



Paper-efficient multi-species conservation and management are not always field-effective: The status and future of Western Indian Ocean leatherbacks



Linda R. Harris^{a,*}, Ronel Nel^a, Herman Oosthuizen^b, Michael Mejer^b, Deon Kotze^b, Darrell Anders^b, Steven McCue^b, Santosh Bachoo^c

^a Coastal and Marine Research Institute, Department of Zoology, PO Box 77000, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa

^b Branch: Oceans and Coasts, Department of Environmental Affairs, Cape Town, South Africa

^c Ezemvelo KwaZulu-Natal Wildlife, Private Bag X3, Congella, Durban, 4000 KwaZulu-Natal, South Africa

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ABSTRACT

Threatened species are dependent on conservation, with strategic approaches underpinned by the principle of complementarity to find efficient solutions. But are paper-efficient designs always field-effective? After 51 years of monitoring a 56-km-long overlap of two turtle rookeries, there are contrasting population-recovery trends: Vulnerable loggerhead abundance is increasing; and Critically Endangered leatherback abundance is remaining constant, despite leatherback individuals having a higher reproductive output. This questions the efficacy of the conservation programme (annual monitoring and land–sea protection in a World Heritage Site). We use biotelemetry to test if the disparate recovery is biased by differences in detectability in the monitored section of the rookery, and if the reserve confers equal protection. The species' movement ecology contrasts strongly, with implications for nest-event detectability: ~66% of leatherback nesting is outside the monitoring area, compared to ~12% of loggerhead nesting. The marine reserve also strongly favours loggerheads at 95% protection, versus 25% protection for leatherbacks. We hypothesize that variability in leatherback movement ecology, and nest placement, is from ocean currents shaping their behaviour as hatchlings, potentially also determining the proportion of the population at risk of capture in pelagic fisheries. Efficient multi-species conservation strategies need to be carefully designed and adaptive to be effective.

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1. Introduction

A plethora of taxa globally are declining in both species richness and abundance (Dirzo et al., 2014) to the point that both extinction rates and the need for conservation and management interventions are unprecedented (Pimm et al., 2014; Hoffmann et al., 2010). Conserving migratory species is of particular importance given the key role they play in large-scale ecological processes and functions, including capabilities to alter energy, trophic and biodiversity dynamics across multiple habitats (Bauer and Hoye, 2014). However, achieving their conservation is a challenge (Runge et al., 2014): their ranges are too large to feasibly encompass in reserves (Bailey et al., 2012; Stokes et al., 2014; Hays and Scott, 2013), and any initiatives require multi-national co-operation and/or interventions in areas beyond national jurisdiction (Schofield et al., 2013; Ban et al., 2014; Maxwell et al., 2011), neither of which necessarily comes easily. Therefore, strategies with the greatest potential returns for conservation are those that target key bottleneck sites, habitats or refugia along migration routes (Runge et al., 2014; Martin et al.,

2007) and/or critical life-history stages where animals are aggregated at their highest relative densities (Schofield et al., 2013). Two of the most commonly used tools in these cases are protected areas and population monitoring programmes. However, these are rarely implemented with a single species or objective in mind, and are invariably constrained by limited budgets. Thus, understandably, solutions are adopted that are underpinned by the principle of complementarity and efficiency (Chadés et al., 2015; Tulloch et al., 2013). Unless very carefully planned, there is a risk that multi-species or multi-objective plans are (unintentionally) in favour of a single species or objective, which may ultimately bias the perceived and/or actual benefits afforded to the other species or objectives in the long term (e.g., Christianen et al., 2014). In turn, this may compromise the efficacy of the conservation strategy, lead to misinformed threat-status classifications, and/or undermine conservation efforts and investments.

To explore these questions, we consider an exceptional example. Two species of threatened sea turtles nesting in South Africa have received decades of the strongest conservation attention possible: land–sea protection over their breeding grounds in iSimangaliso Wetland Park – a Ramsar Site, World Heritage Site, and Site of International Importance for Sea Turtles – and population monitoring over 56 km of coast during the full six-month-long breeding season for 51 years. The

* Corresponding author at: Department of Zoology, PO Box 77000, NMMU, Port Elizabeth 6031, South Africa.

E-mail address: harris.linda.r@gmail.com (L.R. Harris).

monitored area represents the overlap in the two species' nesting grounds from the Mozambique border to Mabibi (Fig. S1-1); south of this, the nesting density is considered very low and inefficient to monitor. In spite of the enormous investment in turtle conservation, both species have not responded equally: the Vulnerable loggerhead, *Caretta caretta*, population is increasing exponentially (currently ~1000 females nesting per annum), but the Critically Endangered leatherback, *Dermochelys coriacea*, population increased in the first decade of protection but has since remained low (currently <100 females nesting per annum; Nel et al., 2013). This is an interesting conundrum, given that the reproductive biology of leatherbacks suggests that this species should have recovered faster than loggerheads (Nel et al., 2013).

Of the four hypotheses that potentially explain the contrast in population recovery (Nel et al., 2013), differences in detectability of the two species on the nesting grounds appears to have the strongest support. The questions this raises regarding the efficacy of the multi-species conservation and management strategy are imperative to address because, for example, the perceived limited recovery of the leatherback population might in fact be an artefact of lower detectability rather than a true trend. It could also mean that detectability issues are rather reflecting the (fairly arbitrary) configuration of the marine reserve not conferring sufficient protection to leatherbacks (e.g., from fisheries operating in the area) while they are aggregated off the nesting beaches. Because support for the hypothesis of differences in detectability comes from evaluations of data only from inside of the monitoring area (Nel et al., 2013; Thorson et al., 2012), we aim to test the efficacy of the multi-species conservation and management strategy more explicitly using biotelemetry. Specifically, our objectives are to quantify and compare the turtles' (a) internesting movement ecology; (b) detectability, based on nest placement relative to the configuration of the monitoring area; and (c) protection afforded by the two contiguous marine protected areas (MPAs).

2. Methods

2.1. Ethics statement

Satellite tagging was undertaken with ethical clearance from the Nelson Mandela Metropolitan University Animal Ethics Committee: A13-SCI-ZOO-012, and the direct attachment of satellite tags to leatherbacks was done in the presence of a qualified veterinarian.

2.2. Data collection

Sea turtles migrate from distant foraging grounds to their breeding grounds (natal philopatry) where they mate, nest multiple times in one season (internesting period; the focus of this study), and then remigrate back to their foraging grounds. They can nest for several seasons, but not usually in consecutive years (Saba et al., 2007; Hays et al., 2014). Seventeen leatherbacks were each fitted with a Wildlife Computers tag (SPOT 4, SPOT 5 and Splash) or Sirtrack (Kiwisat) tag over several years. Initially, the tags were attached to custom-designed harnesses that were fitted to the first twelve turtles (Fig. S1-2A). More recently, technological advances allowed direct attachment of the Kiwisat tags to the central, cartilaginous ridge of the soft shell (Fig. S1-2B). Tagging took place in the middle of the nesting season, in December (2006: $n = 6$) and January (2008: $n = 3$; 2009: $n = 3$; and 2014: $n = 5$), to facilitate data capture of the turtles' at-sea distributions for multiple research and management objectives. Because the nesting density is so low for these animals, a large area was searched between Adlams Reef (occasionally down to Cape Vidal) and as far north as Black Rock; these vehicle patrols started from Sodwana in 2006–2009, and from Manzengwenya in 2014 (see Fig. S1-1). Similarly, 24 loggerheads were each fitted with a SPOT 5 (Wildlife Computers) or Kiwisat (Sirtrack) tag in December (2010: $n = 12$; and 2011: $n = 9$) and January (2011: $n = 3$). In 2010/2011 loggerheads were satellite

tagged near Bhanga Nek, and in 2011/2012 they were tagged near Manzengwenya, occasionally outside of the monitored area. Tags were attached directly to the loggerheads' hard shell using epoxy adhesive (RS 553-614/850-956 Component quick-set epoxy) and epoxy cement (Sika Anchorfix 2), and painted with anti-fouling paint (Fig. S1-2C). All turtles tagged were sexually-mature females that had hauled out onto the beach to nest, with tagging commencing on their return to the sea. The tags were linked to Service Argos (CLS, 2015), running continuously.

2.3. Data analysis

All analyses were performed in R version 3.0.1 (R Development Core Team, 2012) unless stated otherwise; see also SOM1 for more details on the methods. The raw tracking data were cleaned by implementing the DAR filter in Movebank (www.movebank.org), with filter parameters set following the recommendations by Douglas et al. (2012). With outliers and improbable locations removed, movement tracks for each turtle were reconstructed using state-space modelling (SSM) routines (hierarchical first difference correlated random walks with behaviour switching) using the bsam package (Jonsen et al., 2013), which calls JAGS (Plummer, 2003). These movement tracks were then split into interesting loops by identifying nest events along the track in ArcGIS 10.2 (ESRI), and were converted to trajectories (adehabitatLT; Calenge, 2011). Trajectory parameters, per individual and interesting loop, were then summarized (adehabitatLT; Calenge, 2011) and statistically compared between and within species using appropriate univariate tests for differences, depending on the outcomes of the relevant assumption tests. Detectability was quantified by counting locations of nests along each movement track in different sections along the shore. These data were augmented with those from a snapshot vehicle-patrol survey of nests laid both inside and outside of the monitoring area (Bhanga Nek to Cape Vidal) three days after a very strong wind cleared the beach of all tracks. The number of nests was compared among coastal sections, particularly comparing nest abundance inside and outside of the monitored area. To delineate the turtles' home ranges, we used the movement-based kernel density estimation (MBKDE/BRB) method that calculates animal utilization distributions (UDs) using biased random bridges (Benhamou, 2011; Benhamou and Cornéris, 2010; Benhamou and Riotte-Lambert, 2012). Protection afforded by the MPAs to each turtle species was determined by calculating Zonal Statistics (Spatial Analyst; ArcGIS 10.2) of the turtles' UD within and outside of the MPAs, and compared with paired-sample t-tests.

3. Results

The internesting movement ecology of the two species contrasts strongly, with significant differences in all metrics evaluated (Fig. 1, Table S2-1, see also SOM1). Leatherbacks swim further (mean \pm standard deviation across all internesting loops per species: 461.8 ± 147.0 km), faster (1.9 ± 0.5 km.h⁻¹) and more directionally ($78.3 \pm 19.6^\circ$) during shorter internesting intervals (time between consecutive nesting events; 10.4 ± 2.0 days) compared to that for loggerheads (respectively: 148.3 ± 48.2 km; 0.5 ± 0.2 km.h⁻¹; $87.0 \pm 14.1^\circ$; 13.1 ± 1.5 days). Their net displacement north (61.0 ± 65.4 km), south (86.1 ± 79.0 km) and offshore (59.6 ± 46.1 km) of the nesting beaches is also significantly further than that of loggerheads (respectively: 8.9 ± 11.2 km; 8.2 ± 6.0 km; 8.4 ± 3.4 km).

Within species, leatherbacks show strong variability in internesting behaviour (Figs. 2 and 3). This is best explained by inter-annual variation, and by their remigration-track type following the breeding season – either heading north in the longshore current close along the coast (the “coastal clingers”), or south in the Agulhas Current much further offshore (the “ocean rovers”; see SOM1). By this latter explanatory variable, coastal clingers have significantly shorter (distance)

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