2007). Leatherback nesting at Lababia occurs mainly in the dry season (October to March). The beach is subject to tidal inundation and erosion during the wet season (Kinch 2006). Nightly beach patrols comprising 3 local community rangers were conducted each nesting season over a 3 mo period (ca. mid-November to mid-February) along the Lababia beach. Accurate data exist for beach monitoring activity for 2002 to 2009, during which an average of 3 to 4 d were missed due to weather, presence of crocodiles or other factors. Unfortunately, metadata on daily activity prior to this are not available. Patrols started at 18:00 h and continued until 06:00 h or until no further nesting was evident. Every leatherback encountered was tagged and any nesting activity recorded. Turtles were tagged at first encounter using Monel flipper tags (National Brand & Tag Company) prior to 2004 and thereafter with shoulder-inserted passive integrated transponder (PIT) tags (see Dutton et al. 2005 for details of PIT tags). Turtles flipper-tagged in earlier years were PIT-tagged when resighted in later years. We do not explicitly account here for tag loss, but turtles in earlier years were all retagged with PIT tags as they were encountered, and have been subsequently resighted on numerous occasions, with several PIT-tagged turtles retaining Monel flipper tags to this day. Data were recorded on field data sheets and passed weekly to a coordinator for review. All data were maintained in the Turtle Research and Monitoring Database System (TREDS), a joint initiative of the Western Pacific Regional Fisheries Management

Council and Secretariat of the Pacific Regional Environment Programme to coordinate marine turtle monitoring efforts in the western Pacific region (Trevor 2010). TREDS allowed us to identify individual histories for each turtle through time. Kinch (2006) provided a thorough overview of this local community-based monitoring effort along the Huon Coast. The data set we used comprised the CMR histories for all nesting female leatherbacks tagged over 10 austral summer nesting seasons (2000/2001 to 2009/2010).

### Statistical modelling approach

We compiled CMR histories for 178 nesting leatherbacks tagged at Lababia over the 10 yr sampling period. The primary sampling occasions consist of the 10 annual nesting seasons with 6 approximately fortnightly secondary sampling occasions within each primary occasion (~60 sampling occasions); this primary and secondary sampling structure comprises an open robust CMR sampling design. The 2 wk secondary periods within each season approximate the 14.1 d intra-seasonal nesting cycle of leatherbacks at Lababia (Kisokau 2005), allowing the staggered arrival and departure of nesting turtles during each season to be explicitly accounted for (Kendall & Bjorkland 2001). We then used the MSORD statistical modelling approach where nesting probabilities are conditional on previous nesting (or are state dependent) to estimate key demographic parameters (Kendall 2004, Converse et al. 2009). The 2 states in our multistate framework were the nesters (observed and available for capture) and the nonbreeder state for those female leatherbacks that skipped nesting in a particular season. The MSORD approach assumes that nester and nonbreeder (unobserved) states have the same survival probability (Converse et al. 2009), and there is no reason to assume that nesters were at any greater risk of mortality than nonbreeders for this stock, given the lack of nearshore fisheries and beach mortality at Lababia. The arrival, departure and detection parameters for the nonbreeder state were fixed to 0 since they were not available for capture (see Converse et al. 2009). Goodness-of-fit and assumptions for the model mirrored those used by Prince & Chaloupka (2012). In particular, Cormack-Jolly-Seber (CJS) model assumptions such as transience (seen once and never again) and capture heterogeneity (known as trap-dependence) were evaluated using the program U-CARE (Choquet et al. 2009), while CJS goodness-of-fit was assessed

using U-CARE and the median  $c$ -hat approach implemented in the program MARK (White et al. 2006). If there was evidence of transience, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure (separate survival probability estimates for the newly and previously tagged nesters) as per Prince & Chaloupka (2012). See Chaloupka & Limpus (2002) for more details on time-since-marking CJS models for sea turtles, while the application of the MSORD framework for marine turtles can be found in Prince & Chaloupka (2012).

## RESULTS

### Exploring goodness-of-fit

Our data set consisted of 408 total encounters, in which 178 individual leatherbacks were identified, along with 164 within-season recaptures and 66 inter-season returns of the same animals. Of the 178 turtles, 86 had been tagged with Monel tags and 92 with PIT tags. A subset of 26 of the Monel tagged animals were re-encountered in later years, at which point they also were tagged with PIT tags. By 2010, only 2 recaptured turtles still carried Monel tags while all others carried PIT tags. Given the nature of the data collection programme, tag scars were not recorded, so we have no way of identifying previously tagged turtles which lost tags.

We assessed the time-dependent CJS model assumptions using variants of TESTS 2 and 3 in U-CARE (Choquet et al. 2009) as per Prince & Chaloupka (2012), which indicated failure of 2.CT (N statistic for trap-dependence/capture heterogeneity = 2.28,  $p = 0.022$ ). Differences with the hawksbill study by Prince & Chaloupka (2012) were in the Test 3.SR results, which was found adequate with some suggestion of transient behaviour (individuals just passing through the study area and never seen again) evident (N statistic for transience = 1.18,  $p = 0.12$ ). The CJS model goodness-of-fit assessment sug-

gests that our MSORD modelling approach accounting for temporary emigration (due to skipped breeding) and transient behaviour was appropriate.

### MSORD model summary

Only a limited range of MSORD models could be applied due to the sparse data set, which especially restricted the use of fully time-dependent models. The most general model we could fit comprised ageclass-specific survival and time-dependent breeding state transition, arrival, departure and detection probabilities (Model 8, Table 1), but many transition probabilities were inestimable. Models imposing a more restricted structure on parameters such as the probability of remaining in the area were included to explore if length of time since arrival that season (so-called time-since-marking) was apparent (Model 4, Table 1). The most parsimonious MSORD model fitted to the 178 CMR histories selected using QAICc (see Anderson et al. 1998) comprised (1) constant 2-ageclass-specific (time-since-marking) survival, (2) constant

Table 1. *Dermochelys coriacea*. Summary of 10 MSORD model fits to capture-mark-recapture histories for 178 leatherbacks that nested over a 10 yr period at Lababia (Huon Coast, Papua New Guinea). Model descriptions follow similar notation by Kendall & Bjorkland (2001) appropriate for the MSORD approach (Kendall 2004). QAICc: sample size and overdispersion-corrected Akaike Information Criterion based on assessment of a previous primary-sessions-only CJS model fit;  $\Delta$ QAICc: difference between each model and the best-fit model 1; QAICc weight: weight of evidence in support of a particular model given the data;  $\phi^*_{a2}(\cdot)$ : constant ( $\cdot$ ) 2-ageclass-specific (time-since-marking) annual survival probabilities;  $\phi^*(\cdot)$ : constant annual survival probability;  $\psi(\cdot)$ : annual breeding transition probabilities = constant transition probability from the nester state in year<sub>*t*</sub> to skipped nesting state in year<sub>*t+1*</sub> ( $\psi^{BN}$ ), from Breeder to Non-breeder state, and constant transition from skipped nester state in year<sub>*t*</sub> to nester in year<sub>*t+1*</sub> ( $\psi^{NB}$ ), from Non-breeder to Breeder state; *pent*: probability of arrival in study area;  $\phi$ : probability of remaining in study area ( $1 - \phi$  = probability of departure); *p*: probability of detection in study area; *pent*(*tt*) or  $\phi$ (*tt*) or *p*(*tt*): time-specific within- and between-season probabilities; *pent*( $\cdot$ ) or  $\phi$ ( $\cdot$ ) or *p*( $\cdot$ ): constant within- and between-season probabilities;  $\phi$ (*tsm*): time-since-marking within season but constant between-season probability of remaining in the study area

Model no.	Description	QAICc			
		QAICc	$\Delta$ QAICc	Weight	Deviance
1	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(t), \phi(tt), p(tt)$	908.907	0.00	0.907	861.145
2	$\phi^*_{a2}(\cdot), \psi(t), pent(t), \phi(tt), p(tt)$	913.659	4.75	0.084	851.484
3	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(\cdot), \phi(tt), p(tt)$	918.643	9.74	0.007	863.756
4	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(\cdot), \phi(tsm), p(tt)$	922.734	13.83	0.000	865.436
5	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(t), \phi(tt), p(tt)$	926.424	17.52	0.000	861.782
6	$\phi^*(\cdot), \psi(\cdot), pent(t), \phi(tt), p(tt)$	927.965	19.06	0.000	865.790
7	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(\cdot), \phi(\cdot), p(tt)$	928.687	19.78	0.000	873.800
8	$\phi^*_{a2}(\cdot), \psi(tt), pent(tt), \phi(tt), p(tt)$	936.251	27.34	0.000	837.745
9	$\phi^*_{a2}(\cdot), \psi(\cdot), pent(\cdot), \phi(\cdot), p(\cdot)$	1141.325	232.42	0.000	1126.930
10	$\phi^*(\cdot), \psi(\cdot), pent(\cdot), \phi(\cdot), p(\cdot)$	1148.268	239.36	0.000	1135.973

conditional breeding state transition, (3) constant intra-seasonal but time-dependent inter-seasonal arrival probabilities and (4) time-dependent departure and detection probabilities. By far the strongest weight of evidence was in support of this model given the data (Model 1, Table 1). There was little weight of evidence (<10%) in support of the next best model (Model 2, Table 1). This is a sparse data set, so it was only possible to fit the 10 models summarised in Table 1 by collapsing the 6 within-season sampling periods into 3 monthly periods within each season (mid-November to mid-February). Otherwise, the models were over-parameterised and either failed to converge or produced models with very few estimable parameters. This modified sampling structure was therefore needed to derive survival and breeding probability estimates, given the data limitations, but then compromised clutch frequency estimation as discussed below.

#### Ageclass-specific survival probabilities

The estimated annual apparent survival probability derived from the best-fit MSORD model (Table 1) was 0.461 (95% CI: 0.25–0.69) for the newly-marked ageclass or 'transient' nesters in the model, and 0.854 (95% CI: 0.66–0.95) for the previously-marked or 'resident' nesters. The 'transient' nester estimate does

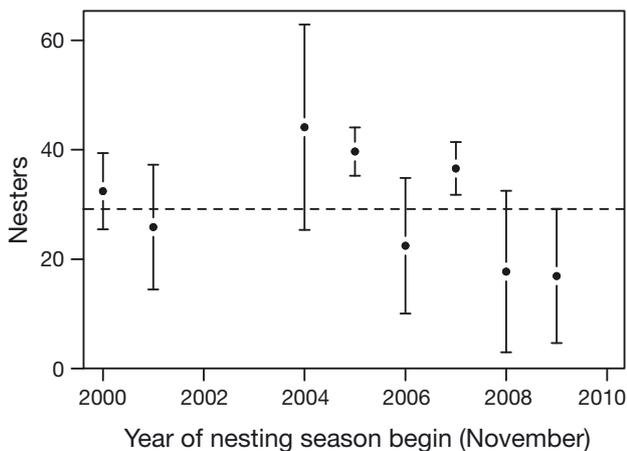


Fig. 2. *Dermochelys coriacea*. Annual nester abundance estimates (solid dot) derived from the best-fit MSORD model in Table 1. Vertical bars show 95% confidence intervals, and dashed horizontal line shows mean abundance over the 10 yr sampling period. Abundance during the seasons 2002/2003 and 2003/2004 could not be estimated using this data set because no recaptures of previously tagged turtles were made in those seasons

not reflect a survival estimate in any meaningful sense; it is simply a device to account for those seen only once.

#### Conditional or state-dependent nesting probabilities

The estimated annual nesting probability for leatherbacks that skipped the previous nesting season was 0.41 (95% CI: 0.23–0.62). The probability of skipping 2 nesting seasons consecutively was 0.59 (95% CI: 0.38–0.77). The nesting probability for leatherbacks that had also nested the previous season (probability of 2 consecutive nesting seasons) was 0.06 (95% CI: 0.02–0.19). Conversely, the probability of skipping a season given that the turtle had nested the previous season was 0.94 (95% CI: 0.81–0.98).

#### Intra-seasonal dynamics

On average, ca. 71% of the leatherbacks nesting each season arrived during the first 2 wk, with the remaining 29% (95% CI: 9–48) arriving over the remaining five 2 wk sampling periods. The mean probability of an individual remaining in the study area during each consecutive secondary sampling period within a season over the entire 10 yr was ca. 0.33, so that the probability of remaining in the study area by the end of the beach patrols each season averaged over the entire 10 yr was <0.11 ( $0.33 \times 0.33$ ), or the probability of being seen over 2 consecutive sampling periods (one of the first 5 and the last one). In other words, on average, ca. 89% of each year's nesters had departed the study area by the end of the beach patrols each season. Mean annualised capture probabilities for the 10 seasons were low and ranged from ca. 0.05 to 0.32 (mean = 0.16).

#### Derived parameter estimates

The estimated leatherback nesting population at Lababia was small and fluctuated around a long-term mean of ca. 30 nesters per season (Fig. 2). The precision of the abundance estimates was poor due to the low capture probabilities (itself a consequence of the sparse data), and so no meaningful interpretation of abundance trend was possible.

## DISCUSSION

Reliable estimates of key demographic parameters such as survival and breeding probabilities are needed for modelling the risk of marine turtle population exposure to anthropogenic hazards (Chaloupka 2003) and for diagnosing any trends in population abundance (National Research Council 2010). Deriving such estimates for long-lived marine species such as leatherback turtles that live in vast oceanic habitats is a major challenge. Most studies on leatherback turtles have focussed on nesting females because they are accessible and readily monitored using beach surveys (Chan & Liew 1996, Hughes 1996, Troëng et al. 2004, Hitipeuw et al. 2007, Thome et al. 2007). However, beach surveys of unmarked animals do not provide estimates of key demographic parameters. CMR studies do enable such parameters to be estimated but face a number of specific challenges, such as accounting for skipped breeding behaviour. The MSORD CMR-based approach used here offers great flexibility in modelling the demography of sea turtles that skip breeding opportunities and in cases where sampling is based only at nesting beaches (Kendall & Bjorkland 2001, Kendall 2004). We therefore used this approach to estimate survival and breeding probabilities for a leatherback nesting population using a community-based CMR study in northeast Papua New Guinea. Danielsen et al. (2009) identified 5 types of community-based monitoring scheme based on the level of local involvement in design, analysis and interpretation of monitoring results. Our study used a Category 2 scheme that comprised community participation in data collection only.

Annual survival probability for nesting leatherbacks has been previously estimated at 0.89 (95% CI: 0.87–0.92) for a Caribbean rookery (Dutton et al. 2005) and 0.91 (95% CI: 0.75–0.97) for a French Guiana rookery (Rivalan et al. 2005). These Atlantic nesting beach CMR studies also accounted explicitly for skipped breeding behaviour, but only Dutton et al. (2005) used the open robust design to account for staggered seasonal arrival and departure of nesters. Our annual survival probability estimate of 0.85 (CI: 0.66–0.95) was lower than both the Atlantic rookery estimates, which might reflect higher mortality for the Lababia population given exposure to anthropogenic hazards in the Pacific such as subsistence hunting (Suarez & Starbird 1996) or incidental capture in pelagic fisheries (Lewison et al. 2004). Few other estimates of leatherback nester survival are

available (but see Santidrián Tomillo et al. 2007), but these are all based on methods that do not account for the skipped breeding behaviour characteristic of leatherback nesting populations and so provide biased estimates of marine turtle annual survival based on sampling a nesting population (Dutton et al. 2005, Rivalan et al. 2005, Troëng & Chaloupka 2007, Prince & Chaloupka 2012).

The low recapture probabilities found in our study could imply lower nesting beach fidelity at the Lababia rookery. Although satellite telemetry findings (Benson et al. 2007) have documented a move between rookeries within a season, this might be an infrequent occurrence. However, a single nesting beach CMR study on the Huon Coast for leatherbacks with low beach fidelity is still likely to confound mortality with permanent emigration and hence result in underestimated survival probabilities (Brownie et al. 1993). Our study did not account for movement between rookeries within and between seasons, so a multi-site CMR study along the Huon Coast is needed to resolve whether our lower survival probability estimate was an artefact of lower nesting beach fidelity or, more importantly, due to higher mortality than is the case for Atlantic leatherback populations. Lower nesting beach fidelity and low recapture probabilities may also have been a consequence of inadequate spatial coverage that needs to be addressed when using a community-based sampling approach. Tag loss is another possible cause of lower survival estimates but is unlikely, since we used mainly PIT tags (especially in more recent years), which are considered reliable permanent markers for leatherback CMR studies (Dutton et al. 2005, Rivalan et al. 2005).

Breeding probabilities are among the most important demographic parameters needed for developing a better understanding of marine turtle population dynamics, yet few estimates have been made for any marine turtle species (National Research Council 2010, Prince & Chaloupka 2012). We found annual breeding behaviour to be breeding-state-dependent, with an adult female leatherback more likely to be a nonbreeder once she had nested at least once in a particular season than to nest 2 seasons consecutively; this is consistent with findings for 2 other leatherback populations (Dutton et al. 2005, Rivalan et al. 2005, Santandrián Tomillo et al. 2007). The probability of nesting given that an individual had skipped the previous season was 0.41, while the probability of skipping 2 consecutive nesting seasons was higher at 0.59. Lababia adult female leatherbacks are more likely to rest for 1 or

more seasons before nesting again, which is characteristic of most leatherback nesting populations (Saba et al. 2008). The probability of Lababia leatherback turtles skipping 2 consecutive seasons was higher than estimated for leatherback nesters at the French Guiana rookery (0.29, Rivalan et al. 2005). This skipped annual breeding behaviour is presumably due to the high energy demands of reproduction likely modulated by environmental fluctuations affecting food supply (Saba et al. 2007, Reina et al. 2009). While the probability of Lababia leatherbacks nesting in 2 consecutive seasons was low (ca. 0.06), it was nonetheless higher than estimated for nesters at the 2 Atlantic rookeries in French Guiana (0.009, Rivalan et al. 2005) and in the Caribbean (0.006, Dutton et al. 2005). This ocean basin difference might be due to Huon Coast nesting beaches being in closer proximity to oceanic foraging habitats than is the case for the more dispersed foraging habitats indicated for some Atlantic leatherback stocks (e.g. the stock that nests in French Guiana). Benson et al. (2011) found that the post-nesting migrations for Lababia leatherback turtles followed substantially shorter southeast tracks to the Eastern Australian Current Extension and the Tasman Front rather than crossing the entire Pacific as did females from West Papua.

It is important to note here that most studies of nesting marine turtles use a metric known as the remigration interval as a surrogate measure of breeding rate (National Research Council 2010). The remigration interval is the number of seasons between consecutive nesting seasons. This metric is only a simple return rate and is not an informative measure of breeding rate. In order to be a meaningful measure of breeding rate, the remigration interval would need to be adjusted by the following: (1) survival probability for each year of the interval between consecutive nesting seasons, (2) the probability of skipped breeding and (3) the probability of detection given that the turtle migrated that year and was detected on the beach. No remigration intervals presented for any marine turtle population correct for these 3 key sampling problems. The MSORD statistical modelling approach for CMR data adopted in our study, and by Prince & Chaloupka (2012), does account explicitly for all 3 sources of error. Similarly, the approaches used by Dutton et al. (2005), Rivalan et al. (2005) and Troëng & Chaloupka (2007) also account for these sources of error in estimating key demographic parameters for nesting marine turtle populations that are subject to skipped breeding behaviour.

The intra-seasonal nesting population dynamics based on estimates of the arrival and departure probabilities revealed a major limitation of our sampling coverage. The departure probabilities indicate that most nesters had left the study area by the time that beach patrols ceased each season so that coverage of the later part of the nesting season was reasonable. However, the estimated arrival probabilities indicated that a proportion of each season's nesting population had already arrived at Lababia prior to the start of the sampling periods used in this study. In more recent years, beach patrols have started earlier to ensure more adequate seasonal coverage. Ensuring full coverage of the nesting season is needed to maximise the benefits of using the MSORD approach for modelling CMR data.

The nesting population at Lababia (Fig. 2) was small compared to other leatherback rookeries around the world (see Table 2 in Troëng et al. 2004). However, the Lababia rookery is only 1 of 7 leatherback nesting sites along the Huon Coast of northeast New Guinea (Benson et al. 2007), which in turn is one of the largest leatherback nesting regions in the western Pacific (Dutton et al. 2007). Moreover, there is evidence of some level of seasonal movement between nesting beaches in the region (Benson et al. 2007), which may be indicative of lower nesting beach fidelity, suggesting that a Huon Coast regional multi-site CMR study would be useful. This should be possible in the future, as several other community-based CMR studies have commenced in recent years along the Huon Coast to complement the current Lababia study (Kinch 2006). Community-based monitoring is increasingly used to engage local communities in natural resource conservation in remote locations (Mellors et al. 2008, Danielsen et al. 2009) and has already been used successfully for marine turtle conservation and monitoring in Brazil (Marcovaldi & Marcovaldi 1999).

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#### LITERATURE CITED

- Alfaro-Shigueto J, Dutton P, van Bresselem M, Mangel J (2007) Interactions between leatherback turtles and Peruvian artisanal fisheries. *Chelonian Conserv Biol* 6: 129–135
- Anderson D, Burnham K, White G (1998) Comparison of Akaike Information Criterion and consistent Akaike

- Information Criterion for model selection and statistical inference from capture-recapture studies. *J Appl Stat* 25: 263–282
- Benson S, Kisokau K, Ambio L, Rei V, Dutton P, Parker D (2007) Beach use, internesting movement, and migration of leatherback turtles, *Dermochelys coriacea*, nesting on the north coast of Papua New Guinea. *Chelonian Conserv Biol* 6:7–14
- Benson S, Eguchi T, Foley D, Forney K and others (2011) Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere* 2: art 84, doi:10.1890/ES11-00053.1
- Brownie C, Hines J, Nichols J, Pollock K, Hestbeck J (1993) Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187
- Chaloupka M (2003) Stochastic simulation modelling of loggerhead sea turtle population dynamics given exposure to competing mortality risks in the western south Pacific. In: Bolten A, Witherington B (eds) *Loggerhead sea turtles*. Smithsonian Institution Press, Washington, DC, p 274–294
- Chaloupka M, Limpus C (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Mar Biol* 140: 267–277
- Chaloupka M, Limpus C (2005) Estimates of sex- and age-class-specific survival probabilities for a southern Great Barrier Reef green sea turtle population. *Mar Biol* 146: 1251–1261
- Chan E, Liew H (1996) Decline of the leatherback population in Terengganu, Malaysia, 1956–1995. *Chelonian Conserv Biol* 2:196–203
- Choquet R, Lebreton J, Gimenez O, Reboulet A, Pradel R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* 32:1071–1074
- Converse S, Kendall W, Doherty P, Ryan P (2009) Multistate models for estimation of survival and reproduction in grey-headed albatross (*Thalassarche chrysostoma*). *Auk* 126:77–88
- Danielsen F, Burgess N, Balmford A, Donald P and others (2009) Local participation in natural resource monitoring: a characterization of approaches. *Conserv Biol* 23: 31–42
- Dutton D, Dutton P, Chaloupka M, Boulon R (2005) Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol Conserv* 126:186–194
- Dutton P, Hitipeuw C, Zein M, Benson S and others (2007) Status and genetic structure of nesting populations of leatherback turtles (*Dermochelys coriacea*) in the western Pacific. *Chelonian Conserv Biol* 6:47–53
- Gaspar P, Benson SR, Dutton PH, Réveillère A and others (2012) Oceanic dispersal of juvenile leatherback turtles: going beyond passive drift modeling. *Mar Ecol Prog Ser* 457:265–284
- Hitipeuw C, Dutton P, Benson S, Thebu J, Bakarbesy J (2007) Population status and interesting movement of leatherback turtles, *Dermochelys coriacea*, nesting on the northwest coast of Papua, Indonesia. *Chelonian Conserv Biol* 6:28–36
- Holmberg J, Norman B, Arzoumanian Z (2009) Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. *Endang Species Res* 7:39–53
- Hughes G (1996) Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963–1995. *Chelonian Conserv Biol* 2:153–158
- Kendall W (2004) Coping with unobservable and misclassified states in capture-recapture studies. *Anim Biodivers Conserv* 27:97–107
- Kendall W, Bjorkland R (2001) Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57:1113–1122
- Kinch J (2006) Socio-economic baseline study of communities involved in leatherback turtle nesting beach projects along the Huon Coast, Morobe Province, Papua New Guinea. Western Pacific Regional Fishery Management Council, Honolulu, HI. Available at [www.wpcouncil.org/protected/Documents/Kinch%20report\\_final.pdf](http://www.wpcouncil.org/protected/Documents/Kinch%20report_final.pdf)
- Kisokau KM (2005) Community-based conservation and monitoring of leatherback turtles at Kamiali Wildlife Management Area. Final Report 04-WPC-025. Western Pacific Regional Fisheries Management Council, Honolulu, HI
- Lewison R, Freeman S, Crowder L (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol Lett* 7:221–231
- Marcovaldi M, Marcovaldi G (1999) Marine turtles of Brazil: the history and structure of Projeto TAMAR-IBAMA. *Biol Conserv* 91:35–41
- Mellors J, McKenzie L, Coles R (2008) Seagrass-Watch: engaging Torres Strait Islanders in marine habitat monitoring. *Cont Shelf Res* 28:2339–2349
- Miller J (1997) Reproduction in sea turtles. In: Lutz P, Musick J (eds) *The biology of sea turtles*. CRC Marine Science Series. CRC Press, Boca Raton, FL, p 51–81
- National Research Council (2010) Assessment of sea turtle status and trends: integrating demography and abundance. National Academies Press, Washington, DC
- Prince R, Chaloupka M (2012) Estimating demographic parameters for a critically endangered marine species with frequent reproductive omission: hawksbill turtles nesting at Varanus Island, Western Australia. *Mar Biol* 159:355–363
- Reina RD, Spotila JR, Paladino FV, Dunham AE (2009) Changed reproductive schedule of eastern Pacific leatherback turtles *Dermochelys coriacea* following the 1997–98 El Niño to La Niña transition. *Endang Species Res* 7:155–161
- Rivalan P, Prévot-Julliard A, Choquet R, Pradel R, Jacquemin B, Girondot M (2005) Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* 145:564–574
- Saba V, Pilar S, Reina R, Spotila J, Musick J, Evans D, Paladino F (2007) The effect of the El Niño Southern Oscillation on the reproductive frequency of eastern Pacific leatherback turtle. *J Appl Ecol* 44:395–404
- Saba VS, Spotila JR, Chavez FP, Musick JA (2008) Bottom-up and climatic forcing on the worldwide population of leatherback turtles. *Ecology* 89:1414–1427
- Santidrián Tomillo P, Vélez E, Reina R, Piedra R, Paladino F, Spotila J (2007) Reassessment of the leatherback turtle (*Dermochelys coriacea*) nesting population at Parque Nacional Marino Las Baulas, Costa Rica: effects of conservation efforts. *Chelonian Conserv Biol* 6:54–62
- Schaub M, Gimenez O, Schmidt B, Pradel R (2004) Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* 85:2107–2113

- Schwarz C, Stobo W (1997) Estimating temporary migration using the robust design. *Biometrics* 53:178–194
- Spotila J, Dunham A, Leslie A, Steyermark A, Plotkin P, Paladino F (1996) Worldwide population decline of *Dermochelys coriacea*: Are leatherback turtles going extinct? *Chelonian Conserv Biol* 2:209–222
- Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV (2000) Pacific leatherback turtles face extinction. *Nature* 405:529–530
- Stewart K, Sims M, Meylan A, Witherington B, Brost B, Crowder L (2011) Leatherback nests increasing significantly in Florida, USA; trends assessed over 30 years using multi-level modeling. *Ecol Appl* 21:263–273
- Suarez A, Starbird C (1996) Subsistence hunting of leatherback turtles, *Dermochelys coriacea*, in the Kai Islands, Indonesia. *Chelonian Conserv Biol* 2:190–195
- Thome J, Baptistotte C, de Moreira L, Scalfoni J, Almeida A, Rieth D, Barata P (2007) Nesting biology and conservation of the leatherback sea turtle (*Dermochelys coriacea*) in the state of Espirito Santo, Brazil, 1988–1989 to 2003–2004. *Chelonian Conserv Biol* 6:15–27
- Trevor A (2010) Turtle Research and Monitoring Database System (TREDS): Annual Report 2009. Secretariat of the Pacific Regional Environment Program, Apia, Samoa
- Troëng S, Chaloupka M (2007) Variation in adult annual survival probability and remigration intervals of sea turtles. *Mar Biol* 151:1721–1730
- Troëng S, Chacón D, Dick B (2004) Possible decline in leatherback turtle *Dermochelys coriacea* nesting along the coast of Caribbean Central America. *Oryx* 38:395–403
- Troëng S, Harrison E, Evans D, de Haro A, Vargas E (2007) Leatherback turtle nesting trends and threats at Tortuguero, Costa Rica. *Chelonian Conserv Biol* 6:117–122
- Wallace B, Seminoff J, Kilham S, Spotila J, Dutton P (2006) Leatherback turtles as oceanographic indicators: stable isotope analyses reveal a trophic dichotomy between ocean basins. *Mar Biol* 149:953–960
- White G, Kendall W, Barker R (2006) Multistate survival models and their extension in Program MARK. *J Wildl Manag* 70:1521–1529

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