Reproductive synchrony in a recovering bottlenecked sea turtle population

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Summary

1. The assessment of species extinction risk has been well established for some time now. Assessing the potential for recovery in endangered species is however much more challenging, because complementary approaches are required to detect reliable signals of positive trends.

2. This study combines genetics, demography and behavioural data at three different time-scales to assess historical and recent population changes and evidence of reproductive synchrony in a small population of olive ridley sea turtle *Lepidochelys olivacea*. *Lepidochelys* is considered as the most extraordinary example of reproductive synchrony in reptiles, yet to date, it has only been reported in large populations.

3. Using Bayesian coalescent-based models on microsatellite nuclear DNA variability, we demonstrate that effective population size in olive ridleys nesting in French Guiana has dramatically declined by 99% over the last 20 centuries. This low current population size is further illustrated by the absence of genetic mitochondrial DNA diversity in the present nesting population. Yet, monitoring of nesting sites in French Guiana suggests a possible recovery of the population over the last decade.

4. Satellite telemetry shows that over the first 14 days of their 28-days inter-nesting interval, i.e. when eggs maturation is likely to occur, gravid females disperse over the continental shelf. They then gather together with a striking spatiotemporal consistency close to the nesting site, where they later emerge for their second nesting event.

5. Our results therefore suggest that reproductive synchrony also occurs in small populations. Olive ridleys may ensure this synchrony by adjusting the duration of the second half of their inter-nesting interval prior to landing, possibly through social mediation.

6. Such reproductive synchrony may be related to the maintenance of some species-specific strategy despite former collapse and may contribute to the present population recovery. The gregarious behaviour of reproductive individuals close to shore where human-induced perturbations occur is however a cause for conservation concern for this still poorly known species.

Key-words: population history, population recovery, reproductive synchrony, satellite tracking, sea turtles

Introduction

Amongst life-history traits, reproductive synchrony (Darling 1938) is an important reproductive strategy that contributes to population dynamics and species resilience. Reproductive synchrony is the process by which certain plants and animals time their reproduction to be temporally more clustered than would have been explained by environmental seasonality alone (for review see Ims 1990). Reproductive synchrony may occur at different times of the breeding cycle, from gametogenesis to parturition, and is expected to allow populations to persist and grow under environmental and demographic conditions that would otherwise make it impossible

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(Henson, Cushing & Hayward 2011). Previous studies have focused on the proximate factors acting as cues to maintain synchronous breeding within a population, and on the ultimate factors that act as selective forces giving survival values to the adaptation. There is a considerable variation in the degree of synchrony amongst species, and the complex mechanisms underlying this phenomenon are still not fully understood.

So far, three main types of proximate causes for reproductive synchrony have been proposed (review in Ims 1990): environmental cues directly connected to climatic seasonality (e.g. photoperiod, temperature, humidity, food availability, lunar and tidal rhythms); internal cues from the organisms' own endogenous rhythms (i.e. biological clocks); and social cues based on the exchange of signals between individuals within a population. Early studies of reproductive synchrony in colonially nesting birds led to the hypothesis that this behaviour had evolved through reduced risks of predation to individual offspring (Darling 1938). The most widely proposed mechanism for this predator hypothesis is predation dilution by which an individual's risk of predation is reduced owing to lower probability of encountering predators through swamping (Ims 1990). This predator hypothesis has further been validated in numerous species, from corals to mammals (e.g. Gaillard *et al.* 1993; Hovel & Morgan 1997). However, synchronous reproduction is unlikely to have evolved solely in response to predation on offspring (Rutberg 1987). Indeed, synchrony within populations has also been proposed to result from the selection of parturition timing by individuals to produce offspring at the best time for ambient conditions, food and water supply for optimal survival, growth and recruitment (e.g. Rutberg 1987; Ogutu *et al.* 2010). Both predator and seasonality hypotheses may be not exclusive but rather operate over a gradient depending on the actual environmental and ecological contexts (Ims 1990). Further environmental cues may be involved in synchrony, the most widely reported being related to lunar rhythms (e.g. Hanafy *et al.* 2010). Reproductive synchrony may also be socially driven, as shown in mass-nesting marine olive ridley turtle *Lepidochelys olivacea* (Plotkin *et al.* 1997), birds (Henson, Cushing & Hayward 2011) and mammals (e.g. Berger 1992), where egg laying and/or ovulation synchrony increases with population density through pheromonal and/or olfactory cues. Reproductive synchrony may further affect operational sex ratio, extra-pair mating and paternity and ultimately may enhance total population size (e.g. Henson, Cushing & Hayward 2011).

Reproductive synchrony has mostly been investigated in species with parental care. Much less information is available about the mechanisms and adaptive values of synchronous nesting and hatching in species without parental care (but see Spencer, Thompson & Banks 2001 for the freshwater turtle *Emydura macquarii,* Colbert, Spencer & Janzen 2010 for the painted turtle *Chrysemys picta*, Plotkin 2007 for the olive ridley turtle). In the case of sea turtles, females lay eggs at night on tropical sandy beaches without any further care. Amongst sea turtles, the olive ridley turtle is one of the most

extraordinary examples of reproductive synchrony, also referred as *arribada* (Pritchard 1969). Hundreds to thousands of gravid females synchronously come ashore on tropical sandy beaches within a spatially limited area, for a very limited period of time, to lay eggs. *Arribada* have been suggested to result from group-coordinated responses to environmental conditions such as rainfall (Plotkin *et al.* 1997) and/or to hormonally driven physiological cues (Plotkin 2007). However, these hypotheses have not actually been tested. It has been suggested that *arribada* reduce adult female depredation ashore by predator satiation (Plotkin 2007). *Arribada* have also been suggested to enhance multiple mating with genetic benefits to both maternal and offspring fitness (Plotkin 2007), which may partially explain why the olive ridley turtle is considered to be the most abundant sea turtle world-wide (Spotila 2004).

Like other sea turtles, olive ridley turtles are however considered to be an endangered species on a world-wide basis. Sea turtles are emblematic of marine biodiversity erosion as they show some of the sharpest historical population declines (Lotze & Worm 2009), as evidenced by archaeological and historical records of human exploitation on sea turtles (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008), and by more recent demographic surveys of nesting activity (IUCN 2009 Red List). It is therefore critically important to have a sound knowledge of the historical population baseline, current population dynamics and current genetic structures of such endangered species to implement the appropriate conservation strategies. Genetic diversity is critical for the fitness and long-term survival of endangered species (Frankham 2005). In addition, genetic structure and demographic history need to be taken into account for successful conservation action plans (Lande 1988). Yet, recent demographic history has not been investigated in any small sea turtle population. Indeed, the complex reproductive biology of these species (Bowen & Karl 2007), further influenced by global change (Reece, Castoe & Parkinson 2005), has considerably complicated our understanding of their current population dynamics and genetic structures. Furthermore, reproduction and survival of sea turtles are both highly influenced by their ecology at sea, as recently evidenced by satellite telemetry and turtle–fishery interaction models (e.g. Ferraroli *et al.* 2004). Yet the links between individual behaviour at sea, nesting activity on land and expected population restoration have never been concurrently explored in any given sea turtle population.

In this study, we used an original approach based on three different time-scales combining genetic, demographic and behavioural data to investigate recent demographic history and population trend in a population of olive ridleys and examine the potential mechanisms involved in these trends. In this species, *arribada* were historically reported in the large populations in Mexico, Costa Rica, India, and to a lesser extent in Suriname, western Atlantic Ocean (Pritchard 1969). These populations have dramatically declined, mostly due to egg poaching and fisheries bycatch, even though some may have recently started recovering, such as in the Guianas

(Guiana, Suriname, French Guiana; Kelle, Gratiot & De Thoisy 2009). The Guianese olive ridley population is therefore considered now as the largest population in the Atlantic Ocean (Kelle, Gratiot & De Thoisy 2009) and is a case study for recent restoration in a population of marine vertebrates.

Materials and methods

GENETIC ANALYSES

Current genetic diversity of the population and demographic history were investigated using both mitochondrial and nuclear DNA variability. Skin samples were obtained from female olive ridley whilst nesting on beaches of Cayenne and Rémire-Montjoly (French Guiana) in 2006. Sequences ($N = 30$) of cytochrome *b* and control region (mitochondrial DNA) genes were obtained with primers GLUDG tRNA Glu and H THR8 (Shaffer, Meylan & McKnight 1997) and LCM15382 and H879lo (Lopez-Castro & Rocha-Olivares 2005), respectively, using the conditions defined by the authors. All sequences were deposited in the GenBank data base (accession numbers of cytochrome *b* sequences from FJ795374 to FJ795403; accession numbers of control region sequences from FJ795404 to FJ795433). Low diversities on the cytochrome *b* and control region sequences (see Results) precluded any further inference of past demographic investigations with mitochondrial markers.

Nuclear genetic variability was investigated using 11 nuclear microsatellite loci OR1, OR2, OR4, OR7, OR9, Ei8, OR11, OR14, OR16, OR18 and OR22, according to the conditions reported in Aggarwal *et al.* (2004, 2008) for 46 females. Haplotypic and nucleotide diversity in mitochondrial DNA were investigated with DNASP 4.20.2 (Rozas *et al.* 2003). As far as nuclear DNA is concerned, the Markov chain method was used to assess Hardy–Weinberg equilibrium and observed heterozygote excess of microsatellites (GENEPOP 1.2, Raymond & Rousset 1995); nucleotidic diversity was calculated with FSTAT 2.9.3.2 (http://www2.unil.ch/popgen/softwares/fstat.htm). Absence of significant dropout, stuttering and null alleles was confirmed with MICRO-CHECKER 2.2.3. (Van Oosterhout *et al.* 2004; http://www.microchecker.hull.ac.uk/); absence of linkage disequilibrium amongst the 11 microsatellite loci was confirmed with GENEPOP 1.2. We used a Bayesian clustering approach (software STRUCTURE 2.3.1, Falush, Stephens & Pritchard 2007) to determine whether there was any hidden population structure that could falsely generate a signature of population collapse (Wakeley & Aliacar 2001). This method uses a Markov Chain Monte Carlo (MCMC) approach to group individuals into K ($K = 1$ from $K = 4$) populations based on their genotypes without prior information, using the admixture population model, 1 000 000 iterations, 500 000 burn-in replicates and five independent replicates per K value.

Markov Chain Monte Carlo simulations were used to estimate the posterior distribution of the genealogical history, including (i) mutational and coalescent events and (ii) a demographic parameter, including growth rate and time elapsed since expansion or decrease, to assess long-term changes in historical population size. LogCombiner and Tracer (BEAST 1.4.7, Drummond & Rambaut 2007) were used to obtain the ratio between ancestral and current population sizes by combining five runs (2×10^9 iterations each) performed with MSVAR0.4 (Storz & Beaumont 2002). Respective effective ancestral and current population sizes and time since collapse or expansion were obtained in a similar way, with MSVAR0.4 and MSVAR1.3 (Storz & Beaumont 2002). To assess adult population sizes, we used an effective population size/adult population size ratio of 0·08, as this

value is the mean of compiled ratios previously assessed in reptiles (Frankham 1995). A priori mutation rates of nuclear DNA ranged from $5·7 \times 10^{-4}$ to $9·6 \times 10^{-3}$, as previously set in several marine turtle species (Fitzsimmons 1998). Generation time for olive ridley was set at 13 years (Zug, Chaloupka & Balazs 2006). Bottleneck populations can produce distinctive genetic signatures in expected heterozygosity (Cornuet & Luikart 1996). When a population experiences a reduction in its effective size, it generally develops excess gene diversity at neutral loci, because the rare alleles that were lost contributed little to the overall heterozygosity (Cornuet & Luikart 1996). We assessed the olive ridley population for a deficiency of low frequency allele classes using Sign and Wilcoxon tests, as implemented in the program BOTTLENECK (Cornuet & Luikart 1996) under the two-phase mutation model (TPM) with 95% single-step mutations.

NESTING ACTIVITY MONITORING

Nesting beaches at Cayenne/Rémire-Montjoly (French Guiana) were patrolled nightly from sunrise to sunset during the nesting season (early May to early September) from 2002 to 2010 to count individual nesting events and tracks. The Grubbs' test statistic (Snedecor & Cochran 1989) for the detection of outliers, based on median absolute deviation, was used to identify peaks of turtle landing from 2002 to 2008.

SATELLITE TELEMETRY

Ten olive ridley turtles ($N = 5$ in 2006 and $N = 5$ in 2007) were individually equipped with a Satellite Relay Data Logger (SRDL 9000X; Sea Marine Research Unit, SMRU, St Andrews, UK, http://www.smru.st-and.ac.uk/) whilst nesting on beaches at Cayenne/Rémire-Montjoly (French Guiana, $N = 9$) and Eilanti (Suriname, $N = 1$). SRDL units were glued on the highest scale of the carapace using two-component fast set epoxy. Location data were recovered from Collecte Localisation Satellites (http://www.cls.fr) before being processed using IKNOS TOOLBOX software (Tremblay, Robinson & Costa 2009). Saltwater switch data were used to identify haul-out events for defining the start and the end of the inter-nesting period (time between two consecutive nesting events). In addition, SRDLs provided 24-h summary statistics of diving behaviour: these statistics include mean ± SD of dive duration (± 10 s) and dive depth (± 1 m) and were used to assess individual daily diving behaviour. SRDLs also recorded *in situ* water temperatures ($\pm 0·1$ °C).

Results

POPULATION GENETICS AND RECENT DEMOGRAPHIC HISTORY

We investigated the genetic diversity of the olive ridley population nesting in the Guianas with both mitochondrial and nuclear DNA markers. The control region (795 bp) had a nucleotide diversity $\theta = 0·00063 \pm 0·00002$ (mean ± SD) and a haplotype diversity $h = 0·239 \pm 0·096$ for three identified haplotypes. Theta and *h* diversities of the cytochrome *b* (1144 bp) were nil, with only one haplotype observed. For nuclear DNA, simulations revealed that $K = 1$ ancestral population was the most likely (estimated Ln probability of data $= -1378$, vs. -1418 for $K = 2$, -1456 for $K = 3$, -1500 for $K = 4$). Genetic diversity and

observed heterozygosity averaged over loci were 0.61 ± 0.20 and 0.62 ± 0.20, respectively. The population showed a small (Fis $= -0.0075$) departure from the Hardy–Weinberg equilibrium ($P < 0.05$), although both Chakraborty & Jin (1992) and Brookfield (1996) methods did not reveal any significant deviation from panmixia.

The demographic parameters of the Guianese population were investigated using microsatellite variability (see Materials and methods). Significant excess gene diversity suggested a recent population decrease, although only the Sign test was significant ($P = 0.03$). Assessment of ancestral and current population sizes with MCMC simulations supported this result. The mean strength of the posterior distribution of the ratio between ancestral population size N_1 and current population size N_0 was $\log(N_0/N_1) = -2.085 \pm 0.156$ (linear population expansion model) and $\log(N_0/N_1) = -2.106 \pm 0.147$ (exponential population expansion model) (Fig. 1a). The posterior distribution of $\log(T)$, T being the time since the population collapsed, was 2.18 ± 0.30, indicating that the decrease in the Guianese population occurred some 150 ± 10 generations ago, i.e. 1950 ± 130 years ago. The posterior distributions for $\log(N_1)$ and $\log(N_0)$ had very limited overlap of 4.37 ± 0.64 and 1.86 ± 0.35 for N_1 and N_0, respectively (Fig. 1b).

BEACH PATROLLING AND CURRENT POPULATION TRENDS

The nesting activity of the present population was monitored from 2002 to 2010 by daily patrols of the beaches surrounding Cayenne, French Guiana. An average of 2015 ± 284 nests per year was reported (Fig. 2a). Importantly, current field data showed a significant increase in the number of nests per year (Spearman's correlation $R_S = 0.933$, $P < 0.001$, $N = 9$ years, Fig. 2a).

Daily beach patrols performed from 2002 to 2008 also revealed mass landings of nesting turtles with peaks of 104 ± 11 nests (overall mean, $N = 53$ peaks, range 17–335 nests per peak) within 2 ± 0 nights ($N = 53$ peaks, range 1–6 nights). The two largest landings occurred in 2008, when 302 and 319 females emerged in 1 and 2 nights, respectively (Fig. 2b).

SATELLITE TRACKING AND CURRENT AT-SEA BEHAVIOUR

After nesting, the 10 satellite-tracked olive ridley turtles left the beach for 28.5 ± 1.9 days (range 18.0 to 39.8 days, Fig. 3a; Table 1) but remained relatively close to the beach (mean maximum distance from the beach 18.4 ± 2.9 km, $N = 10$ turtles, range 23.8 to 73.8 km, Fig. 3b). A concurrent analysis of dispersion and diving patterns indicated that the inter-nesting period could be divided into two distinct periods. During the first half of the inter-nesting period (14.1 ± 0.6 days, $N = 10$ turtles), turtles dispersed from 17.3 ± 0.1 to 50.8 ± 0.6 km from the beach (overall mean 26.4 ± 3.3 km, $N = 10$ turtles). A wide range of diving
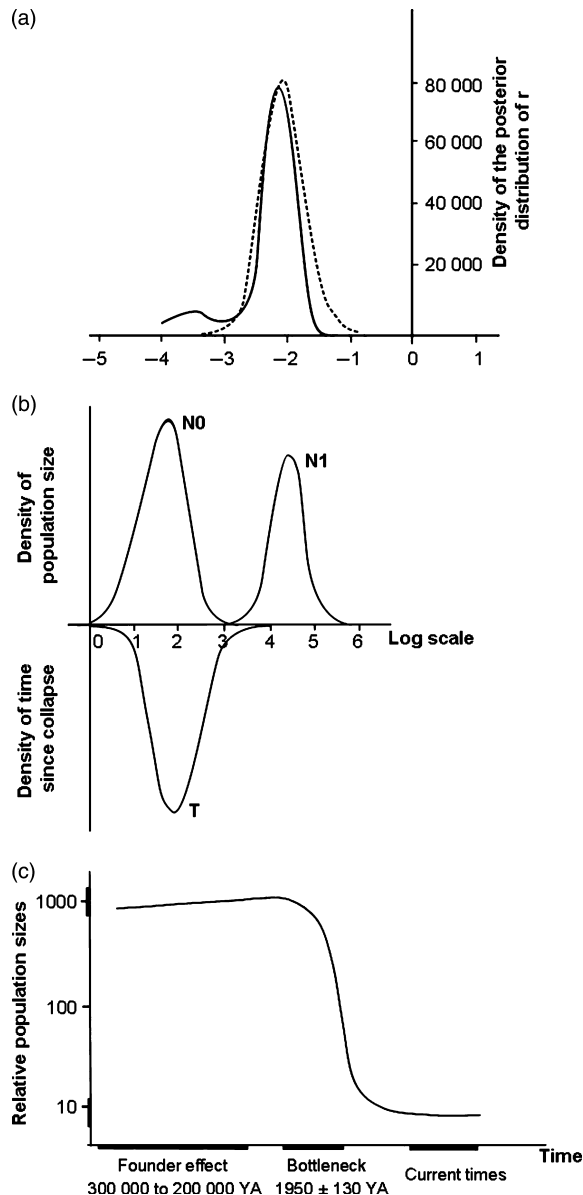

Fig. 1. Demographic history of the Guianese olive ridley population. (a) Population size change. Posterior distribution of $r = N_0/N_1$, representing the ratio on a logarithmic scale of present (N_0) to past (N_1) population sizes. Solid curve: exponential model of population size change; dash curve: linear model of population size change. (b) Past and present population sizes and time since the size has changed. Posterior distributions of past (N_1), current (N_0) and time since collapse (T, in generations). (c) Schematic demographic history of the Guianese olive ridley population. After a founder effect faced by their Atlantic ancestral stock that colonized the Atlantic 300 000–200 000 year ago (YA) (Bowen *et al.* 1998), the population faced a dramatic bottleneck (1950 ± 130 YA), resulting in a 130-fold decrease in the effective population size (this study).

behaviours was observed amongst individuals, with mean dive depths ranging from 6.8 to 37.9 m (overall mean 14.8 ± 3.0 m, overall max $= 50$ m, $N = 10$ turtles) with a mean dive duration of 24.9 to 64.1 min (overall mean 42.6 ± 4.4 min, overall max $= 130$ min, $N = 10$ turtles). During the second half of the inter-nesting period, all turtles
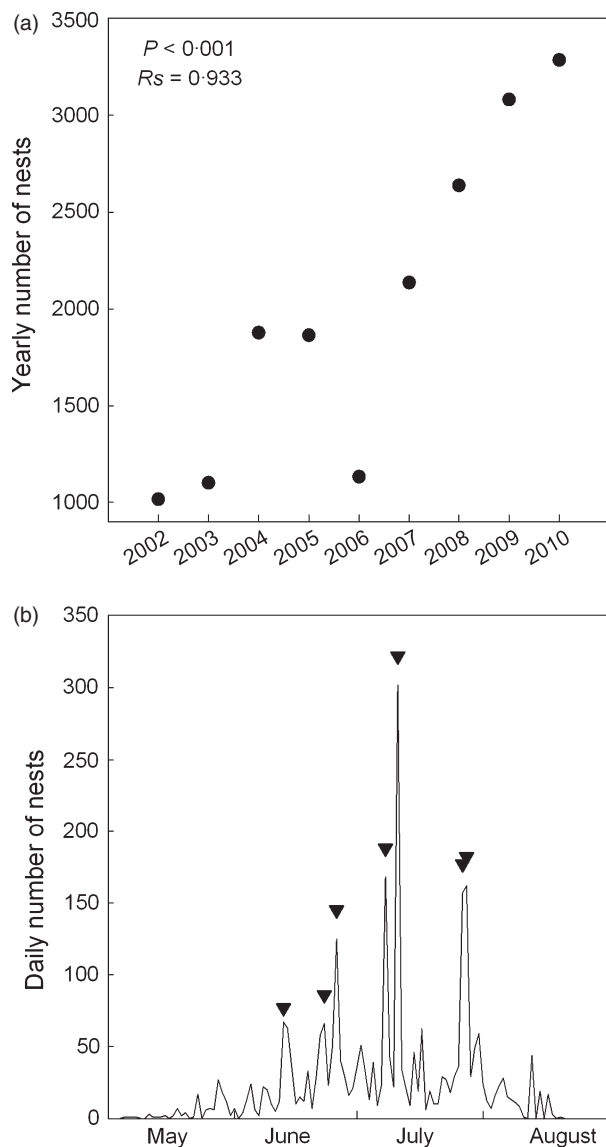
Fig. 2. Nesting activity of the population of olive ridley turtles on Cayenne beaches. (a) Recent annual trends. Yearly nesting activity of olive ridley has been increasing since 2002. (b) Daily nesting activity monitoring. Olive ridley females exhibit landing peaks (black triangle-down, identified by Grubbs' test), indicating an *arribada*-like behaviour (data 2008).

showed a striking consistency in their movements and diving patterns = (Fig. 3b–d). They all returned within very close vicinity of the departure beach (overall mean 8.7 ± 1.5 km, $N = 10$ turtles) in very shallow (< 12 m), relatively warmer waters (phase 1: 27.2 ± 0.1 vs. phase 2: 28.6 ± 0.1 °C; GLMM, with dive depth as covariate: $P < 0.001$, $F = 131.02$, ddl $= 1$). They then all ceased erratic diving in favour of sustained dives, which were systematically regular, constant, very shallow (overall mean 4.1 ± 0.3 m, range 3.4–6.5 m, $N = 10$ turtles) and short (overall mean 6.3 ± 0.9 min, range 3.6–11.6 min, $N = 10$ turtles). These dives differed significantly from those observed in the first phase (GEE$_{depth}$: $P < 0.001$, Wald $\chi^2 = 20.96$, ddl $= 1$; GEE$_{duration}$: $P < 0.001$, Wald $\chi^2 = 73.1$, ddl $= 1$). The

turtles returned ashore for their second nest at locations *c.* 7.8 ± 1.9 km (range 2.9–23.9 km, $N = 10$ turtles) from the first nest.

CUES OF ARRIBADA-LIKE LANDING

There was a negative correlation between the duration of the first phase of the inter-nesting period and the mean water temperature experienced by the 10 satellite-tracked turtles during this phase ($R_S = 0.932$, $P < 0.001$, $N = 10$ turtles). However, no such relation was found during the second phase, or indeed over the entire inter-nesting period ($R_S = 0.04$, $R_S = 0.55$, respectively, $P > 0.05$ in both cases).

Discussion

Investigating historical population baseline, current population dynamics and genetics is critical for assessing population status, particularly in the case of critically endangered species. Major population declines have been reported in both terrestrial (e.g. Goossens *et al.* 2006) and marine vertebrates (e.g. Baker & Clapham 2004), including sea turtles (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008). However, understanding how severely depleted populations can recover has been proved to be much more challenging. This study investigates how a small population of sea turtles may be able to recover owing to its specific reproductive strategy, i.e. reproductive synchrony. This is to the best of our knowledge the first dedicated study based on a multidisciplinary approach at three different time-scales.

RECENT DEMOGRAPHIC HISTORY

Models using Bayesian coalescent-based approach of microsatellite nuclear DNA variability (Storz & Beaumont 2002) have recently allowed the investigation into recent population history in large endangered vertebrates (e.g. Goossens *et al.* 2006). Using similar Bayesian coalescent-based models of microsatellite nuclear DNA variability, our study suggests that the present population of olive ridley turtles nesting in Suriname and French Guiana originates from an ancestral population 130 times larger. This ancestral population may then have experienced a dramatic decline over the last 2000 years and now consists of a non-substructured population, as revealed by Hardy–Weinberg equilibrium. Our simulations suggest that the effective ancestral population was about 20 000 breeding animals, whilst the effective current population is estimated to be between 100 and 150 breeding animals. Simulations of the effective current population correspond to an estimated current population of 1250–1850 breeders. As the ratio of total/efficient population size is not set specifically to olive ridleys, this kind of interpolation should be considered with caution. However, these theoretical estimates correspond very well to our field data of 1343 females nesting yearly, when considering that olive ridley turtles produce on average 1.5 nests per breeding year
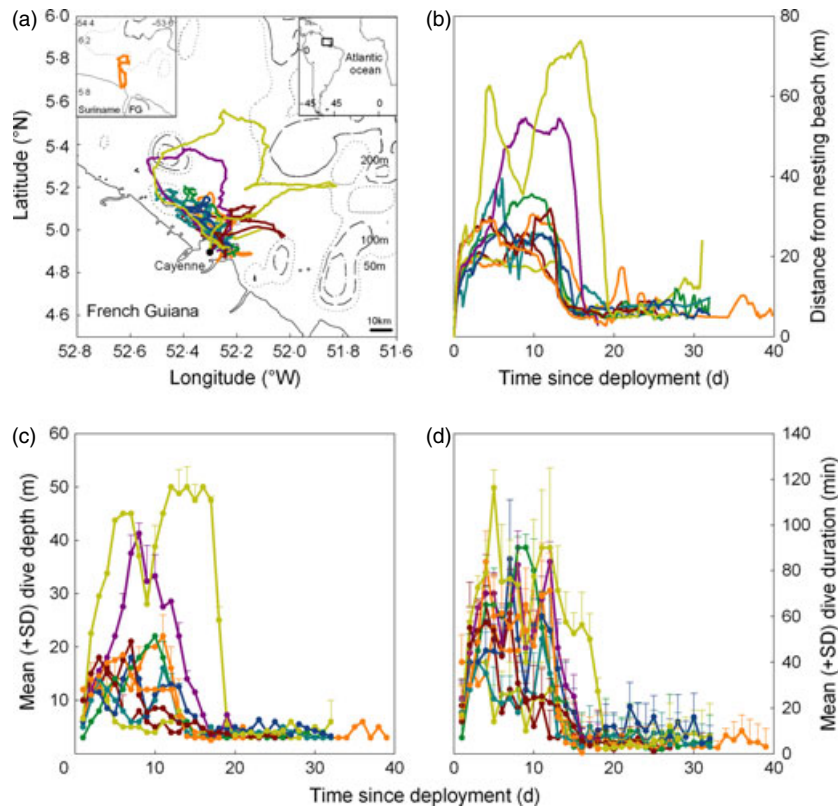
Fig. 3. At-sea ecology of 10 satellite-tracked olive ridley turtles during their inter-nesting period. (a) Reconstructed at-sea movements of olive ridley turtles nesting in French Guiana (FG) and Suriname (insert). The turtles remained in shallow coastal waters between two consecutive nesting events. (b) Distance travelled from the deployment site. The turtles dispersed during the first half of the inter-nesting period before remaining close to the nesting beach for the last 2 weeks spent at sea. (c, d) Diving behaviour, in terms of daily dive depth and duration. Vertical and horizontal patterns amongst individuals were consistent.

(Plotkin 2007), indicating that our simulation outputs are highly reliable.

The magnitude of this 130-fold population decline is similar to that reported in the Caribbean, where today's sea turtle populations (green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata*) represent only 0·3% (i.e. a 333-fold decline) of their historical abundance owing to human exploitation (McClenachan, Jackson & Newman 2006). Similar declines have been reported in populations of whales (99·9% decrease Baker & Clapham 2004), or orang-utans *Pongo pygmaeus* (95% decrease, Goossens *et al.* 2006) for instance, although these massive population collapses occurred over a shorter period of time. Amongst current species declines, the population collapse observed in the Guianese olive ridley is undeniably one of great magnitude.

The recent population decrease suggested by our results is further supported by the significant excess of gene diversity and particularly by the dramatically low level of mitochondrial genetic diversity in the observed control region compared to those reported in Pacific (Lopez-Castro & Rocha-Olivares 2005) and Indian olive ridley populations (Shanker *et al.* 2002; Aggarwal *et al.* 2008). Indeed, such a low DNA diversity may be attributed to two major demographic events: either a founder effect explained by a recent (300 000 years ago) colonization of the western Atlantic by

olive ridley turtles (Bowen *et al.* 1998) or an extensive and recent population collapse as suggested by our results (Fig. 1c). The mitochondrial mutation rate used in our study to estimate when this decline occurred is not specific to olive ridleys, yet it encompasses the range of values calculated for other marine turtles (Fitzsimmons 1998). Accordingly, the time-scale at which the population has been estimated to decline (i.e. during the last 2000 years) should be interpreted as first-order approximation. This is however consistent with archaeological records reporting local overexploitation, leading to the depletion of sea turtles (*Chelonidea*) in Mexico between *c*. 2300 and 5500 years ago (Kennett *et al.* 2008). This bottleneck may be related to human exploitation of sea turtles, both historically and more recently (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008). In the case of the Guianese olive ridley, it is more likely that the collapse observed within the last 2000 years was due to egg poaching and/or selective harvesting of nesting females during mass landing, rather than to more recent interactions with fisheries. Indeed, selective harvest (i.e. of a specific age and sex class) has been reported to drive population fluctuations (Bunnefeld *et al.* 2009). Dramatic environmental effects, which have yet to be identified, may also be linked to the decline in the Guianese olive ridley population.

Table 1. Summary of the horizontal and vertical behaviour during the inter-nesting interval of 10 satellite-tracked olive ridley turtles from French Guiana (N = 9) and Suriname (N = 1*)

	Entire inter-nesting interval (IP)					First phase of the inter-nesting interval (IP1)				Second phase of the inter-nesting interval (IP2)				
Turtle's ID	Duration (days)	Water temperature (°C)	Distance from the beach (km); mean ± SE; [max]	Dive depth (m); mean ± SE; [max]	Dive duration (min); mean ± SE; [max]	Duration (days)	Distance from the beach (km); mean ± SE; [max]	Dive depth (m); mean ± SE; [max]	Dive duration	Duration (days)	Distance from the beach (km); mean ± SE; [max]	Dive depth (m); mean ± SE; [max]	Dive duration (min); mean ± SE; [max]	Distance between the 2 nests' sites
A	27·0	27·0	12·9 ± 0·2 [26·0]	6·0 ± 0·7 [16·0]	16·5 ± 3·4 [65·0]	13·9	18·9 ± 0·2 [26·0]	8·2 ± 1·1 [16·0]	27·2 ± 5·0 [65·0]	13·2	6·5 ± 0·1 [8·9]	3·6 ± 0·1 [4·0]	4·9 ± 0·5 [4·0]	5·7
B	39·8	27·1	12·7 ± 0·2 [30·6]	7·4 ± 0·9 [22·0]	18·3 ± 3·3 [70·0]	15·7	21·1 ± 0·2 [30·6]	13·3 ± 1·3 [22·0]	39·8 ± 4·7 [70·0]	24·1	7·3 ± 0·1 [17·3]	3·7 ± 0·2 [6·0]	4·9 ± 0·5 [10·0]	5·3
C	31·0	27·0	12·2 ± 0·3 [23·8]	4·9 ± 0·5 [14·0]	13·7 ± 2·2 [40·0]	13·9	17·3 ± 0·1 [20·2]	6·8 ± 0·8 [14·0]	24·9 ± 2·7 [40·0]	17·1	8·0 ± 0·1 [23·9]	3·6 ± 0·2 [6·0]	4·9 ± 0·5 [19·0]	23·9
D	31·9	26·5	15·2 ± 0·3 [35·6]	7·3 ± 1·1 [22·0]	26·0 ± 5·1 [90·0]	13·9	26·2 ± 0·3 [35·6]	12·4 ± 1·6 [22·0]	52·4 ± 7·0 [90·0]	18·1	6·7 ± 0·1 [12·0]	3·4 ± 0·1 [4·0]	5·5 ± 0·7 [10·0]	9·1
E	32·0	27·3	14·3 ± 0·2 [39·4]	6·1 ± 0·6 [16·0]	15·0 ± 2·2 [50·0]	11·8	23·3 ± 0·3 [39·4]	9·8 ± 1·0 [16·0]	29·0 ± 2·7 [50·0]	20·2	9·1 ± 0·1 [24·5]	3·9 ± 0·2 [6·0]	3·6 ± 0·6 [12·0]	9·7
F	32·0	27·8	13·4 ± 0·2 [28·5]	7·3 ± 0·4 [18·0]	24·6 ± 1·9 [85·0]	13·8	21·8 ± 0·2 [28·5]	10·8 ± 0·4 [18·0]	42·1 ± 2·5 [85·0]	18·2	7·0 ± 0·1 [17·1]	4·6 ± 0·2 [8·0]	10·4 ± 1·0 [45·0]	5·4
G	18·0	26·3	35·4 ± 0·6 [54·5]	20·4 ± 1·4 [45·0]	47·0 ± 3·1 [100·0]	13·9	39·3 ± 0·6 [54·5]	24·1 ± 1·4 [45·0]	56·5 ± 2·7 [100·0]	4·1	21·7 ± 1·3 [51·4]	6·5 ± 1·0 [12·0]	11·6 ± 2·3 [26·0]	2·9
H	24·1	26·6	16·4 ± 0·3 [54·5]	8·2 ± 0·6 [22·0]	22·4 ± 2·2 [85·0]	14·8	22·8 ± 0·3 [32·0]	11·6 ± 0·7 [22·0]	35·3 ± 2·6 [85·0]	9·3	6·3 ± 0·1 [7·4]	3·5 ± 0·1 [6·0]	4·4 ± 0·6 [20·0]	6·5
I*	20·1	27·1	15·9 ± 0·3 [29·2]	10·7 ± 0·7 [20·0]	41·3 ± 3·6 [95·0]	11·8	22·7 ± 0·2 [29·1]	13·5 ± 0·5 [20·0]	55·1 ± 3·3 [95·0]	8·3	6·3 ± 0·2 [14·5]	4·0 ± 0·4 [10·0]	8·3 ± 1·8 [24·0]	4·6
J	28·0	26·2	35·5 ± 0·7 [73·8]	27·1 ± 1·9 [50·0]	45·0 ± 3·6 [130·0]	17·9	50·8 ± 0·6 [73·8]	37·9 ± 1·5 [50·0]	64·1 ± 3·3 [130·0]	10·1	8·5 ± 0·5 [48·3]	4·5 ± 0·2 [6·0]	4·3 ± 0·6 [6·0]	5·1
All	28·5 ± 1·9	26·8 ± 0·1	18·4 ± 2·9 [73·8]	10·5 ± 2·3 [50·0]	27·0 ± 4·0 [130·0]	14·1 ± 0·6	26·4 ± 3·3 [73·8]	14·8 ± 3·0 [50·0]	42·6 ± 4·4 [130·0]	14·3 ± 2·0	8·7 ± 1·5 [48·3]	4·1 ± 0·3 [6·0]	6·3 ± 0·9 [6·0]	7·8 ± 1·9

Dispersion and diving parameters are given for each individual (turtles' ID from A to J) during their entire inter-nesting interval (IP), and during the two phases of the inter-nesting periods (i.e. IP1 and IP2).

CURRENT OLIVE RIDLEY POPULATION TRENDS IN GUIANAS AND WORLD-WIDE

Despite this relatively recent dramatic decline, the monitoring of nesting beaches in French Guiana reveals that the annual number of nests has increased from *c*. 1000 in 2002 to 3300 in 2010, with an average of 2015 nests per year, i.e. 1343 turtles nesting yearly. In sea turtles, where inter-annual variations in nesting numbers may reflect different remigration intervals, estimates of population trends over such a short period of time should be interpreted with caution (e.g. Hays 2000). However, as olive ridley turtles show a low variability in remigration intervals by nesting every 1 or 2 years (Plotkin 2007), we are confident that our results calculated over 10 years are good estimates of the actual trends of the Guiana's population. With three additional years of data, this study also supports the increase recently reported in the olive ridley nesting population in French Guiana (Kelle, Gratiot & De Thoisy 2009). Such an increase has been interpreted as a shift of nesting females from neighbouring Suriname to French Guiana rather than by recruitment of new breeders (Kelle, Gratiot & De Thoisy 2009). In southern neighbouring Brazil, da Silva *et al*. (2007) suggest that conservation efforts contributed to a 10-fold increase in nesting activity over the last 11 years, resulting in similar population size (2600 nests, i.e. *c*. 1700 breeding females in 2003. At-sea survey estimates of olive ridley abundance in the eastern tropical Pacific also suggest an increase in their population numbers (from *c*. 1·1 million in 1998 to 2·9 millions in 2006), which is consistent with the dramatic increase reported in olive ridley nesting populations over the last decade in Mexico and Costa Rica (see Eguchi *et al*. 2007). In contrast, the olive ridley nesting population in India, renowned for its massive *arribada*, is reported to have declined since 1994 mostly due to fishery-related mortality of adults (Shanker, Pandav & Choudhury 2003). Nevertheless, compared to these large nesting populations found in the Pacific and in India, the size of the Guianese population (1000–5000 effective breeders) even though increasing remains close to the critical level required to maintain long-term evolutionary potential (Lynch & Land 1998). This result suggests that efficiency of reproductive activity may therefore play a critical role in the recovery of this population.

PRESENT BEHAVIOURAL SYNCHRONY IN GUIANESE OLIVE RIDLEYS

In French Guiana, olive ridley turtles show evidence of mass nesting similar to *arribada*, yet to a lesser extent than reported in some of the largest populations in Mexico and Costa Rica (Eguchi *et al*. 2007). First, daily beach patrolling showed that individuals emerge on land during peaks that may account for up to 11% and 12% of the annual nesting activity, and 30% and 32% of the estimated number of breeding females. Secondly, satellite tracking indicated that the mean duration of the inter-nesting interval of olive ridley turtles in the Gui-

anas is similar to inter-nesting intervals of mass-nesting olive ridley in Costa Rica (Plotkin *et al*. 1997; Plotkin 2007). This suggests that in this species, reproduction synchrony is not limited by population size, although mass landing occurs to a lesser extent in smaller populations.

Satellite-relayed behavioural data collected in this study provided further evidence of synchrony patterns during the inter-nesting interval. Until now, our knowledge of at-sea behaviour in olive ridley turtles prior to *arribada* was based on a unique direct observation in Costa Rica, where individuals were reported to gather and remain motionless on the seabed in shallow waters close to the shore (Plotkin, Polak & Owens 1991). Here, we show that gravid olive ridley turtles do not adopt such motionless behaviour during the entire inter-nesting interval. During the first half (14 days) of the 28-days inter-nesting interval, the turtles travelled a fairly long distance (up to 70 km) over the continental shelf whilst performing long (> 40 min) and deep (up to 50 m) dives. This pattern of long and deep dives is quite unlike the simple near-surface and repetitive diving conducted by animals that are simply travelling (e.g. Hays *et al*. 2001) and may rather be interpreted as benthic dives for either resting or foraging purposes (Hays *et al*. 1999; McMahon, Bradshaw & Hays 2007). Such active horizontal and vertical activity during the first phase of the inter-nesting interval is similar to that reported in the leatherback turtle *Dermochelys coriacea* during the nesting season in French Guiana (Fossette *et al*. 2007; Georges *et al*. 2007), which has been interpreted as foraging attempts (Fossette *et al*. 2008).

Several tracking studies in other sea turtle species have shown a common behaviour where breeding females decrease their dive duration in the few days preceding a nesting event (green turtles: Hays *et al*. 1999; hawksbill turtles: Houghton *et al*. 2008; leatherback turtles: Fossette *et al*. 2007; olive ridley turtles: Hamel, McMahon & Bradshaw 2008; this study). This may be related to the approach and selection of the nesting beach. However, the changes in behaviour we recorded are fundamentally different from these other observations, in that we showed a striking consistency across individuals in terms of horizontal and vertical movements, so that they all gathered together close inshore at the same time. Such dramatic behavioural changes strongly suggest a group-coordinated pattern, anticipating a mass landing event.

PROXIMATE CUES OF SYNCHRONY IN THE OLIVE RIDLEY TURTLE

To date, environmental and social cues are the main factors considered to mediate *arribada* in the olive ridley turtle. *Arribada* have been suggested to occur at the end of heavy rainfall in Costa Rica, although this relationship has to be statistically validated (Plotkin *et al*. 1997). However, it is not clear yet how olive ridleys assess rainfall when at sea prior to landing. Moreover, rain rather affects sand humidity which in turn may affect embryonic development and hatching success in sea turtles (Kraemer & Bell 1980). Thus, more investigations are needed to understand the links between

rainfall and *arribada*, and its potential costs/benefits for olive ridley populations.

We found a negative relationship between the water temperature experienced by the turtles and the duration of the first half of the inter-nesting interval, but significance failed for the duration of the second half and for the entire inter-nesting interval. Consistent with the ectothermic physiology of sea turtles, previous studies have reported the inter-nesting interval to increase in cooler waters, with a mean raise from 10 to 25 days for water temperatures declining from 28 to 22 °C (Sato *et al.* 1998; Hays *et al.* 2002). If this relation holds for olive ridleys in French Guiana, where water temperature averages *c.* 27 °C (Table 1), female turtles would perform inter-nesting intervals of about 13 days. However, our results showed that in French Guiana, females performed inter-nesting intervals of 28 days, similar to those reported in olive ridleys nesting in *arribada* in Costa Rica (Plotkin 2007), yet with a first – thermal dependent – phase of 14 days. This suggests that the first half of the inter-nesting interval may be associated with temperature-dependent egg maturation, whereas the second half of the inter-nesting interval may be related to landing synchrony. Indeed, despite the fact that all satellite-tracked females showed a consistent two-phased behaviour at sea, some of them did not lay their first nest during a mass landing event. For instance, turtles B, D, G and H missed a peak by 2–5 days for their first clutch. During the following inter-nesting interval, they then exhibited a regular first phase (*c.* 14 days) but had a longer (turtles B and D) or a shorter (turtles G and H) second phase before they eventually all nested again during a landing peak (Table 2). This suggests that olive ridley turtles adjust the duration of the second part of their inter-nesting period to synchronize their second clutch with a landing peak. The second half of the inter-nesting interval being thermally independent, it is most likely that behavioural synchronization prior to mass landing is socially mediated through pheromone-like exocrine secretions (Weldon *et al.* 1990). Hormone-mediated induction has already been described in social animals from invertebrates to mammals (e.g. Berger 1992; Watson *et al.* 2003).

Conclusions

In French Guiana, where the olive ridley population is recovering from the dramatic collapse of the last 2000 years, gravid females present *arribada*-like behaviour, indicating that reproductive synchrony may occur in small populations. This further suggests that in this population, it is possible that the ancestral *arribada* behaviour has not evolved over the short period since the reported population decline, and that the observed increase in the current population has resulted in the maintenance of this species-specific behaviour. One key result of our work is that olive ridleys synchronize their behaviour at sea before mass landing by adjusting the duration of the second half of the inter-nesting interval whilst maintaining the first half of the inter-nesting interval (when *in utero* egg maturation is likely to occur). Further studies are required to assess the actual costs/benefits of adjusting the duration of each phase of the inter-nesting interval in terms of eggs development and fitness.

Despite the striking consistency observed in their at-sea behaviour, the temporal pattern of the landing peaks of olive ridley turtles in French Guiana is not as clear as those known in larger populations. Further research based on long-term monitoring is required to better assess the potential links between population density and proximate cues. This may be achieved by comparing neighbouring populations presenting synchronous/non-synchronous nesting patterns and/or different population trends. Finally, as we have shown that some synchrony occurs in female olive ridleys, a similar approach should focus on reproductive males to better estimate the reproductive/genetic value of such pattern and ultimately the adaptive value of the observed synchronized behaviour.

Table 2. Summary of the nesting events of 10 satellite-tracked olive ridley turtles from French Guiana ($N = 9$) and Suriname ($N = 1*$)

| Turtle's ID | First nest | | Second nest | |
	Deployment date	No of days before/after a landing peak	Date of the 2nd nesting event	No of days before/after a landing peak
A	30/06/2006 03:33	2/2	27/07/2006 04:03	15/12
B	30/06/2006 08:13	2/2	09/08/2006 03:13	–/1
C	07/07/2006 01:39	5/3	07/08/2006 02:37	26/1
D	07/07/2006 03:35	5/3	08/08/2006 01:05	0
E	20/07/2006 04:00	8/19	21/08/2006 04:00	–/13
F	03/07/2007 05:36	4/3	04/08/2007 04:36	1/4
G	03/07/2007 02:22	4/3	21/07/2007 01:52	0
H	03/07/2007 04:17	4/3	27/07/2007 07:19	0
I*	10/07/2007 05:27	1/7	30/07/2007 06:57	2/4
J	29/06/2007 02:58	0	27/07/2007 03:58	0

The dates of the two nesting events and the time related to an observed landing peak are indicated for each individual (turtles' ID from A to J). '–' means that no landing peak has been identified before the considered nesting event.

In terms of conservation, gathering together in a very restricted coastal area during the last 2 weeks of their inter-nesting interval may expose gravid females to high levels of human activity (e.g. marine navigation, fisheries, pollution) that may jeopardize their survival. As such potential inter-actions are likely to occur during the critical reproductive period, restoration of the small population of olive ridley turtles in the Guianas will depend on adequate conservation strategies ensuring the efficiency of reproductive activity and survival. The immediate mitigation of threats and the fact that this small population has maintained the ancestral *arribada* reproductive strategy are undeniable key factors for the recovery of this species in the western Atlantic Ocean.

Acknowledgements

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