



Population trends and survival of nesting green sea turtles *Chelonia mydas* on Aves Island, Venezuela

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ABSTRACT: Long-term demographic data are valuable for assessing the effect of anthropogenic impacts on endangered species and evaluating recovery programs. Using a 2-state open robust design model, we analyzed mark-recapture data from green turtles *Chelonia mydas* sighted between 1979 and 2009 on Aves Island, Venezuela, a rookery heavily impacted by human activities before it was declared a wildlife refuge in 1972. Based on the encounter histories of 7689 nesting females, we estimated the abundance, annual survival, and remigration intervals for this population. Female survival varied from 0.14–0.91, with a mean of 0.79, which is low compared to survival of other populations from the Caribbean (mean = 0.84) and Australia (mean = 0.95), even though we partially corrected for tag loss, which is known to negatively bias survival estimates. This supports prior suggestions that Caribbean populations in general, and the Aves Island population in particular, may be more strongly impacted than populations elsewhere. It is likely that nesters from this rookery are extracted while foraging in remote feeding grounds where hunting still occurs. Despite its relatively low survival, the nesting population at Aves Island increased during the past 30 years from approx. 500 to >1000 nesting females in 2009. Thus, this population, like others in the Caribbean and the Atlantic, seems to be slowly recovering following protective management. Although these findings support the importance of long-term conservation programs aimed at protecting nesting grounds, they also highlight the need to extend management actions to foraging grounds where human activities may still impact green turtle populations.

KEY WORDS: *Chelonia mydas* · Survival · Open robust design model · Population trends

INTRODUCTION

Worldwide, many species have suffered large population declines as a result of anthropogenic pressures on ecosystems (Balmford et al. 2003, Ehrlich & Pringle 2008). One of the greatest challenges for the conservation of threatened species is to detect changes in their abundance and understand the effect of specific threats in their population dynamics (Bonebrake et al. 2010). Demographic parameters (e.g. survival, re-

cruitment, population size) are essential for understanding population dynamics and often provide insights to effective management strategies — selection of adequate life stages or habitats, minimum viable populations, time frames over which 'success' can be assessed — and future research (Noon et al. 1992).

Sea turtles have been among the many threatened marine vertebrates, with populations in many regions suffering overexploitation (Parsons 1962, Jackson 1997). Despite unequivocal signs of recovery of

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some populations following the protection of nesting beaches (Balazs & Chaloupka 2004, Dutton et al. 2005, Antworth et al. 2006), others continue to decline (NMFS & USFWS 2007, Fonseca et al. 2009, Tapilatu et al. 2013, Seminoff et al. 2014). Recovery of sea turtle populations tends to be slow because population turnover rates are low (Heppell et al. 2003), and high natural hatchling mortality and slow maturation result in a small proportion of any given cohort reaching adulthood (Miller 1997, Miller et al. 2003). In this context, high subadult and adult survival are essential for maintaining populations because population growth is most sensitive to variations in survival in these stages (Crouse et al. 1987, Congdon et al. 1993, Heppell 1998). Furthermore, females are philopatric, most returning to their natal beaches to reproduce, which tends to make each nesting beach, or rookery, a relatively independent demographic unit vulnerable to local extinction (Bowen et al. 1992, Encalada et al. 1996, Bjørndal et al. 2005a, 2006, Formia et al. 2006, Wallace et al. 2010). However, reliable estimates of abundance and survival of individuals in these life stages are difficult to obtain because subadult and adult turtles spend their lives in open water and only females return to land to nest.

Despite their extensive geographic distribution across tropical and subtropical seas, many green turtle (*Chelonia mydas*) populations have historically been depleted and in some cases were considered extirpated, e.g. in Bermuda, Cayman Islands (King 1982, Groombridge & Luxmoore 1989). Overexploitation of eggs and females on nesting beaches, and juveniles and adults on foraging grounds, as well as unintentional take in fisheries (bycatch), and degradation of feeding and nesting habitats are among the major threats to green turtles (Parsons 1962, Lutwidge et al. 1997, Pritchard 2004, Seminoff 2004, McClenachan et al. 2006, Lagueux et al. 2014). Although some populations have been recovering in recent decades due to conservation measures (Balazs & Chaloupka 2004, Broderick et al. 2006, Chaloupka & Balazs 2007, Chaloupka et al. 2008, Mortimer et al. 2011, Weber et al. 2014), the green turtle remains listed as Endangered by the IUCN (Seminoff 2004) and is protected under multiple treaties and laws (CITES 1995, República de Venezuela 1996, 1998) due to continued threats, depleted status, and insufficient recovery of many populations.

Recently, important efforts have been made to estimate population abundance and survival of green turtles based on long-term population monitoring using mark-recapture methods of nesting females

(Balazs & Chaloupka 2004, Troëng & Rankin 2005, Koch et al. 2007, Troëng & Chaloupka 2007) in foraging aggregations (Chaloupka & Limpus 2001, Bjørndal et al. 2003, 2005b, Seminoff et al. 2003, Campbell & Lagueux 2005, Patrício et al. 2011, 2014, Colman et al. 2015) and remote tracking of individuals using satellite telemetry (Pelletier et al. 2003). However, a large variation has been observed among species, regions, and even populations (Casale et al. 2007, Troëng & Chaloupka 2007). For example, survival estimates for green turtles tend to be lower (0.82–0.85) (Campbell & Lagueux 2005, Troëng & Chaloupka 2007) than those for other sea turtles in the Caribbean, e.g. leatherbacks *Dermochelys coriacea* (0.89; 95% CI = 0.87–0.92) (Dutton et al. 2005) and hawksbills, *Eretmochelys imbricata* (0.95; 95% CI = 0.91–0.97) (Kendall & Bjørkland 2001), which has been attributed to targeted extraction of green turtles in the Caribbean (Campbell & Lagueux 2005, Troëng & Chaloupka 2007, Lagueux et al. 2014). In Australia, 1 unexploited green turtle population was estimated to have a relatively high mean annual survival of 0.95 (Chaloupka & Limpus 2005). While some of these may reflect true differences in survival related to human-induced impacts or life-history differences, others may be the result of methodological differences.

Aves Island, Venezuela, is one of the largest green turtle nesting colonies in the Caribbean (Peñaloza 2000, Vera & Buitrago 2012), but the abundance and population trends here are unclear, with some studies pointing to a 90% decline between 1947 and 1994 (Seminoff 2004), while others suggest population stability during an overlapping period (1979–1997) (Peñaloza 2000). Moreover, Vera & Buitrago (2012) suggested a more recent increase in the abundance of nesters at this rookery (2001–2008). However, previous studies that estimate demographic parameters at Aves Island have used methods based on enumeration, composite life tables, and catch curve analysis (Bjørndal 1980, Frazer 1983, Peñaloza 2000, Vera & Buitrago 2012). A major limitation of the methods described above is that they do not account for imperfect detection (Kéry et al. 2009, Pfaller et al. 2013). Mark-recapture models based on maximum likelihood estimation (Lebreton et al. 1992, Kendall et al. 1995, 1997, Spindel et al. 1995, Kendall 2010) can account for imperfect detection, and more recently, have also incorporated temporary emigration (Schwarz & Stobo 1997, Kendall & Nichols 2002) which is another important source of bias (Kendall et al. 1997, Schaub et al. 2004) that occurs when females 'skip' a breeding season. Most green turtles do not nest in

consecutive years, and non-nesters (or 'skip-breeders') are not present at the nesting beach and cannot be sampled during that time (Burnham & Rexstad 1993, Kendall et al. 1997, Kendall & Bjorkland 2001). Such models also account for staggered entry and exit from the rookery, which if unaccounted for may bias survivorship (Schwarz & Stobo 1997, Kendall & Bjorkland 2001, Kendall & Nichols 2002, Thorson et al. 2012). More reliable demographic estimates from Aves Island would not only contribute to a better understanding of the causes of variation in adult green turtle survival in the Caribbean, but also help resolve the controversy surrounding the status and trends of this colony.

In the present study, we examined the dynamics of the Aves Island green turtle population, estimated nesting female abundance, survival, recruitment, remigration interval, and residence time. We used a 26-year dataset consisting of mark-recapture records of nesting females, collected by the NGO, Fundación para la Defensa de la Naturaleza (FUDENA), and the Venezuelan government agency, Ministerio para el Poder Popular para el Ambiente (MINPPA) as part of their monitoring and conservation programs.

MATERIALS AND METHODS

Study site

Aves Island is a flat (<5 m high) sand spit located 670 km north of the Venezuelan mainland (63° 37' 00" W, 15° 40' 00" N) (Schubert & Laredo 1984). The island is approx. 540 m long and varies in width from 30 to 125 m. Aves Island is the only outcrop of the Aves Ridge, a north-south submarine mountain range extending 500 km from Margarita Island to the vicinity of St. Croix (Fig. 1). The island consists of calcareous sandy beaches with scarce vegetation on a beach-rock platform surrounded by a fringing reef. The beaches on Aves Island are highly dynamic. They may change drastically from year to year, or even disappear in the short term, because of the exposure of the coastline to strong wave action during periods of high wind or when equatorial Atlantic and Caribbean hurricanes pass over or near the island (Zuloaga 1955, Gremone & Gómez 1983, Schubert & Laredo 1984, Baamonde 2007). Aves Island was declared a wildlife refuge in 1972, granting protection to nesting green turtles, which had been impacted by commercial guano extraction at their nesting habitats and by the removal of nesting individuals by fishermen (Harris 1958, Parsons 1962). In 1978, due to the

island's geopolitical importance, the Venezuelan Naval Forces established a permanent station on the island (Baamonde 2007). A year-round military presence provides technical and operational support for scientific research among other activities.

Aves Island is also one of the most important green turtle nesting sites in the Caribbean (Carr et al. 1978, Seminoff 2004, Vera & Buitrago 2012). Green turtles nest there year round, with a peak from August to September. Females tagged on the island have been recaptured in feeding grounds throughout the Caribbean and South Atlantic, including Maranhao, Brazil (over 2870 km away) (Sole 1994). Aves Island green turtles have long been hypothesized to be a distinct colony, based on differences in adult size from other Caribbean populations (Pritchard & Trebbau 1984). The presence of unique mitogenomic variants at Aves Island, and significant differences between the Aves Island and Surinam populations, determined using microsatellite data, further indicate a demographically isolated population (Shamblin et al. 2012, Naro-Maciel et al. 2014).

Data collection and processing

Sampling effort varied between the 2 observer teams that collected mark-recapture data: FUDENA sampled almost year-round from 1979 to 1997, whereas MINPPA sampled mainly from June to

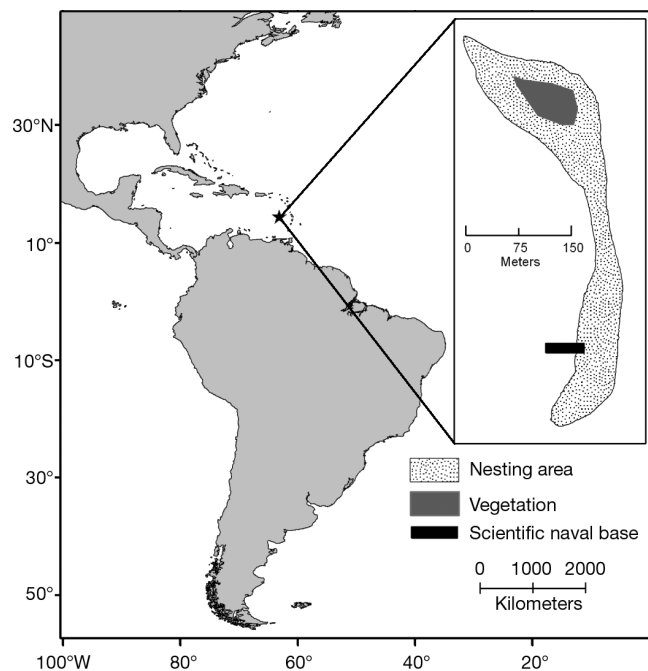


Fig. 1. Location of Aves Island, Venezuela

November between 2001 and 2009 (excluding 2003 and 2004). Both teams conducted daily patrols between 20:00 h to 03:00 h, weather permitting (Gremone & Gómez 1983, Vera 2004); however, the number of patrollers, usually 2 or 3, was reduced to 1 during 2001 and 2002. Turtles were mainly tagged while nesting on the beach, as they do not react to handling during this time (Balazs 1999). Individuals were tagged between the second and third scale of the trailing edge of a front flipper using a single Monel or Inconel tag, bearing a unique alpha numeric code, a reward message, and a return address. Tag numbers of newly and previously tagged turtles were recorded each night. Curved carapace length (CCL; from the nuchal scute at the midline to the posterior tip of the supracaudal scutes), and curved carapace width (CCW; across the carapace at its widest point) were measured at least once for each turtle with a flexible fiberglass tape (Gremone & Gómez 1983, Bolten 1999, Vera 2004).

Mark-recapture methods

Live encounter histories and framework selection.

Live encounter histories were compiled and analyzed for all nesting females observed between 15 June and 15 November of each year, when >90% of all sightings occurred. Because green turtles often lay more than 1 clutch per nesting season, they can be recaptured several times in a season. We pooled observations into 11-night-long sampling sessions, which was the mode of the interval between a given female's successive nesting attempts within a season (i.e. re-nesting interval). Therefore, any individual sighted at least once during each 11-night sampling session was recorded as seen (1) or not seen (0). Re-nesting and remigration intervals were thus determined by estimating the mean time between successive captures for each turtle within and between nesting seasons.

Multistate open robust design (MSORD). Given that females temporarily emigrate from the nesting beaches, which can result in a downward bias in survival estimates (Kendall et al. 1997), we used a 'multistate open robust design' framework (MSORD) to model arrival and departure (Kendall & Bjorkland 2001) using an unobservable state to represent the portion of the population that was away from the study area during a primary period (Kendall 2004, 2010). To do this, we divided our data into 26 primary sessions, corresponding to nesting seasons or years between 1979 and 2009, and further subdivided each

into 9–14 secondary sampling sessions of 11 nights each. In any given year, we considered females to be in the observable state (nester; N) if they migrated to the study area, or in the unobservable state (skip-breeder; S) if they had skipped nesting for that year, and remained away from the study area. This model allows for the arrival and departure of turtles from their nesting beaches in a staggered fashion, a pattern common to most nesting populations (Kendall & Bjorkland 2001). We used the 'RMark' package ver. 2.1.1 (Laake 2012) in R (R Development Core Team 2012) as a front end interface to specify models for mark-recapture data analysis in the program MARK ver. 6.1 (White & Burnham 1999).

Goodness of fit. We used a χ^2 goodness-of-fit test (GOF) to evaluate the underlying assumptions of equal catchability of marked and unmarked turtles and transient behavior of newly marked turtles. Transients are individuals having zero probability of being recaptured after their initial capture because they permanently leave the study area, and their presence in a population can cause a downward bias in survival estimates (Pradel et al. 1997). Currently, there is no readily available software to assess the overall fit of the MSORD model, so we tested these assumptions for each of the 26 primary periods using χ^2 -tests for the fully-time-dependent (all parameters vary with time) Cormack-Jolly-Seber model for closed populations implemented in program U-CARE (Croquete et al. 2005). We then added χ^2 -statistics across all years (Chaloupka 2002, Chaloupka & Limpus 2005) and estimated the variance inflation factor (\hat{c} indicating the degree of overdispersion in the data or lack of fit of our general framework), as the quotient between the sum of the χ^2 statistics divided by the sum of the degrees of freedom across all years ($\hat{c} = \sum \chi^2 / \sum df$) (Lebreton et al. 1992). Signed-statistics were also estimated for each year to detect evidence for trap-dependence in recapture rates (Croquete et al. 2005) and for the presence of transients (i.e. newly marked individuals that are not seen in subsequent primary sessions) (Pradel et al. 1997).

Alternative models. We built 20 alternative models (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n029p103_supp.pdf) to examine how tagging status (newly vs. previously tagged), state or emigration status, observer, or climatic events affected model performance. Tag loss can occur after a faulty application of a tag, as demonstrated by double tagging, and may cause downward bias in survival probability estimates (Limpus 1992, Bjorndal et al. 1996). If it occurs shortly after tag application, its bias on sur-

vival estimates can be reduced by separating newly marked turtles, which were either first-time nesters (cohort 0) or previous nesters that had lost a tag, from all other nesting females (cohorts 1–29). To test whether turtles emigrate in a non-random, Markovian fashion we compared random ($\psi_{\text{time}}^{\text{N to S}} = \psi_{\text{time}}^{\text{S to S}}$) to Markovian ($\psi_{\text{time}}^{\text{N to S}} \neq \psi_{\text{time}}^{\text{S to S}}$) emigration models. We also modeled emigration probability as dependent on state (*state*), where nesters had a constant probability of leaving the nesting beach year after year ($\psi_{\text{constant}}^{\text{N to S}}$), and skip-breeders had a time-dependent or constant probability of returning to the nesting beach ($\psi_{\text{state,time}}^{\text{S to N}}$ or $\psi_{\text{state,constant}}^{\text{S to N}}$). For each nesting season, the probability of entering the study area was modeled as a quadratic function of the secondary session ($\text{mlogit}(\text{pent}_{\text{year,time}}^{\text{N}}) = \beta_0 + \beta_{\text{time}} + \beta_{\text{time}^2}$), where β denotes constants, as we expected more turtles to arrive at the nesting beach as the season progressed, up to the peak or approximately mid-season, and to decline thereafter. The probability of leaving the study area within a primary period was assumed to be a linear function of time since arrival at the nesting beach ($\text{logit}(\phi_{\text{year,time}}^{\text{N to S}}) = \beta_0 + \beta_{\text{time-arrival}}$), because turtles were more likely to leave as the number of clutches they had deposited increased. Capture probabilities were allowed to vary between primary sessions or set constants from year to year and in secondary sessions. We created the grouping variable ‘observer’ (*obs*) to represent which institution did the sampling each year and tested for an observer bias effect on capture rates or survival estimates. Finally, we tested if parameter estimates were influenced by hurricanes in the Caribbean by including the number of hurricanes reported by NOAA as a covariate for survival or remigration probability. Models were built by testing different parameter structures one by one and keeping those that substantially reduced the Akaike values (the 20 best performing models [lowest AIC values] are shown in Table S1 in the Supplement).

Model selection and parameter estimates. We used the quasi Akaike Information Criterion (qAIC) to compare models because \hat{c} values indicated considerable overdispersion of the data (Akaike 1981). The ‘best’ models were those that best accounted for the variation in the data, which was indicated by the lowest qAIC values. We obtained our final parameter estimates by model-averaging, i.e. we estimated a weighted-average for each model by using the qAIC weights (w ; model support scaled from 0 to 1 for each model under consideration) for all models with $w > 0.05$. Model-averaging includes model selection uncertainty in the estimates and precision of parameters (Buckland et al. 1997). Parameters that could

not be estimated due to their low precision were identified using a threshold value of the vector of conditioned singular values (*S*) of the Hessian matrix, which result from the singular value decomposition of the Hessian divided by the maximum value in this vector (Viallefont et al. 1998). We obtained the number of green turtles nesting in the study area each year ($N_{\text{year}}^{\text{N}}$) and their expected residence or stopover time ($R_{\text{year}}^{\text{N}}$) as derived parameters from the ‘best’ models (Kendall & Bjorkland 2001, Kendall 2010). To detect temporal trends in population size, annual survival and re-nesting intervals, we used linear regression, evaluated temporal autocorrelation, and normality of residuals using R statistical software (R Development Core Team, 2012). We also compared the size distribution (CCL) of nesters arriving every year at Aves Island with a reference distribution in 1979, when the study began, using a nonparametric smoothing method in the R package ‘sm’ (ver. 2.2-5.4) (Bowman & Azzalini 2014).

RESULTS

Green turtle nesting patterns on Aves Island

A total of 7689 female green turtles were tagged in 26 primary sampling sessions, or yearly nesting seasons (Fig. 2). The number of turtles observed nesting varied between years, but there were new captures and recaptures in every nesting season. Nesting turtles laid 1–9 clutches each year, with an average of 2.4 observed clutches per female (SE = 0.020, N =

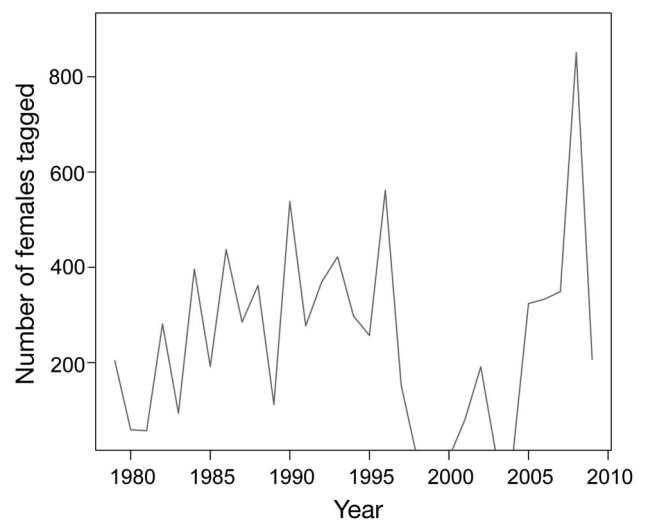


Fig. 2. Number of green turtles *Chelonia mydas* tagged at Aves Island, Venezuela, from 1979 to 2009

8658) and a mode of 11 d between successive clutches. Each year, most turtles left Aves Island between October and November. Of those tagged, 58.7% were not seen again; these could have been transient turtles, or individuals that lost their tags or died. The mean interval between successive captures was 2.37 yr (SE = 0.032) and 80.2% of remigrants were recaptured 2 or 3 yr after tagging.

The combined GOF tests for the 26 primary periods revealed evidence for immediate trap dependence on marked turtles; during secondary sessions, the probability of capture immediately after first tagging was higher possibly because nesting turtles tended to abandon the nesting beach after the second nesting event. We also found evidence for the presence of transient turtles (i.e. turtles that were not observed again after their first capture). The variance inflation factor ($\hat{c} = 1.27$) indicated slight but significant overdispersion in the data ($\chi^2 = 690$, $df = 545$, $p < 0.001$). Therefore, the AIC values and deviances, and confidence interval estimates were adjusted accordingly (Schwarz & Arnason 2007).

MSORD models

The best 3 models had similar qAIC values, within 2 units of each other (Table 1), and included the parameter structures: (1) survival probability dependent on year and tagging status ($\text{Surv}_{\text{tag,year}}^N$), (2) temporary emigration probability dependent on the nesting status (i.e. first-order Markovian) and the number of hurricanes ($\psi_{\text{state,hur}}^{\text{NtoS}} \neq \psi_{\text{constant}}^{\text{StoS}}$), (3) probability of arriving at the nesting site dependent on the secondary session date ($\text{pent}_{\text{time}}^N$), (4) probability of leaving the nesting site dependent on time since arrival, ($\phi_{\text{time-arrival}}^N$), and (5) capture probability de-

pendent on year and observer ($p_{\text{obs,time}}^N$). The cumulative qAIC weights for these 3 models indicated a relative support of 99.9% (Table 1).

The threshold values for the conditioned S vectors identified the following 11 non-estimable parameters: annual survival in 1989, 2002, 2005, 2006 and 2008, temporary emigration probability (ψ^{NtoS}) in 2001 and 2005, and temporary remigration probability (ψ^{StoS}) in 1979, 1997, and 2002. Capture probabilities during some of these years (2001, 2002, and 2005) were particularly low (< 0.05), possibly because of a reduction in the number of patrollers collecting data. Therefore, we do not show values for demographic parameters estimated between 1998 and 2004.

Interseasonal dynamics: survival and remigration

Maximum likelihood estimates for annual survival varied considerably among years for both of the turtle groups modelled (newly tagged and remigrant). As expected, remigrant turtles had a significantly higher mean annual survival (mean = 0.79, 95% CI = 0.73–0.84) than newly tagged turtles (mean = 0.39, 95% CI = 0.30–0.48) (Fig. 3B). Despite the reduction in model deviance achieved by treating these groups separately, a large proportion of the variation in the annual survival of remigrant turtles remained unexplained. Although the second ranked model included the effect of hurricanes on female temporary emigration, the small difference in AIC values between this and the first ranked model indicated this covariate had a negligible effect on model performance.

The probability of an individual entering the study area in a particular year depended on whether it was observed during the previous nesting season. Turtles that nested in year i almost always skipped nesting

Table 1. Ranking of the best 3 models developed using the Multistate Open Robust Design (MSORD), based on the corrected quasi-Akaike's Information Criteria (qAIC). We modeled survival probability (Surv), temporary emigration probability (ψ), entry or arrival probability (pent), departure probability (ϕ) and capture probability (p), or as functions of the tagging status (tag; newly tagged vs. remigrant), the observer (observer; MINNPA vs. FUDENA program), the emigration status (state; nester vs. skip-breeder), the incidence of hurricanes (hur), the breeding season (year), a quadratic function of the time since the beginning of the breeding season (time-quadratic), or as a linear function of the time since arrival within a breeding season (time since arrival). Model weight (w_i) and deviance (Q_{deviance}) indicate relative support and fit of each model. See 'Materials and methods: Alternative models' for detailed description of model structure, and Table S1 in the Supplement for descriptions of the best 20 models

Rank	Surv	ψ	pent	ϕ	p	No. of parameters	qAIC	w_i	Q_{deviance}
1	(tag, year)	(state, year ^a)	(time-quadratic)	(time since arrival)	(year)	85	54846.5	0.546	54675.3
2	(tag, year)	(state, hur, year ^a)	(time-quadratic)	(time since arrival)	(year)	86	54848.0	0.256	54674.8
3	(tag, year)	(state, year ^a)	(time-quadratic)	(time since arrival)	(year, observer)	86	54848.5	0.198	54675.3

^aEmigration of skip-breeders for years preceded by sampling gaps (2001 and 2005) were estimated separately from all other years

in year $i + 1$; that is, their probability of temporarily emigrating from Aves Island was high (0.99). On the contrary, those that skipped nesting in year i either returned or did not return during the following season depending on the particular year, but their mean probability of returning was nevertheless low (0.24) (Fig. 3C). This means that, on average, the permanency or length of time turtles remained as skip-breeders (S) was 4.64 yr [permanency = $-1/\ln(\psi^{S \text{ to } S})$]. Linear regression analyses did not detect temporal trends in annual survival ($F_{(1,16)} = 0.75$, $R^2 = 0.044$, $p = 0.395$) or re-nesting intervals ($\psi^{S \text{ to } N}$) ($F = 0.69$, $R^2 = 0.01$, $p = 0.418$).

Intraseasonal dynamics: arrival, departure and residence time

Turtle arrival and departure from Aves Island was staggered, as expected. The estimated mean residence time of turtles (R_{year}^N) indicated that females spent an average of 38 days on the island during a nesting season in which they were present. Despite the peak in the number of turtles toward the middle of the season, due to overlap of early and late arrivals, the arrival probability was highest at the beginning of the nesting season, after which it gradually decreased (Fig. 4A). Departure probability was best described as a function of the time since arrival. Because most turtles arrived at the beginning of the season, the number of departing turtles increased as the season progressed (Fig. 4B). Within each breeding season, capture probabilities did not vary significantly with date (secondary session). The small difference in AIC values between the model including *obs* and all other models without this grouping variable indicated that there was no significant bias in the capture probability associated with the observer.

Nester population size

Derived estimates of population sizes suggested that 146–767 females nested on Aves Island every

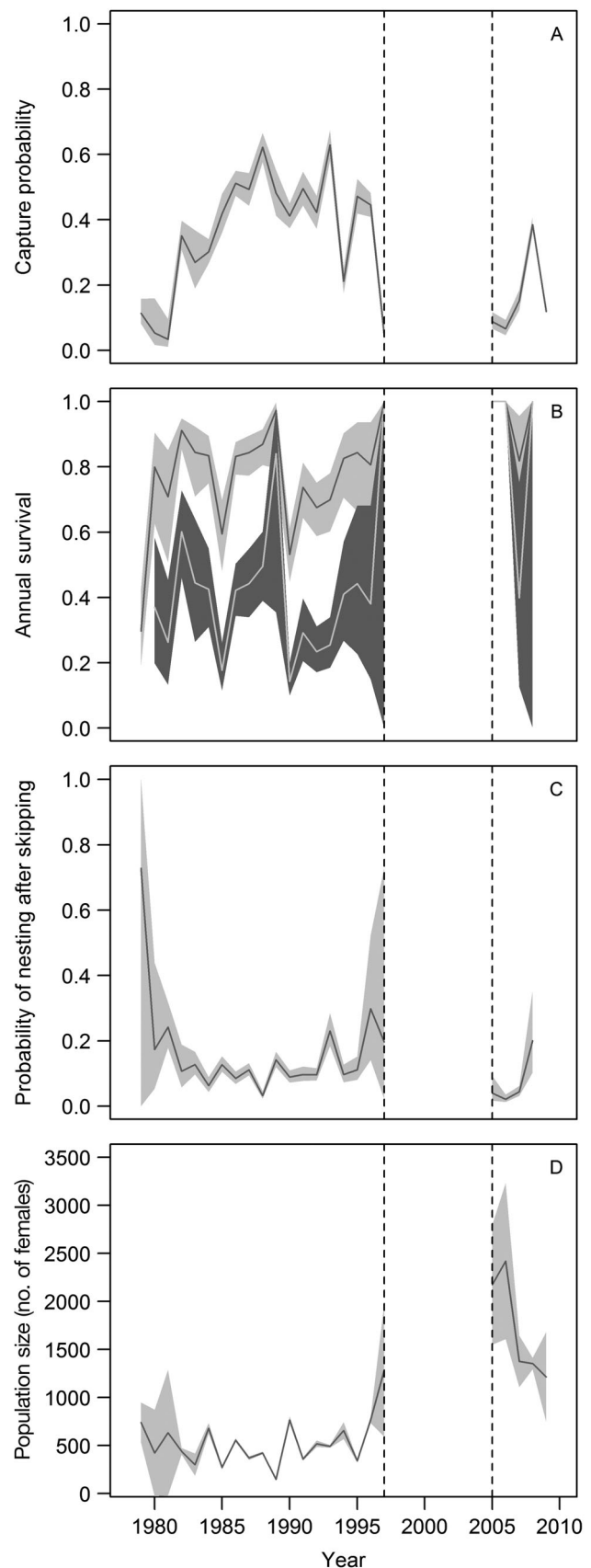


Fig. 3. Temporal trends in (A) capture probability, (B) annual survival, (C) probability of nesting after 'skipping' a nesting year, and (D) population size for the population of green turtles nesting on Aves Island, Venezuela. Areas between the dotted lines indicate years with low capture effort, for which demographic parameters could not be estimated. Shaded areas indicate 95% CI. Annual survival is shown separately for newly tagged (dark grey) and remigrant (lighter grey) females

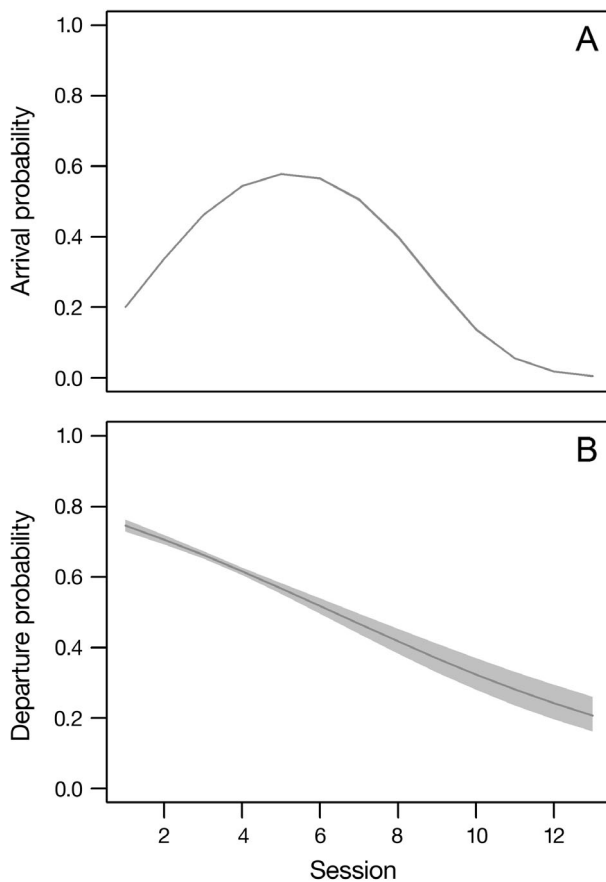


Fig. 4. Probabilities of (A) arrival, and (B) departure of green turtles nesting on Aves Island, Venezuela, as defined by the 3 top ranking models developed using the Multistate Open Robust Design (MSORD). Shaded areas indicate 95% CI (narrow and therefore not visible for arrival probability)

year from 1979 to 1997, with alternating years of high and low abundance (Fig. 3D). Population size estimates between 1998 and 2004 are not shown because they had high levels of uncertainty due to a substantial decrease in sampling effort and capture probabilities during that period (Fig. 3A). The number of observers was reduced to 1 during 2001 and 2002, and no data were collected for 2003 or 2004. Despite the broader confidence intervals due to this reduction in sampling effort in 1997 and 2005–2009, the number of nesters appears to have increased above 1000 during these years (Fig. 3D). A reduction in the number of nesters was observed at the end of the study (2006–2009), but more recent data are not available to assess whether this trend continued in subsequent years. A regression analysis indicated that, despite the fluctuations in estimates, the number of nesting turtles increased at an average rate of 4.5% per year from 1979–2009 [$\ln(N) = (-81.40300 +$

$0.04407 \times \text{year})]$ ($F_{(1,19)} = 11.71$, $R^2_{\text{adj}} = 0.381$, $p = 0.003$). Additionally, a leftward-shift in the size distribution of nesters (CCL) during 2008 and 2009 compared to previous years suggests the recruitment of smaller and likely younger females at the end of the study (Fig. 5).

DISCUSSION

Survival of green turtle females from the Aves Island nesting population

Despite the protected status of nesting females at Aves Island Wildlife Refuge, the annual survival of nesting green turtle females (mean = 0.79) (Fig. 2B) was no higher than survival probabilities estimated for other populations in other parts of the Caribbean (Bjorndal 1980, Campbell & Lagueux 2005, Troëng & Chaloupka 2007). Temporary emigration or tag loss may result in a downward estimate bias, nonetheless, the use of a substantial dataset and estimation methods that correct for this potential bias did not reveal a higher survival. Additionally, survival at Aves Island was considerably lower than the survival probability estimated for a protected population in Australia (mean = 0.95) (Chaloupka & Limpus 2005).

Because we corrected for the largest possible sources of negative bias in our survival estimates—tag loss from newly tagged females and the presence of transient females—these are likely to reflect the true biological patterns of green turtles at Aves Island. Therefore, mean survival for this colony appears to be lower than for other colonies in the Caribbean. Although the Aves Island Wildlife Refuge seems to be safe for nesting green turtles, most of these females forage throughout the Caribbean in regions where extraction still occurs, e.g. coastal waters of Nicaragua (Campbell & Lagueux 2005, Lagueux et al. 2014) and the Gulf of Venezuela (Montiel-Villalobos 2012). Furthermore, the legal green turtle fishery in Nicaragua, where turtles from the Aves Island rookery are known to forage, has among the highest take in the Atlantic basin (Lagueux et al. 2014). If our low survival probabilities are a result of these high levels of extraction, protection of nesting habitat on Aves Island may not be enough to ensure that survival rates increase to levels similar to undisturbed populations and necessary for population sustainability or growth, such as those estimated for green turtles in Australia (95%).

Nonetheless, we were not able to correct for all negative biases in our analyses. By separating neo-

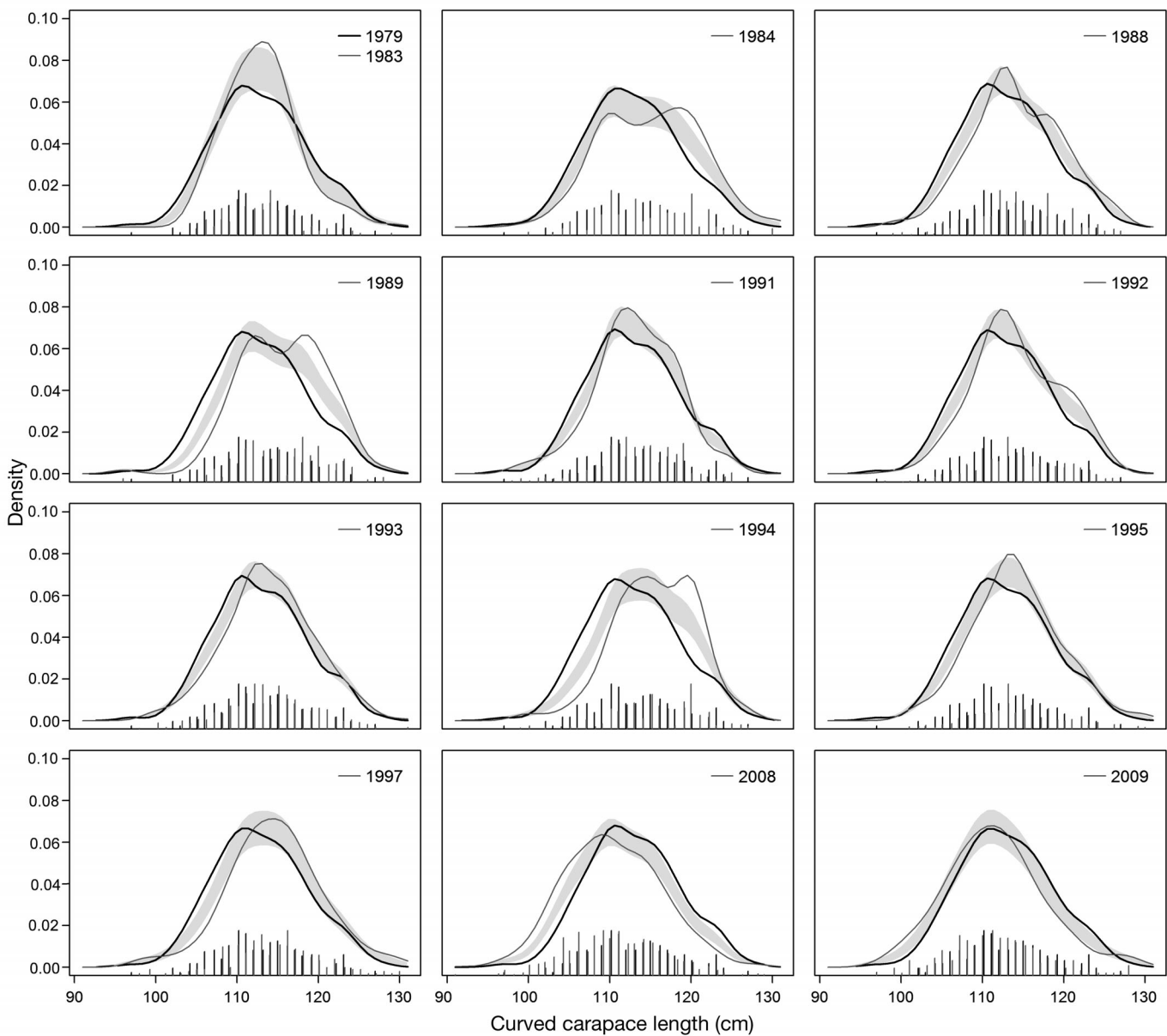


Fig. 5. Kernel density plots showing changes in the frequency distribution of the curved carapace length (CCL) of nesting green turtles each year in relation to 1979. Only years for which significant differences were detected in the frequency distribution of size are shown ($p < 0.05$ for all comparisons). Before 1997, females tended to be larger than in 1979 (right-shift) but, after 2001, females were smaller on average than in 1979 (left-shift). The difference in CCL frequency distribution was tested using the *sm* package in R (Bowman & Azzalini 2014). Spike histograms indicate where the data points for each group lie with respect to the kernel density curves

phytes from remigrant females, we reduced the bias that first-year tag loss and the presence of transient turtles may have on survival; however, tags may also be lost after the first year (Limpus 1992, Bjørndal et al. 1996, Troëng et al. 2003). Tag loss has been previously identified as an important source of error in turtle survival estimates (Frazer 1983, Limpus 1992, Bjørndal et al. 1996, Peñaloza 2000, Troëng et al. 2003, Troëng & Chaloupka 2007).

Furthermore, survival probabilities varied considerably between years. Annual variation in survival has been reported for several populations of nesting turtles (Troëng & Chaloupka 2007, Phillips et al. 2014) although its cause is not well understood. Several authors have tried to link this variation to particular climatic events (Carr & Carr 1970, Hays 2000, Solow et al. 2002) but its effects appear to be associated more with reproductive output, time to maturity

or remigration. It has been suggested that El Niño Southern Oscillation (ENSO) may influence green turtle nutrient intake, producing a decline in growth rates and delaying sexual maturity (Carrion-Cortez et al. 2010). Nutrient deficiencies caused by ENSO can also reduce the reproductive output of green turtles by not allowing nesting females to reach the required body condition to breed. This may drive inter-annual variation in nesting numbers, as has been reported on the northern coast of Australia (Limpus & Nicholls 1988), and implies that sea turtle remigration intervals can also be influenced by environmental conditions and climate cycles (Carr & Carr 1970, Hays 2000, Solow et al. 2002). Additionally, extreme climatic events such as hurricanes affect up to 97% of the world's sea turtle nesting beaches and are common in coastal areas, impacting turtle populations by changing the quality of nesting habitat through coastal erosion and accretion processes, and reducing hatching and emergence success through nest flooding and erosion (Dewald & Pike 2014). Nonetheless, we did not detect an effect of hurricanes on annual survival or remigration patterns in spite of Aves Island's extreme exposure to wind and wave action.

Number of nesting females on Aves Island

Despite large yearly fluctuations in the number of nesting females, the population of green turtles nesting at Aves Island made a slow but sustained recovery between 1979 and 2009 (Fig. 2D), with the estimated number of nesting females in 2008–2009 at 1283 (95% CI = 1213–1352). In general, such a recovery may be due to increased recruitment, higher juvenile survival, subadult or adult survival, or shorter re-nesting intervals (increased fecundity); however, evidence appears most compelling for increased recruitment. Females nesting at Aves Island in any given year almost certainly skipped breeding the following year, but the probability of returning after a skipped breeding season varied from year to year. Although the recovery of populations elsewhere has been linked to an increase in nesting frequency (Limpus et al. 1994, Troëng & Chaloupka 2007) due to improving food sources (Hirth 1997), we did not observe a reduction in the re-nesting interval during the study period. Annual survival was also variable, but had no clear trend indicating an increase in adult survival. This leaves increased recruitment rates as the most likely explanation. In Australia, for example, Fordham et al. (2007) found that populations

with lower adult survival tended to have higher recruitment rates, which the authors attributed to compensatory density-dependent responses. Changes in the size of nesting females between 1979 and 2009 support the hypothesis of increased recruitment to adult classes on Aves Island; females toward the end of the study period were smaller than they were at the beginning of the study, suggesting that younger turtles nested in more recent years (Fig. 5).

Although human disturbance has been minimal at this rookery in the past 42 years, the number of nesting females appears not to have stabilized, and continues to increase. This population is probably still recovering from past human disturbances on the island, when green turtles were intensely exploited and their nesting habitats were continuously perturbed by commercial guano extraction (Harris 1958, Parsons 1962). Several green turtle nesting populations have increased in the decades following protection from human impact (Chaloupka et al. 2008), demonstrating the importance of long-term conservation programs in green turtle rookeries. However, the low survival of adult female turtles at Aves Island compared with a fully-protected Australian population (in nesting and foraging habitats) suggests that this population may be exposed to higher mortality, possibly in foraging grounds in Nicaragua, the Dominican Republic and/or the Gulf of Venezuela (Solé 1994), which highlights the need to consider these areas in management programs.

CONCLUSIONS

This study presents one of the most comprehensive mark-recapture analyses to date for a green turtle nesting population in the Caribbean, and reveals important patterns in green turtle survivorship and population size. The population at Aves Island is increasing in numbers particularly through the recruitment of smaller nesters, although the nesters' survival is still lower than in other protected populations. Our model successfully accounted for the bimodal behavior of staggered arrival and the monotonically increasing probability of departure of females from the nesting beach, as well as skipped breeding by females (i.e. temporary emigration), and bias in survival estimates resulting from higher apparent mortality of neophyte nesters, due to the higher incidence of tag loss in newly tagged females or presence of transients. As tagging efforts on beaches around the world continue to grow into ever-larger datasets (Bjorndal et al. 1999, Balazs & Chaloupka

2004, Troëng & Rankin 2005, Troëng & Chaloupka 2007, Pfaller et al. 2013), these methods will be increasingly valuable tools for monitoring populations of this endangered species worldwide. Nonetheless, because tag loss after the second year continues to be a potential cause of negative bias in survival estimates, future marking efforts on Aves Island should adopt double-tag application as a standard practice, as have other marking efforts worldwide (Bjorndal et al. 1996).

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