ECOLOGY, REPRODUCTIVE BIOLOGY AND CONSERVATION OF THE LEATHERBACK TURTLE *DERMOCHELYS CORIACEA* (VANDELLI, 1761): A GLOBAL REVIEW WITH IMPLICATIONS FOR GREAT NICOBAR ISLAND, INDIA

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1. SCOPE AND APPROACH OF THE REVIEW

For the Literature Review, greater evidential weight was assigned to leatherback-specific empirical studies, long-term datasets and systematic reviews. Studies concerning other turtle species were used only where they supplied transferable methods or comparative ecological principles. The available literature is geographically uneven. Research is comparatively strong for the Atlantic, Caribbean and eastern Pacific; moderate for the western Pacific and western Indian Ocean; limited for the eastern Indian Ocean; and especially sparse for Great Nicobar Island. Consequently, the literature supports a strong global conceptual framework but does not provide a complete local ecological explanation for the Great Nicobar population, indicating lacunae in research in Great Nicobar.

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2. THEMATIC FRAMEWORK

2.1 Evolutionary Distinctiveness, Taxonomy and Global Distribution

The leatherback is the only extant member of the family Dermochelyidae and represents an evolutionarily distinctive marine-turtle lineage. Fossil material indicates that dermochelyids possessed a much wider historical distribution and were characterised by reduction of the conventional bony shell, loss of keratinised scutes and development of a mosaic of polygonal dermal ossicles (Zvonok, Danilov and Syromyatnikova, 2013). Molecular phylogenetic studies similarly place leatherbacks as an early-diverging marine-turtle lineage distinct from Cheloniidae (Bowen,

Nelson and Avise, 1993). The species combines tropical nesting with temperate and subpolar foraging. Physiological adaptations, including large body size, insulating tissues, counter-current heat exchange and activity-generated heat, permit leatherbacks to exploit waters much colder than those ordinarily occupied by reptiles. Their distribution extends across the Atlantic, Pacific and Indian oceans, with migrations sometimes exceeding several thousand kilometres (James, Davenport and Hays, 2006; Piboon *et al*., 2025).

This global distribution does not imply ecological uniformity. Eastern and western Pacific turtles use markedly different migratory corridors and foraging habitats (Bailey *et al*., 2012), while Atlantic nesting populations also exhibit population-specific movement strategies and reproductive schedules (Dutton *et al*., 2013). Leatherback conservation must therefore operate simultaneously at rookery, regional management-unit and ocean-basin scales.

2.2 Population Structure, Natal Philopatry and Connectivity

Leatherbacks present an important biological paradox: adults undertake basin-scale migrations, yet nesting females display maternally inherited population structure. Early mitochondrial DNA studies revealed shallow global genealogy but significant differentiation among nesting populations, supporting natal homing without deep Atlantic–Indo-Pacific separation (Dutton *et al*., 1999; Bowen and Karl, 2007). Subsequent studies using mitochondrial and nuclear microsatellite markers detected structure that mtDNA alone could not fully resolve. Dutton *et al*. (2013), for example, showed that Atlantic nesting populations could be separated into biologically meaningful stocks through combined marker systems. Long-term identification and genetic evidence from St Croix further revealed close female relatives and probable mother–daughter recruitment, providing direct support for natal philopatry and the delayed benefits of nest protection (Dutton *et al*., 2005).

The Andaman Sea evidence is especially relevant to Great Nicobar. Piboon *et al*. (2025) reported multiple mitochondrial haplotypes and two genetic clusters among Thai nesting areas, suggesting that incompletely sampled or cryptic population units may persist in the eastern Indian Ocean. However, the genetic relationship among Thai, Andaman–Nicobar, Sri Lankan, Indonesian and western Indian Ocean rookeries remain unresolved.

2.3 Reproductive Cycles, Clutch Frequency and Remigration

Leatherback reproduction involves repeated nesting within a season, followed by one or more non-breeding years. Individual females commonly return at intervals of approximately 9-11 days during a nesting season, although clutch frequency and remigration vary among individuals, populations and environmental conditions. At Pacuare, Costa Rica, long-term monitoring produced an estimated remigration interval of approximately 2.5 years and demonstrated a positive relationship between female body size and clutch size (Rivas, Fernández and Marco, 2015). At St Croix, robust-design capture–mark–recapture indicated an annual nesting probability of about 0.46, equivalent to an average remigration interval of approximately 2.2 years (Dutton *et al*., 2005). In Gabon and Congo, Casale *et al*. (2023) estimated a mean inter-nesting interval of 10.13 days, a bias-corrected remigration interval of 2.33 years and approximately 5.0–7.7 clutches per female per season.

These estimates demonstrate why annual nest totals cannot be interpreted directly as numbers of breeding females. Nest counts are affected by clutch frequency, remigration, nesting outside monitored sectors, observer effort, tag loss and variation in the probability of encountering individual females. Long-term individual histories are therefore essential for estimating reproductive parameters and population trends. Reproductive schedules are also influenced by foraging success. Atlantic populations using more productive feeding environments generally show shorter remigration intervals and greater

reproductive output than eastern Pacific populations inhabiting less predictable systems (Saba *et al*., 2008). Thus, reproductive output observed on a beach may partly reflect ecological conditions encountered thousands of kilometres away.

2.4 Nesting-Site Fidelity and Inter-Nesting Movement

Leatherbacks generally exhibit nesting-site fidelity, but it is probabilistic rather than absolute. Casale *et al*. (2023) found that movements between successive nesting events were usually local, averaging approximately 4.1 km, whereas movements between breeding seasons averaged approximately 25.1 km. However, Byrne *et al*. (2009) recorded individual females travelling hundreds of kilometres during inter-nesting intervals. Satellite telemetry in Gabon similarly showed that females regularly moved beyond protected-area boundaries during the breeding season (Witt *et al*., 2008). Great Nicobar females may therefore use multiple beaches, offshore resting areas and waters outside any narrowly defined nesting-beach protection zone. A turtle encountered for the first time should not automatically be classified as a new recruit. It may previously have nested on an unsurveyed beach, avoided detection or lost its tags (Chevallier, Mourrain and Girondot, 2020; Casale *et al*., 2023). This has direct implications for estimating recruitment and philopatry.

2.5 Nesting-Beach Selection and Geomorphology

Leatherbacks generally select broad, accessible beaches with relatively steep profiles, coarse or permeable sand, unobstructed access and proximity to deep water. Nevertheless, the effective nesting area may be much smaller than total beach area. At Yalimapo–Awala, suitable nests were concentrated within a restricted portion of the physical beach, producing density-dependent nest overlap and destruction (Girondot *et al*., 2002). Beach elevation, width, slope, vegetation, sand texture, water table, tidal reach and seasonal erosion influence nest placement and survival. On Bioko Island, clutch elevation relative to the high-tide line was among the strongest predictors of hatching success, with vegetation distance, grain size, temperature and conductivity also contributing (Veelenturf *et al*., 2021). At Grande Riviere, Trinidad, seasonal erosion altered the distribution of nesting activity and increased risks in foreshore zones (Mycoo and Gobin, 2013). In French Guiana, dynamic mudbanks and erosion were estimated to destroy a substantial proportion of nests in some years (Chevallier *et al*., 2023). These findings show that nest counts alone do not measure habitat quality. Great Nicobar requires repeated beach-profile measurements, erosion–accretion mapping and nest-level elevation data linked to reproductive outcomes.

2.6 Egg Production, Incubation and Embryonic Development

Leatherback clutches normally contain yolked eggs together with variable numbers of smaller yolkless eggs. Hatching success is often lower and more variable than in other sea turtles. Variation may arise from infertility, early embryonic mortality, microbial activity, altered gas exchange, waterlogging, extreme temperature, predation, contamination and management practices. Dennis *et al*. (2020) recorded very low average hatching success in sampled St Kitts nests and found that many failed eggs showed no visible embryonic development. Associations were reported between certain trace elements and hatch success or pathological conditions, although causation was not established.

Nest relocation can prevent complete loss from erosion, inundation or poaching, but it introduces additional risks. At Pacuare, increasing relocation distance was associated with lower hatching success, suggesting that handling time, vibration, rotation or thermal exposure during transport may affect embryos (Quesada-Rodríguez *et al*., 2021). Studies in the Dominican Republic similarly found that relocation outcomes varied among sites and could alter incubation duration or hatching success (Revuelta *et al*., 2014). Relocation should therefore be treated as a targeted risk-response measure, not as an

automatically superior alternative to natural incubation.

2.7 Temperature-Dependent Sex Determination and Climate Change

Like other marine turtles, leatherbacks exhibit temperature-dependent sex determination: relatively cool incubation produces more males, whereas warmer incubation produces more females. Temperature also influences incubation duration, embryonic survival, hatchling morphology and locomotor performance. Large longitudinal datasets show declining incubation duration consistent with warming and increasing female bias, although the pattern varies among beaches and seasons (Ceriani and Casale, 2025). Cooler seasonal periods, shaded sectors and thermally buffered beaches may function as male-producing refugia. Temperature does not act independently. Rainfall, sand moisture, grain size, nest depth, vegetation, clutch metabolism and nest density modify the thermal environment. Girondot et al. (2002) further demonstrated that nest destruction can interact with seasonal temperature patterns: early, cooler and potentially male-producing nests remain in the sand longer and may face greater exposure to destruction, producing an additional pathway towards feminisation. No direct evidence in the earlier literature establishes pivotal temperature, transitional range of temperatures, primary sex ratio or thermal mortality thresholds for Great Nicobar leatherbacks.

2.8 Hatchling Emergence, Orientation and Early-Life Performance

Hatchling production must be separated into hatching success, emergence success and successful entry into the sea. Substrate compaction, nest depth, roots, logs, erosion scarps and artificial illumination can affect emergence and sea-finding. Bourgeois *et al*. (2009) demonstrated that artificial lighting significantly altered leatherback hatchling orientation in Gabon. Moon phase and landward silhouettes modified this response, while badly positioned obstacles could intensify disorientation. Artificial lighting therefore represents both a behavioural and energetic threat: disoriented hatchlings travel farther, remain exposed longer and may reach the sea in poorer physiological condition. Reference intervals for hatchling morphometry and blood variables are beginning to provide tools for assessing early-life health (Perrault *et al*., 2022). Comparable baselines do not exist for Great Nicobar.

2.9 Morphometry, Growth, Body Condition and Maternal Investment

Leatherback growth was once commonly represented by asymptotic models. More recent evidence supports biphasic indeterminate growth: rapid juvenile growth followed by slower but continuing adult growth (Chevallier, Mourrain and Girondot, 2020). Adult growth has also been detected in long-term African capture histories (Casale *et al*., 2023). Adult female size varies among populations and may reflect juvenile growth, foraging conditions, age structure and selective mortality. Atlantic and western Indian Ocean females are generally larger and may have greater reproductive output than many eastern Pacific females (Saba *et al*., 2008). Foraging leatherbacks may also be substantially heavier than nesting females of comparable carapace length because reproductive migration and egg production deplete energy reserves (James *et al*., 2005). Georges and Fossette (2006) developed approaches for predicting body mass, while Robinson *et al*. (2017) emphasised standardisation of curved carapace-length measurements. Without standardised protocols, geographic or temporal differences may partly reflect measurement error.

Great Nicobar lacks validated body-mass equations, adult condition indices, hatchling morphometric baselines and analysis of relationships among maternal size, clutch characteristics and reproductive success.

2.10 Oceanic Movement and Foraging Ecology

Satellite telemetry transformed the perception of leatherbacks from nesting-beach animals into highly mobile oceanic predators. Hays *et al*. (2006) showed that Atlantic females frequently moved

and foraged opportunistically rather than occupying only a small number of fixed feeding grounds. Diving behaviour changed with latitude, time of day and presumed prey distribution. Bailey *et al*. (2012) demonstrated marked segregation between eastern and western Pacific movement systems. Western Pacific turtles used multiple dispersed foraging regions, while eastern Pacific females moved principally into the south-eastern Pacific. Within the Indian Ocean, tracking from Little Andaman showed post-nesting migrations towards Western Australia, Mozambique and Madagascar, using both direct oceanic and shelf-associated pathways (Swaminathan, Namboothri and Shanker, 2019). This is the most geographically relevant movement evidence for the Nicobar context, but it does not establish whether Great Nicobar turtles use identical routes. Movement analyses are increasingly combining horizontal locations, diving behaviour, oceanographic data and fisheries-risk surfaces. Such integration is essential because a surface track alone does not reveal feeding behaviour, depth-specific fishing interaction or mortality exposure.

2.11 Trophic Ecology and Environmental Forcing

Leatherbacks specialise on gelatinous zooplankton. Stable-isotope studies, telemetry and acoustic prey surveys have improved understanding of this trophic relationship (Seminoff *et al*., 2009; Dodge, Logan and Lutcavage, 2011; Graham *et al*., 2010). Saba *et al*. (2008) proposed a bottom-up pathway in which climate variability affects ocean productivity, gelatinous prey, maternal energy accumulation and ultimately reproductive frequency and clutch output. Eastern Pacific leatherbacks occupy comparatively unpredictable foraging systems, helping explain their smaller size, reduced reproductive output and greater demographic vulnerability. Satellite chlorophyll, sea-surface temperature, upwelling and net primary productivity remain indirect proxies. Hays *et al*. (2006) showed that turtles sometimes displayed intensive local use without an obvious surface oceanographic signature. Direct prey sampling is therefore needed to validate remotely sensed habitat models.

2.12 Health, Contaminants and Biological Associations

Leatherback health studies have expanded from gross measurements to plasma biochemistry, haematology, endocrine stress markers, pathology, contaminants and immunogenetics. Blood variables can provide reference information, but interpretation must account for reproductive state, capture method, body condition and handling time (Hunt *et al*., 2016; Kucinick *et al*., 2024). Necropsy evidence from Brazil identified trauma, fisheries interaction and pathological changes during an unusual mortality event (Santos-Costa *et al*., 2020). Contaminants and plastics are additional concerns because leatherbacks may mistake floating debris for gelatinous prey. Epibiont assemblages may also provide information about habitat use, health and movement history, although these relationships remain insufficiently tested (Robinson *et al*., 2016). No systematic contaminant, pathology, blood-health or plastic-ingestion baseline is available for the Great Nicobar nesting population.

2.13 Population Trends and Monitoring Bias

Long-term studies show sharply contrasting trajectories. Florida nesting increased significantly during a 30-year period (Stewart *et al*., 2010), while eastern Pacific populations underwent severe declines. Within Panama, individual beaches displayed increasing, declining or stable trends even though pooled effort-adjusted results suggested broader stability (Gutiérrez Parejo *et al*., 2025). These differences demonstrate that aggregation can conceal local declines. Conversely, increases in nest numbers may reflect higher clutch frequency or temporary improvements in female condition rather than growth of the adult population. Environmental variation can therefore mask underlying demographic decline.

Monitoring is affected by:

- Unequal patrol effort and incomplete temporal coverage.
- Nesting outside monitored sectors.
- Multiple nesting by the same female.
- Non-annual breeding and variable remigration.
- Failed nesting attempts and unidentified tracks.
- Tag loss and tag-induced injury.
- Imperfect detection of tagged females.
- Population interchange among neighbouring beaches.

Casale *et al*. (2023) showed that double-tag loss could become substantial over a decade. Reliable monitoring should combine flipper tags, PIT tags, photographic or genetic identification, effort records and open-population capture–recapture models.

2.14 Threats and Conservation Interventions

Leatherbacks face threats across every life stage. On nesting beaches, these include egg collection, predation, erosion, inundation, artificial lighting, vehicles, tourism, sand extraction, waste, coastal engineering and habitat loss. At sea, fisheries bycatch, vessel strikes, entanglement, plastic ingestion, pollution and climate-driven prey redistribution are major risks. Population modelling consistently shows that protecting eggs alone cannot compensate for high mortality of juveniles and adults (Santidrián Tomillo *et al*., 2008). Nevertheless, sustained nest protection can generate measurable recovery where adult survival is also maintained, as demonstrated at St Croix (Dutton *et al*., 2005).

Protected areas must correspond to actual space use. Telemetry studies show that inter-nesting females frequently move outside protected boundaries (Witt *et al*., 2008). Dynamic fisheries management, gear modification, bycatch monitoring and multinational cooperation are therefore necessary alongside beach protection. For Great Nicobar, conservation planning should integrate nesting beaches, offshore inter-nesting habitat, migratory corridors, development impacts, fisheries interaction and disaster-related coastal change within a single adaptive framework.

3. EVOLUTION OF THE LITERATURE

3.1 Descriptive Natural-History Phase: Before the 1990s

Early work concentrated on nesting behaviour, clutch composition, morphology and broad distribution. Investigators relied mainly on direct beach observation, measurements, tagging and descriptive comparisons (Hirth, 1980). Leatherbacks were studied chiefly when females emerged to nest, leaving males, juveniles and the oceanic phase largely unknown.

3.2 Molecular and Standardisation Phase: 1990s

Research expanded into evolutionary relationships, stock identification and standardised conservation methods. Molecular phylogenetics clarified the leatherback's position among marine turtles (Bowen, Nelson and Avise, 1993), while mtDNA studies revealed shallow global genealogy but significant rookery structure (Dutton *et al*., 1999). Standard field manuals promoted consistent measurement, tagging, nest excavation and data recording (Eckert *et al*., 1999).

3.3 Telemetry and Demographic Phase: 2000–2009

Satellite telemetry revealed transoceanic movement, inter-nesting dispersal and population-specific foraging strategies (James, Eckert and Myers, 2005; Hays *et al*., 2006; Witt *et al*., 2008). Capture–mark–recapture and genetic identification improved estimation of nesting probability, remigration and recruitment (Dutton *et al*., 2005). Research also shifted from single-factor descriptions towards ecological mechanisms. Oceanographic data were linked to foraging and reproduction (Saba *et al*., 2008), while models evaluated the demographic consequences of egg harvest and adult mortality (Santidrián Tomillo *et al*., 2008).

3.4 Integrative Spatial-Ecology Phase: 2010–2019

The 2010s brought larger multi-site datasets, hierarchical trend models, mixed molecular markers, stable isotopes and more explicit treatment of habitat risk. Long-term modelling demonstrated contrasting population trends (Stewart *et al*., 2010), while combined mtDNA and microsatellite studies improved stock discrimination (Dutton *et al*., 2013). Researchers increasingly connected nest location with erosion, elevation, artificial light and coastal development (Mycoo and Gobin, 2013; Revuelta *et al*., 2014). Indian Ocean tracking began to reveal connectivity between the Andaman region and distant foraging areas (Swaminathan, Namboothri and Shanker, 2019).

3.5 Data-Intensive and Climate-Responsive Phase: 2020 Onwards

Recent research is more longitudinal, bias-aware and management-oriented. It employs:

- Robust-design and multistate capture–mark–recapture.
- Hidden Markov behavioural models.
- Thermal drones and remotely piloted aircraft.
- Digital elevation models and repeated topographic surveys.
- Genome-wide and reproductive-genetic tools.
- Large incubation-duration datasets as climate proxies.
- Dynamic fisheries-risk modelling.
- Integrated health and contaminant assessment.

Examples include long-term African reproductive-demography modelling (Casale *et al*., 2023), spatially explicit erosion assessment (Chevallier *et al*., 2023), large-scale climate-related incubation analysis (Ceriani and Casale, 2025), thermal-UAS monitoring (Wilson *et al*., 2025) and reproductive-genetic investigation of multiple paternity (Bispo *et al*., 2025).The perspective has consequently shifted from "how many turtles or nests occur?" to "which biological, environmental and observation processes generate the apparent trend and which intervention changes survival or recruitment?".

4. EVIDENCE MAP BY THEME AND REGION

Theme	Global evidence	Indian Ocean evidence	Great Nicobar evidence
Evolution and taxonomy	Strong historical and molecular foundation	General distributional context	No primary site-specific evidence
Reproductive cycles	Strong long-term estimates from Atlantic and Caribbean	Fragmentary regional summaries	No reliable local clutch-frequency or remigration estimate
Nesting-site fidelity	Strong tagging and telemetry evidence	Limited movement evidence	Unquantified
Beach geomorphology	Strong studies from Atlantic and Caribbean beaches	Limited comparable leatherback work	No integrated beach-profile study identified
Incubation and TSD	Moderate-to-strong global evidence	Scattered Thailand/regional information	No pivotal-temperature or sex-ratio data
Morphometry and growth	Moderate global standardisation and growth evidence	Comparative size information	No validated local baseline

Oceanic movement	Strong Atlantic and Pacific telemetry	Important Little Andaman tracks	Great Nicobar routes unresolved
Foraging ecology	Moderate telemetry, isotope and prey studies	Weak direct prey evidence	No local or linked offshore study
Genetics and stock structure	Strong mtDNA and microsatellite evidence	Emerging Thailand/Indo-Pacific evidence	No definitive stock assignment
Health and contaminants	Moderate but geographically restricted	Very limited	No systematic baseline
Fisheries bycatch	Recognised as a major global threat	Poorly quantified by stock and route	Local exposure and mortality unknown
Monitoring bias	Strong recent statistical treatment	Limited application	Tag loss and detection probability unknown
Conservation interventions	Numerous beach-level programmes	Variable and incompletely evaluated	Effectiveness not evaluated rigorously
Climate vulnerability	Growing thermal and erosion literature	Limited long-term datasets	No integrated climate-risk assessment

5. GAP TABLE: GLOBAL, INDIAN OCEAN AND GREAT NICOBAR

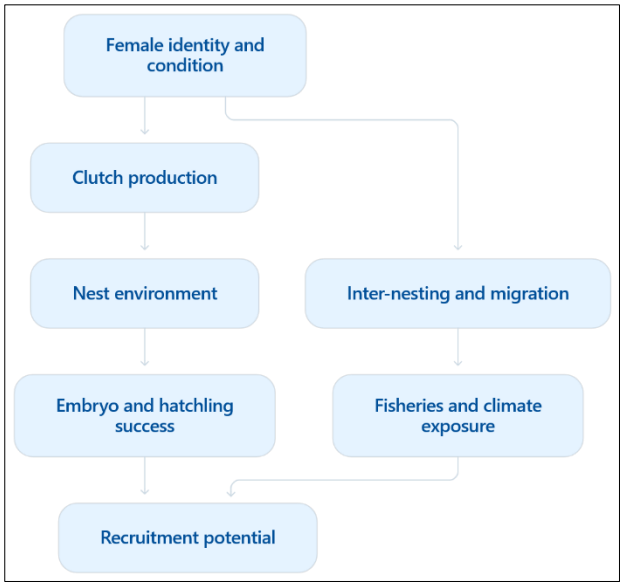
Research domain	**Established global knowledge**	**Indian Ocean evidence**	**Critical Great Nicobar gap**
Population identity	Rookery structure detectable using mtDNA and nuclear markers	Regional structure suggested but incompletely sampled	Genetic identity and management-unit membership unknown
Nesting abundance	Long-term standardised monitoring can detect trends	Uneven and discontinuous coverage	No bias-corrected long-term abundance estimate
Clutch frequency	Commonly around 5–8 clutches, but population-specific	Few robust estimates	Unknown
Remigration	Usually approximately 2–4 years, environmentally variable	Poorly quantified	Unknown
Inter-nesting habitat	Females may range far beyond the nesting beach	Limited telemetry	Spatial extent and protected-area adequacy unknown
Nest-site selection	Influenced by elevation, slope, vegetation and tidal risk	Limited regional validation	Predictors of nest placement unknown
Incubation environment	Temperature, moisture and gases jointly affect development	Sparse rookery-scale datasets	Thermal, moisture and gas profiles absent
Sex ratio	Warmer incubation generally produces females	No comprehensive eastern Indian Ocean series	Primary sex ratio and male-producing refugia unknown
Hatch success	Controlled by interacting natural and anthropogenic factors	Highly variable and inconsistently monitored	Causes and stages of embryo mortality unresolved

Adult growth and condition	Continued adult growth and population size differences documented	Limited standardised regional comparisons	Local growth, body condition and maternal investment unknown
Migration and foraging	Population-specific corridors and flexible foraging established	Little Andaman tracks show basin-wide movement	Great Nicobar routes, prey fields and connectivity unknown
Adult survival	Dominant driver of population persistence	Few stock-specific estimates	Survival and cause-specific mortality unknown
Bycatch	Major global driver of decline	Distribution recognised but mortality poorly quantified	Fisheries overlap and bycatch rate unknown
Climate change	Warming, feminisation, erosion and inundation increasingly documented	Limited long-term empirical tests	Compound thermal–erosion–inundation risk unknown
Conservation effectiveness	Egg protection helps but cannot offset high adult mortality	Mostly programme descriptions	Intervention effects lack controlled evaluation
Monitoring performance	Detection, effort and tag loss can be modelled	Rarely incorporated systematically	Magnitude of bias unknown

6. THE ULTIMATE RESEARCH GAP

The ultimate gap is not merely the absence of another nesting census. It is the absence of a long-term, integrated and bias-aware study connecting Great Nicobar nesting ecology, reproductive performance, individual life histories, beach processes and offshore connectivity. The reviewed literature usually investigates these components separately. Telemetry studies rarely measure nesting-beach thermal ecology; incubation studies seldom identify maternal histories; genetic studies do not usually link stock identity with individual reproductive performance; and beach-conservation programmes often measure hatchling output without evaluating adult survival or offshore mortality.

A Great Nicobar study would therefore be most original if it developed a linked evidence chain:



6.1 Principal Unaddressed Gaps

- Lack of long-term, individual-based reproductive parameters for Great Nicobar.

- Absence of detection- and effort-corrected estimates of annual nesting females.
- Unknown genetic relationship between Great Nicobar and other Indian Ocean rookeries.
- Insufficient understanding of whether Great Nicobar females constitute one rookery or a network of interchangeable nesting beaches.
- Absence of integrated geomorphological, thermal and hydrological assessment of nests.
- No quantified primary sex ratio or identification of male-producing thermal refugia.
- Limited information on causes and developmental stages of egg failure.
- No local adult body-condition or maternal-investment model.
- Unknown offshore inter-nesting habitat and migratory corridors.
- Poorly quantified overlap with artisanal, coastal and pelagic fisheries.
- No evaluation of how coastal development, lighting and vessel activity affect nesting females and hatchlings.
- No controlled comparison of in-situ incubation, relocation and hatchery management.
- Absence of an integrated population model combining reproductive output and survival.
- Insufficient assessment of cumulative climate, infrastructure and disaster-related impacts.
- Lack of a monitoring framework explicitly estimating tag loss and imperfect detection.

7. RESEARCH QUESTIONS REQUIRING INVESTIGATION

- What are the annual nesting abundance and temporal trend of leatherbacks on Great Nicobar after correcting for patrol effort and imperfect detection?
- What is the inter-nesting interval, clutch frequency, seasonal residence time and remigration interval of individually identified females?
- Do Great Nicobar females use discrete nesting beaches, or do they move among beaches within and between reproductive seasons?
- Which beach characteristics—elevation, width, slope, grain size, moisture, vegetation and distance from high tide—predict nesting and hatching success?
- How do erosion, accretion, tidal inundation and storm events affect nest loss?
- How do nest temperature and moisture vary spatially, seasonally and with nest depth?
- What is the pivotal temperature, transitional temperature range and seasonal hatchling sex-ratio pattern?
- At what developmental stages does embryonic mortality occur and which environmental or pathological variables explain it?
- How are female size and body condition related to clutch size, egg dimensions, hatch success and hatchling size?
- Are local body-size distributions changing through recruitment, selective mortality or changing foraging conditions?
- What is the genetic relationship of Great Nicobar leatherbacks to Little Andaman, Thailand, Indonesia, Sri Lanka and western Indian Ocean populations?
- Where do females remain during inter-nesting intervals and what post-nesting migratory routes and foraging areas do they use?
- Which fishing gears, seasons and locations produce the greatest overlap with leatherback habitat?
- Do artificial lighting and coastal infrastructure alter nesting-site selection or hatchling orientation?
- Does nest relocation improve net hatchling production after accounting for transport distance, incubation duration and sex-ratio effects?
- How much do tag loss, missed encounters and beach switching bias estimates of recruitment, survival and population size?

- Which combination of nest protection, habitat management and fisheries mitigation produces the greatest demographic benefit?

8. TESTABLE HYPOTHESES

- **H1:** Annual nest counts differ significantly from the trend in the number of nesting females because clutch frequency and remigration probability vary among years.
- **H2:** Females exhibit significant nesting-area fidelity, but movement among Great Nicobar beaches causes underestimation of clutch frequency at individual index beaches.
- **H3:** Nests at higher elevations and farther above the high-tide line have greater hatching and emergence success than low-elevation nests.
- **H4:** Extreme nest temperature and moisture, rather than temperature alone, best predict embryonic mortality.
- **H5:** Incubation temperatures produce a predominantly female hatchling population, but shaded or early-season sectors function as male-producing refugia.
- **H6:** Larger females produce larger clutches or eggs and greater total hatchling biomass, but not necessarily higher proportional hatching success.
- **H7:** Relocated nests have lower or more variable hatching success than safe in-situ nests after controlling for beach sector and laying date.
- **H8:** Relocation distance and handling duration are negatively associated with hatching success.
- **H9:** Great Nicobar leatherbacks constitute a genetically differentiated nesting unit within the eastern Indian Ocean.
- **H10:** Post-nesting females use more than one migratory corridor and connect Great Nicobar with both eastern and western Indian Ocean foraging areas.
- **H11:** Productive foraging conditions before migration are associated with shorter remigration intervals and greater reproductive output.
- **H12:** Fisheries-risk exposure is concentrated in identifiable seasonal corridors rather than being uniformly distributed.
- **H13:** Multi-method identification using PIT tags, flipper tags and photographic or genetic identity produces higher detection probability and lower apparent recruitment than flipper tagging alone.
- **H14:** Coastal lighting significantly increases hatchling angular deviation, travel distance and time required to reach the sea.
- **H15:** A population model incorporating adult survival predicts substantially different trajectories from one based only on nests or hatchlings.

9. OVERALL SYNTHESIS

Leatherback research has developed from descriptive nesting observations into an integrated science combining genetics, telemetry, reproductive demography, climate analysis, health assessment and spatial conservation. Its central conclusion is that nesting beaches and oceanic habitats form one connected demographic system. Reproductive performance is influenced by female condition and distant foraging environments; nest survival depends on dynamic beach and incubation processes; and population persistence remains highly sensitive to juvenile and adult mortality at sea. However, this scientific integration has not yet been achieved for Great Nicobar. Existing Andaman-region telemetry confirms the importance of Indian Ocean connectivity, but local stock identity, reproductive schedules, nest environments, sex ratios, survival and fisheries exposure remain inadequately resolved. The strongest contribution. would therefore be an integrated, individual-based and spatially explicit account of how maternal biology, nesting habitat, incubation environment and offshore threats jointly determine the conservation status of the Great Nicobar leatherback population.

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