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RESEARCH ARTICLE

Mathematical Modelling of Sea Turtle Nesting Behaviour Incorporating Predation and Carrying Capacity

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Abstract Understanding the ecological balance on sea turtle nesting beaches is essential for developing effective conservation strategies. These environments are shaped by interacting ecological pressures, particularly carrying capacity and predation. In this study, we adapt a Lotka-Volterra predator-prey framework with logistic growth to evaluate the long-term interaction between sea turtle egg abundance and predation pressure at Chagar Hutang Turtle Sanctuary (CHTS), Redang Island, Malaysia. The contribution of this study lies in the site-specific parameterisation of the model using eleven years of field monitoring data (2013-2023), which are used to identify and analyse possible equilibrium states of egg abundance and predation pressure under carrying capacity constraints. Stability analysis indicates that the extinction equilibrium is unstable, whereas the coexistence equilibrium is locally stable under the estimated parameter values. Numerical simulations further show damped oscillations converging towards coexistence, suggesting that long-term nesting outcomes at CHTS are influenced by both the habitat carrying capacity and the persistent predation pressure. These findings suggest that sustainable sea turtle nesting management should focus on maintaining or enhancing habitat carrying capacity while reducing excessive predation pressure, rather than relying solely on predator eradication.

Keywords: Sea turtle ecology, predator-prey interactions, mathematical modelling, carrying capacity, conservation strategy.

Introduction

Sea turtle nesting sites are complex ecological systems shaped by environmental constraints, biological interactions, and density dependent pressures. Reproductive success depends not only on the availability of suitable habitat but also on the ability of nests to persist despite threats such as predation, climatic variability, and spatial limitations [1-3]. Even on protected beaches, these factors can cause significant seasonal fluctuations in hatchling success, with predation representing a major source of egg and hatchling mortality in sea turtle populations globally [4,5]. The impact of predators varies depending on the nesting location and species involved, with common predators including monitor lizards *(Varanus spp.),* ghost crabs *(Ocypode spp.),* fire ants *(Solenopsis spp.),* and several avian species [6,7]. While some predators act in a density independent manner, others exhibit density dependent behaviour, whereby predation pressure increases as nests become more concentrated [8,9].

Although carrying capacity and predation have been studied separately in relation to nesting success, less attention has been paid to how these factors interact over time to shape nesting beach dynamics. This interaction becomes particularly relevant as nesting beaches face increasing pressure from high nest densities and persistent predation. Therefore, mathematical modelling offers an effective framework

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for examining these ecological complexities. The foundational Lotka-Volterra equations have long been used to model predator-prey interactions. However, the classical model assumes unlimited prey growth, which does not reflect real-world limitations such as carrying capacity. Thus, a refined model incorporating logistic limitation is required to account for density dependent constraints within nesting systems [10,11].

Sea turtle nesting dynamics differ from those represented in classical predator-prey models in several keyways. Nest abundance is not a function of local reproduction but is instead driven by migratory females depositing eggs [12,13]. In addition, carrying capacity is determined by environmental constraints, such as available nesting space and sand quality, rather than food availability [1,14]. Nonetheless, the predator-prey modelling framework remains applicable because predator density directly affects nest survival, while nest abundance, in turn, influences predator persistence [6,15]. Furthermore, although mathematical models have previously been applied to sea turtle nesting systems, important limitations remain. Existing studies conducted at CHTS have examined predator-prey interactions in nesting dynamics [16,17]. However, these studies rely largely on assumed parameter values and do not incorporate carrying capacity constraints when exploring the theoretical behaviour of the system. Similarly, many empirical studies of sea turtle nesting success rely on statistical analyses to quantify the impacts of predation on nests and hatchling survival. These studies typically examine relationships between nest fate and predator presence, environmental conditions, or nest density using observational or experimental data [5-9]. While such approaches are effective for identifying patterns and risk factors, they generally treat predation pressure as an external or fixed influence and do not explicitly represent the dynamic feedback between nest availability and predator responses over time. Consequently, they may overlook density constraints and implicitly assume that prey populations can increase without bound. Recent field observations at CHTS, however, suggest that density dependent effects increasingly influence nesting outcomes, highlighting the need to incorporate carrying capacity into mathematical models of the system.

Although the mathematical structure adopted in this study is based on the established Lotka-Volterra predator-prey framework with logistic egg abundance limitation, its contribution lies in applying and parameterising this framework using eleven years of site-specific monitoring data from CHTS. The novelty of the study therefore is not in proposing a new class of differential equations, but in converting long-term field records of egg abundance, carrying capacity, and predator related egg losses into a data informed model of egg abundance and predation pressure for a Malaysian sea turtle nesting beach. This addresses a modelling gap because previous sea turtle predator-prey models for CHTS relied largely on assumed parameter values and did not explicitly combine field-based parameter estimation with environmental carrying capacity constraints [16,17]. Therefore, this study proposes a modified Lotka-Volterra system incorporating logistic growth, in which the seasonal egg input coefficient, egg carrying capacity, egg predation pressure interaction coefficient, and predation pressure decline coefficient are estimated from monitoring data collected from 2013 to 2023. The objectives are twofold with first, to identify and mathematically characterise the equilibrium states of the system, and second, to determine which equilibrium state is most likely under current conditions at CHTS. The insights derived from this model aim to support long-term conservation planning by providing a better understanding of how habitat carrying capacity and predation pressure jointly influence nesting outcomes, rather than treating predator suppression as the sole management option.

Methodology

Study area

CHTS is located at the northernmost part of Redang Island (5°44′–5°50′N, 102°59′–103°05′E) on the east coast of Peninsular Malaysia (Figure 1). The island is well known as a significant nesting site for sea turtles, predominantly favoured by green sea turtles *(Chelonia mydas)* and hawksbill turtles *(Eretmochelys imbricata),* with annual nesting activity ranging from 700 to 1,700 nests and peak nesting occurring from May through July [18]. The beach extends approximately 350 meters in length and is systematically divided into 35 sectors, each 10 meters wide, to facilitate monitoring and data collection. The beach is covered with fine sand suitable for nest excavation, while coastal vegetation covers the upper beach zone. This vegetated area provides shade and thermal regulation and creates a gradual slope that turtles prefer for nesting compared to open, exposed areas. The vegetation helps regulate nest temperature during the day, thereby reducing thermal stress on developing embryos [14,19]. Since 1993, CHTS has been managed and monitored by the Sea Turtle Research Unit (SEATRU), with continuous conservation and research activities conducted for over three decades. The station operates annually from April to October, coinciding with the peak nesting season. During monsoon season from November to March, the beach is closed due to adverse weather conditions and minimal nesting activity.

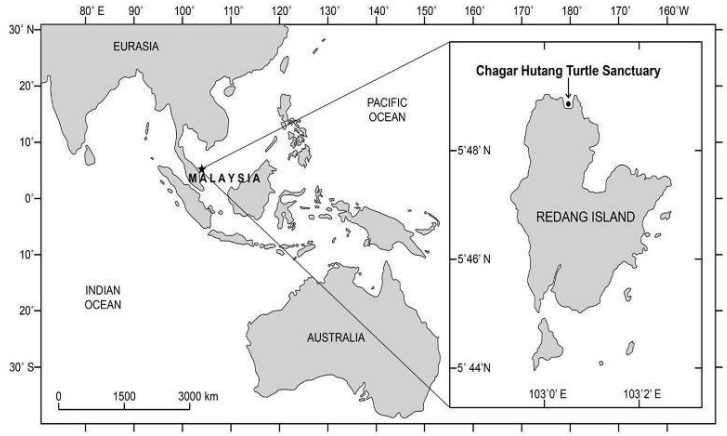

Figure 1. Map showing the location of CHTS on Redang Island, Terengganu [20].

Data collection

Daily and monthly hatching success data from 2013 to 2023 were obtained from SEATRU's long-term monitoring database. This comprehensive dataset includes detailed records of nesting activity, predation events, and hatching outcomes across eleven consecutive nesting seasons. The monitoring protocol remained consistent throughout this period, ensuring data comparability across years. For each recorded nest, the following variables were documented and extracted for analysis: total number of eggs, total number of hatched eggs, and total number of eggs attacked by predators, which were categorised into four predator groups: crabs, ants, monitor lizards, and maggots. However, nests affected by non-predation factors, such as flooding, attacks by the mother turtle, or fungal infection, were recorded separately and excluded from the primary analysis to ensure that the observed patterns reflected predator-prey dynamics rather than environmental stochasticity or anthropogenic effects.

Parameter estimation

The parameters used in the modified predator-prey model were estimated using monthly hatching and predation records obtained from the SEATRU monitoring database for the period 2013-2023. The dataset consisted of monthly records of total eggs, total hatched eggs, total unhatched eggs, and eggs affected by the recorded predator groups, namely ants, crabs, maggots, and monitor lizards. The model used in this study was formulated as:

$$\frac{dE}{dt} = rE\left(1 - \frac{E}{K}\right) - \beta EP,$$

$$\frac{dP}{dt} = \beta EP - mP,$$

where E represents egg abundance, P represents predator-related pressure, r represents the seasonal egg input coefficient, K represents the egg carrying capacity of the nesting beach, β represents the egg-predation pressure interaction coefficient, and m represents the predation-pressure decline coefficient.

Since direct predator abundance was not recorded in the SEATRU monitoring database, P was not treated as the actual biological population size of predators. Instead, P was defined as a predation pressure index calculated from the number of eggs affected by the recorded predator groups. This approach is consistent with sea turtle nest predation studies, in which predation is commonly quantified based on the number or proportion of eggs or nests affected by predators rather than direct estimates of predator population abundance [6,58-61]. Therefore, for each month t, the predation pressure index was calculated as follows:

$$P_t = A_t + C_t + G_t + L_t.$$

Here, A_t, C_t, G_t, and L_t represent the number of eggs affected by ants, crabs, maggots, and monitor

lizards, respectively.

This definition also follows the general Lotka-Volterra modelling assumption that the interaction term is proportional to the interaction between the prey variable and the predator or predator pressure variable [10,15,26]. In ecological systems where one of the interacting variables cannot be measured directly, time series estimation and model calibration can be used to estimate model coefficients from observed changes in the available state variables [62-67]. Previous studies have estimated Lotka-Volterra and differential equation parameters from observed time series data using finite-difference approximations, least-squares fitting, regression-based methods, generalised smoothing, and numerical optimization [62-67]. Therefore, the values of r and m in this study were estimated from the time series form of the model rather than directly measured as field rates.

The carrying capacity, K, was estimated by converting the estimated nesting carrying capacity into an egg carrying capacity. Based on the estimated maximum capacity of 3,004 nests at CHTS and assuming an average clutch size of 100 eggs per nest, the egg carrying capacity was calculated as follows:

$$K = 3004 \times 100,$$
$$K = 300400.$$

Thus, the carrying capacity used in the model is $K = 300400$. The use of K follows the logistic growth framework, where carrying capacity represents the upper limit imposed by environmental and density-dependent constraints [10,24,25,33]. The assumption of approximately 100 eggs per nest is biologically reasonable because green turtle clutches are commonly reported to range from approximately 80 to 120 eggs, and clutch sizes for green turtles on Redang Island have been reported to average around 100 eggs [68,69].

The predation coefficient, β, was estimated using the mean monthly egg abundance during the main nesting and predation period. Since nesting activity at CHTS occurs mainly during the nesting season and peaks between May and July, the May-September period was used to represent the main nesting and predation period [18,20]. Based on the monthly dataset from 2013-2023, the mean egg abundance from May to September was calculated as follows:

$$\bar{E}_{May-Sept} = 13814.34$$

The egg predation pressure interaction coefficient was then calculated as the reciprocal of this mean egg abundance:

$$\beta = \frac{1}{\bar{E}_{May-Sept}}$$
$$\beta = \frac{1}{13814.34}$$
$$\beta = 0.0000723885$$
$$\beta \approx 7.24 \times 10^{-5}$$

Thus, the value used in the model is $\beta = 7.24 \times 10^{-5}$. This coefficient scales the interaction term βEP, which represents egg loss associated with predation pressure. In predator-prey models, the predation coefficient is commonly used to represent interaction strength or encounter based loss between prey and predators [10,15,26]. In the present study, because P represents predation pressure rather than direct predator abundance, β was interpreted as an egg predation pressure interaction coefficient, consistent with the use of affected eggs or nests as measures of predation intensity in sea turtle studies [6,58-61].

The seasonal egg input coefficient, r, was estimated from the egg abundance time series using the finite-difference form of the egg equation. This interpretation is necessary because sea turtle egg abundance on a nesting beach does not increase through the local reproduction of eggs but through seasonal deposition by nesting females. Sea turtles exhibit strong natal homing and return to established nesting beaches, meaning that egg input at the beach is driven by seasonal nesting activity rather than by local reproduction of eggs [12,13]. Therefore, r was treated as a seasonal egg input coefficient.

Starting from:

$$\frac{dE}{dt} = rE\left(1 - \frac{E}{K}\right) - \beta EP$$

The monthly finite-difference approximation is:

$$\frac{E_{t+1} - E_t}{\Delta t} = rE_t\left(1 - \frac{E_t}{K}\right) - \beta E_t P_t$$

Where $\Delta t = 1$ month. Rearranging for r_t:

$$r_t = \frac{\frac{E_{t+1} - E_t}{\Delta t} + \beta E_t P_t}{E_t\left(1 - \frac{E_t}{K}\right)}$$

The final value of r was obtained by estimating the value that minimised the squared difference between the observed and model predicted monthly changes in egg abundance, using the monthly SEATRU egg abundance and predation pressure data from 2013-2023. With $K = 300400$, $\beta = 7.24 \times 10^{-5}$, and $\Delta t = 1$, the estimated seasonal egg input coefficient is:

$$r = 2.351654564$$

This method is consistent with previous parameter estimation approaches for differential-equation population models, in which unknown coefficients are estimated from observed time series data by minimizing differences between observed and model predicted rates of change [62-67]. Mühlbauer et al. [62], for example, developed gauseR for fitting Lotka-Volterra models to time series data, including logistic and multi-species interaction models. Lee [63] also showed that Lotka-Volterra parameters can be determined from measured population data over time, while Ramsay et al. [64] and Ding and Wu [65] developed general parameter estimation frameworks for nonlinear differential-equation models. Rosenbaum and Rall [66] further demonstrated direct parameter estimation by simulating ecological differential-equation models, and Auger-Méthé et al. [67] emphasised the importance of time series modelling when ecological processes are only partially observed.

The predation pressure decline coefficient, m, was estimated from the time series form of the predation pressure equation. Since P represents predation pressure rather than actual predator abundance, m was interpreted as the rate at which predation pressure declines when egg availability is insufficient to sustain the observed predation effects. Starting from:

$$\frac{dP}{dt} = \beta EP - mP,$$

The monthly finite-difference approximation is:

$$\frac{P_{t+1} - P_t}{\Delta t} = \beta E_t P_t - mP_t$$

Where $\Delta t = 1$ month. Rearranging for m_t:

$$m_t = \frac{\beta E_t P_t - \frac{P_{t+1} - P_t}{\Delta t}}{P_t}$$

The final value of m was estimated by minimising the squared difference between the observed and model predicted monthly changes in predation pressure, using the monthly SEATRU predation pressure index from 2013-2023. With $\beta = 7.24 \times 10^{-5}$ and $\Delta t = 1$, the estimated predation pressure decline coefficient was:

$$m = 3.48485048$$

This formulation is appropriate for the present dataset because predator abundance was not directly censused. Instead, predator activity was observed through its effect on eggs. Similar ecological modelling situations frequently rely on time series estimation, state variable approximation, or calibration of unobserved process rates from observed data [62-67]. Therefore, m was not interpreted as direct mortality of individual predators, but as the decline coefficient of the observed predation pressure index.

The final parameter values used in the model were $r = 2.351654564$, $K = 300400$, $\beta = 7.24 \times 10^{-5}$,

and $m = 3.48485048$. These values were then substituted into the modified predator-prey model for equilibrium analysis, stability analysis, and numerical simulation.

Mathematical model development

To capture the interaction between sea turtle egg abundance and predation pressure at CHTS, a mathematical model was developed based on the classical Lotka-Volterra equations, which have been widely used in ecology to describe interacting biological systems [10,11,26]. However, the basic Lotka-Volterra formulation assumes unlimited prey growth in the absence of predation, which is unrealistic for nesting beaches where physical space, nest site quality, sand conditions, and density dependent pressures impose an upper limit on egg or nest abundance. Therefore, the standard formulation was modified to incorporate a carrying capacity term, resulting in a system that accounts for both density dependent limitation and predation pressure. This approach follows the framework of predator-prey models with logistic prey growth [10,11,15], which has been applied to ecological systems where prey growth is constrained by environmental limits [21-23].

The model consists of two coupled ordinary differential equations describing the rates of change in sea turtle egg abundance (E) and predation pressure index (P):

$$\frac{dE}{dt} = rE\left(1 - \frac{E}{K}\right) - \beta EP, \qquad \frac{dP}{dt} = \beta EP - mP, \tag{1}$$

where the notations of $\frac{dE}{dt}$ and $\frac{dP}{dt}$ represent the rates of change in egg abundance and predation pressure over time, respectively. Table 1 presents the parameters used in the model, their revised biological interpretations, values, and sources of estimation.

Table 1. Description of the parameters in Model (1)

Parameters	Description	Value	Source
r	Seasonal egg input coefficient	2.351654564	Estimated from monthly egg abundance time series [62-67]
K	Egg carrying capacity of nesting beach	300400	Calculated from 3004 x 100 eggs [68,69]
β	Egg predation pressure interaction coefficient	7.24×10^{-5}	Calculated from mean May-September egg abundance [58-61]
m	Predation pressure decline coefficient	3.48485048	Estimated from predation pressure time series [62-67]

In the first equation, the term $rE\left(1 - \frac{E}{K}\right)$ represents the seasonal input of eggs into the nesting beach system under density dependent limitation, where the rate of egg input decreases as E approaches K [10,24,25]. This term does not imply that eggs reproduce locally, but rather, r represents the net seasonal input of eggs deposited by nesting females. The term βEP represents egg loss associated with predation pressure and is proportional to both egg abundance and the predation pressure index, consistent with the interaction assumption of Lotka-Volterra models [10,15,26]. In the second equation, βEP represents the increase in predation pressure associated with egg availability, while mP represents the decline of predation pressure when egg availability is insufficient. Since direct predator abundance was not recorded, P is interpreted as a predation pressure index, while m is interpreted as a predation pressure decline coefficient rather than as a measure of direct predator population mortality.

Analytical methods

To address the research objectives of identifying steady states and determining which equilibrium will occur in the future, standard techniques from dynamical systems theory were employed to analyse the model's behaviour [28]. The analytical framework followed a sequential process, as illustrated in Figure 2, consisting of three main steps, namely equilibrium analysis, stability analysis, and numerical simulation.

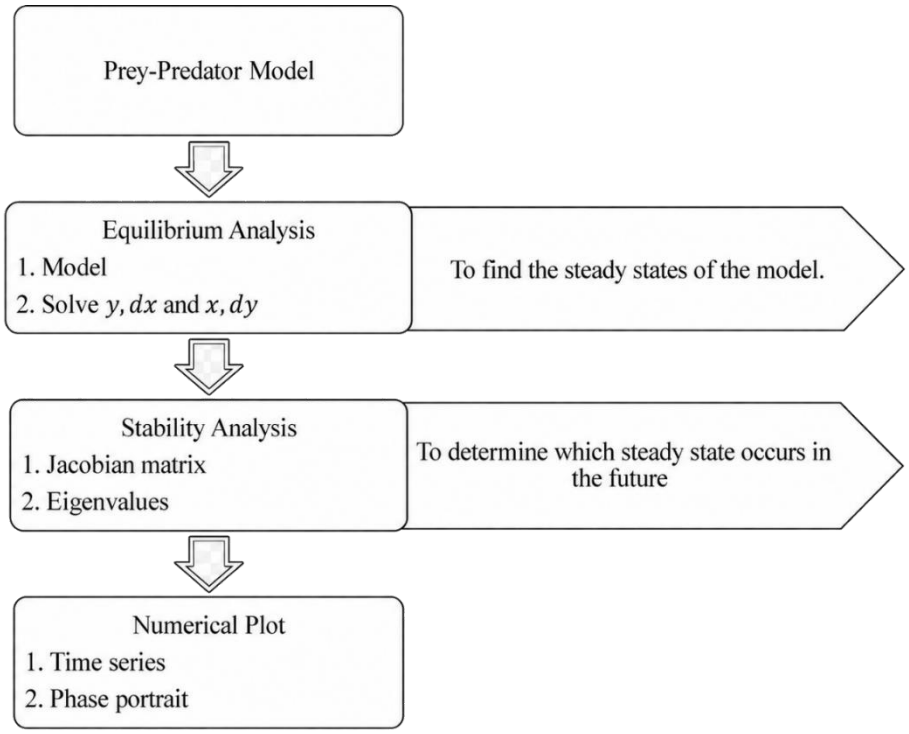

Figure 2. Analytical framework showing the sequential steps of model analysis.

For equilibrium analysis, the steady states of the system were identified by setting both differential equations equal to zero and solving for the values of $\left(\frac{dE}{dt} = 0 \; and \; \frac{dP}{dt} = 0\right)$, and E and P, where egg abundance and predation pressure remain constant over time [29]. These equilibrium points represent potential long-term outcomes of the system under different ecological scenarios, while the mathematical derivation involved solving the system of algebraic equations simultaneously to obtain the equilibrium coordinates (E^*, P^*). As for stability analysis, the stability of each equilibrium point was determined using linearisation and eigenvalue analysis [10, 30]. To assess equilibrium stability, we examined the Jacobian matrix evaluated at each fixed point and analysed the nature of its eigenvalues to determine the system behaviour near equilibrium and whether small perturbations away from the equilibrium grow or decay over time.

Finally, for numerical simulations, the system dynamics were visualised, with the analytical results being validated against numerical solutions of the differential equations computed for various initial conditions. Time series plots were generated using Maple software to show how egg and predator populations evolve over time, while phase portraits were constructed in the $E - P$ plane to illustrate trajectories starting from different initial states and to visualise the basins of attraction for stable equilibria [31]. These simulations help demonstrate which equilibrium the system approaches depending on the initial values of egg abundance and predation pressure.

Results and Discussion

Analytical results

To determine the steady states of the egg-predation-pressure system with carrying capacity, both differential equations were set equal to zero and solved for the equilibrium points [10, 30]:

$$\frac{dE}{dt} = rE\left(1 - \frac{E}{K}\right) - \beta EP = 0, \tag{2}$$

$$\frac{dP}{dt} = \beta EP - mP = 0. \tag{3}$$

From equation (3):

$$\beta EP - mP = 0,$$
$$P(\beta E - m) = 0,$$
$$P = 0 \quad or \quad E = \frac{m}{\beta}$$

When $P = 0$ is substituted into equation (2):

$$rE\left(1 - \frac{E}{K}\right) - \beta EP = 0,$$
$$rE\left(1 - \frac{E}{K}\right) = 0,$$
$$E = 0 \quad or \quad E = K$$

Therefore, $E_0 = (0,0)$ and $E_1 = (K, 0)$ are the first and second equilibrium points respectively.

When $E = \frac{m}{\beta}$,

$$rE\left(1 - \frac{E}{K}\right) - \beta EP = 0,$$
$$\frac{rm}{\beta}\left(1 - \frac{m}{\beta K}\right) - mP = 0,$$
$$\frac{rm}{\beta}\left(1 - \frac{m}{\beta K}\right) = mP,$$
$$mP = \frac{rm}{\beta}\left(1 - \frac{m}{\beta K}\right),$$
$$P = \frac{r}{\beta}\left(1 - \frac{m}{\beta K}\right).$$

Therefore, the third equilibrium point is $E_2 = \left(\frac{m}{\beta}, \frac{r}{\beta}\left(1 - \frac{m}{\beta K}\right)\right)$.

The interpretation for all the steady states is given as follows:

i. $E_0 = (0,0)$: At the extinction equilibrium, both state variables are zero, indicating the absence of recorded egg abundance and observed predation pressure.

ii. $E_1 = (K, 0)$: At the predation-pressure-free boundary equilibrium, egg abundance reaches the carrying capacity of the nesting beach, while the predation pressure index is zero.

iii. $E_2 = (E^*, P^*) = \left(\frac{m}{\beta}, \frac{r}{\beta}\left(1 - \frac{m}{\beta K}\right)\right)$: At the coexistence equilibrium, egg abundance and predation pressure persist simultaneously, which only exists if $\beta K > m$, when the carrying capacity is sufficiently high to support egg input while still allowing measurable predation pressure to remain in the system.

Stability analysis for the steady states

The stability of each equilibrium point was assessed using the Jacobian matrix method [28-29]. The Jacobian matrix, J, for model (1):

$$J(E, P) = \begin{bmatrix} r - \frac{2rE}{K} - \beta P & -\beta E \\ \beta P & \beta E - m \end{bmatrix}.$$

For a 2×2 matrix, the eigenvalues are determined by solving the characteristic equation [30]:

$$\lambda^2 - (a + d)\lambda + (ad - bc) = 0,$$
$$\det(J - \lambda I) = 0.$$

First for $E_0 = (0,0)$, the Jacobian matrix at the extinction equilibrium $(0, 0)$:

$$J(E_0) = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix},$$

$$J(E_0) - \lambda I = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix},$$
$$J(E_0) - \lambda I = \begin{bmatrix} r-\lambda & 0 \\ 0 & -m-\lambda \end{bmatrix},$$
$$\det(J(E_0) - \lambda I) = (r - \lambda)(-m-\lambda) - 0,$$
$$\det(J(E_0) - \lambda I) = (r - \lambda)(-m-\lambda),$$
$$(r - \lambda)(-m-\lambda) = 0,$$

Therefore, the eigenvalues are:

$$\lambda_1 = r, \qquad \lambda_2 = -m.$$

Since $r > 0$, r-value is positive, therefore, this equilibrium, E_0, is unstable. This indicates that the system will move away from the extinction state as long as seasonal egg input continues at CHTS [10, 30].

Secondly, the Jacobian matrix at the predator-free equilibrium $E_1 = (K, 0)$:

$$J = \begin{bmatrix} r-2r & -\beta K \\ 0 & \beta K - m \end{bmatrix},$$
$$J - \lambda I = \begin{bmatrix} r-2r & -\beta K \\ 0 & \beta K - m \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix},$$
$$J - \lambda I = \begin{bmatrix} r-2r-\lambda & -\beta K \\ 0 & \beta k - m - \lambda \end{bmatrix},$$
$$\det(J - \lambda I) = (r - 2r - \lambda)(\beta K - m - \lambda) - (-\beta K)(0),$$
$$\det(J - \lambda I) = (r - 2r - \lambda)(\beta K - m - \lambda),$$
$$(r - 2r - \lambda)(\beta K - m - \lambda) = 0,$$
$$(-r - \lambda) = 0,$$

Therefore, the eigenvalues are:

$$\lambda_1 = -r, \lambda_2 = \beta K - m.$$

The stability of this equilibrium depends on the sign of $\lambda_2 = \beta K - m$. If $\beta K < m$, predation pressure cannot be sustained as both eigenvalues are negative and the equilibrium is stable. However, if $\beta K > m$, predation pressure can increase when eggs are available at carrying capacity, then $\lambda_2 > 0$ and the equilibrium is unstable. For CHTS, where predation events were recorded throughout the study period, we expect $\beta K > m$, making this predator-free equilibrium unstable [10, 28]. We summarise this result in Theorem 1.

Theorem 1. The stability of equilibrium point, E_1, can be classified as follows:

i. If $\beta K > m$, then E_1 is unstable.
ii. If $\beta K < m$, then E_1 is asymptotically stable.

Finally, evaluating the Jacobian matrix at the coexistence equilibrium $\left(\frac{m}{\beta}, \frac{r}{\beta}\left(1 - \frac{m}{\beta K}\right)\right)$:

$$J = \begin{bmatrix} -\frac{rm}{\beta K} & -m \\ r(1 - \frac{m}{\beta K}) & 0 \end{bmatrix},$$
$$J - \lambda I = \begin{bmatrix} -\frac{rm}{\beta K} & -m \\ r(1 - \frac{m}{\beta K}) & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix},$$
$$J - \lambda I = \begin{bmatrix} -\frac{rm}{\beta K} - \lambda & -m \\ r(1 - \frac{m}{\beta K}) & -\lambda \end{bmatrix},$$
$$\det(J - \lambda I) = \left(-\frac{rm}{\beta K} - \lambda\right)(-\lambda) - (-m)\left(r\left(1 - \frac{m}{\beta K}\right)\right),$$
$$\det(J - \lambda I) = \lambda\left(\frac{rm}{\beta K} + \lambda\right) + mr\left(1 - \frac{m}{\beta K}\right),$$
$$\det(J - \lambda I) = \lambda^2 + \lambda\left(\frac{rm}{\beta K}\right) + mr\left(1 - \frac{m}{\beta K}\right),$$

$$\lambda_{1,2} = \frac{-\frac{rm}{\beta K} \pm \sqrt{\left(\frac{rm}{\beta K}\right)^2 - 4mr\left(1 - \frac{m}{\beta K}\right)}}{2}.$$

The stability of the coexistence equilibrium depends on the sign of the real parts of these eigenvalues. Analysis shows that when this equilibrium exists, the eigenvalues have negative real parts, indicating that the coexistence equilibrium is stable, which represents the most biologically realistic outcome for CHTS, where egg abundance and predation pressure remain positive at intermediate levels [15, 28]. We summarise the results on stability of equilibrium point E_1 in the following theorem:

Theorem 2. Suppose that the eigenvalues λ_1 and λ_2 are real. The stability of equilibrium point E_2 can be classified as follows:

i. E_2 is asymptotically stable if $\pm\frac{B}{2} < \frac{A}{2}$.
ii. E_2 is unstable if $\pm\frac{B}{2} > \frac{A}{2}$.

$$\lambda_{1,2} = \frac{-A \pm B}{2} = -\frac{A}{2} \pm \frac{B}{2}$$

where

$$A = \frac{rm}{\beta K}, \qquad B = \sqrt{\left(\frac{rm}{\beta K}\right)^2 - 4mr\left(1 - \frac{m}{\beta K}\right)}$$

$$\lambda_1 = -\frac{A}{2} + \frac{B}{2}$$

$$\lambda_1 = -\frac{A}{2} - \frac{B}{2}$$

Proof.
Case I: Stable, $\lambda_1 < 0, \quad \lambda_2 < 0$.
For λ_1:

$$-\frac{A}{2} + \frac{B}{2} < 0,$$
$$\frac{B}{2} < \frac{A}{2}.$$

For λ_2:

$$-\frac{A}{2} - \frac{B}{2} < 0,$$
$$-\frac{B}{2} < \frac{A}{2}.$$

Therefore, E_2 is stable if $\pm\frac{B}{2} < \frac{A}{2}$.

Case II: Unstable, $\lambda_1 > 0, \quad \lambda_2 > 0$.
For λ_1:

$$-\frac{A}{2} + \frac{B}{2} > 0,$$
$$\frac{B}{2} > \frac{A}{2}.$$

For λ_2:

$$-\frac{A}{2} - \frac{B}{2} > 0,$$
$$-\frac{B}{2} > \frac{A}{2}.$$

Therefore, E_2 is unstable if $\pm\frac{B}{2} > \frac{A}{2}$. ■

However, the equilibrium point E_2 may also have complex eigenvalues.

Theorem 3. Suppose that the eigenvalues can be written as complex numbers, $\lambda_{1,2} = a \pm bi$, the stability of equilibrium point E_2 is as follows:

i. If $a > 0$, then E_2 is a spiral unstable state.

ii. If $a = 0$, then E_2 is a center.
iii. If $a < 0$, then E_2 is a spiral stable state.

The classification follows the standard eigenvalue criteria for two-dimensional autonomous systems [28,30,31].

Numerical simulations

Figure 3 shows the time series plots for egg abundance, $E(t)$, and predation pressure index, $P(t)$, starting from initial conditions away from the coexistence equilibrium, using $K = 300400$ obtained through parameter estimation from CHTS data. The left panel displays the temporal dynamics of egg abundance, while the right panel shows the temporal dynamics of predation pressure, with both state variables exhibiting damped oscillatory behaviour before converging toward their respective equilibrium values. Egg abundance initially increases and then declines through oscillations toward the coexistence level of approximately 48133 eggs, while predation pressure shows a similar oscillatory convergence toward approximately 27277 index units. These damped oscillations are characteristic of stable spiral equilibria in predator-prey type systems [26,28,30,32], where the state variables cycle around the equilibrium point with decreasing amplitude until reaching a steady state. The convergence pattern confirms the analytical prediction that the coexistence equilibrium is stable.

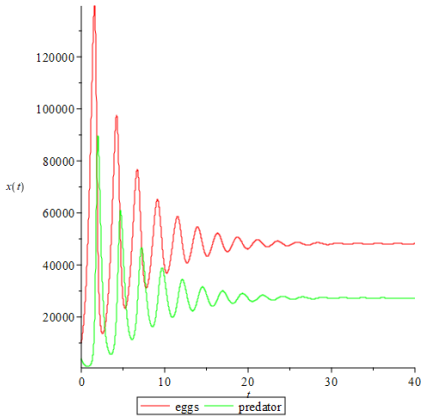

Figure 3. Time-series plot for egg abundance and predation pressure index for $\beta = 7.24 \times 10^{-5}$.

Figure 4 presents the phase portrait showing multiple trajectories in the $E(t) - P(t)$ plane from different sets of initial conditions. Each coloured spiral represents the system's trajectory starting from a different initial egg abundance and predation pressure state. All trajectories, regardless of their starting points, converge toward the coexistence equilibrium located at approximately $(E^*, P^*) = (48133, 27277)$. The direction field, indicated by small arrows throughout the phase space, shows the instantaneous rate of change at each point and guides the trajectories toward the equilibrium. The spiral pattern confirms that the coexistence equilibrium is a stable spiral or focus, meaning that egg abundance and predation pressure approach equilibrium through oscillatory dynamics rather than monotonic convergence [28]. The tightening of the spirals as they approach the centre demonstrates the damping effect, with oscillation amplitudes decreasing over time. This visualisation shows that the coexistence state is an attractor for biologically realistic initial conditions, supporting the conclusion that CHTS will naturally tend towards a state where egg abundance and predation pressure coexist at intermediate levels.

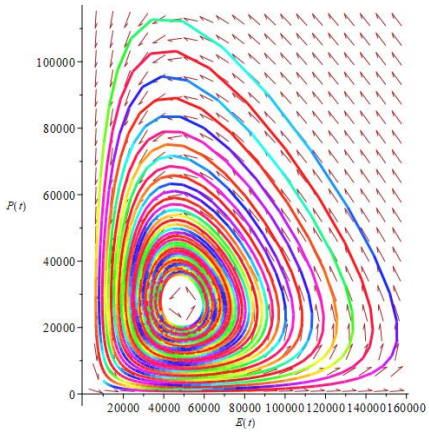

Figure 4. Phase portrait diagram of egg abundance and predation pressure index for $\beta = 7.24 \times 10^{-5}$.

Figure 5 illustrates the behaviour of the system when initialised at the predation-pressure-free equilibrium $(E = K,\ P = 0)$. The left panel shows that egg abundance remains constant at the carrying capacity $K = 300400$ eggs throughout the simulation period, exhibiting no oscillations or deviations from this value. The right panel confirms that the predation pressure index remains at zero for the duration of the simulation. This demonstrates that in the complete absence of recorded predation pressure, egg abundance can theoretically be maintained at carrying capacity, limited only by the physical and environmental constraints of the beach [10,14,24,25,33]. However, as shown by the stability analysis, this equilibrium is unstable when predation pressure can be reintroduced or sustained, meaning that even a small positive value of P would cause the system to move away from this boundary state toward the coexistence equilibrium. This theoretical result has important implications for management: complete removal of predation pressure may temporarily allow maximum egg abundance, but it does not represent a stable long-term state if predation pressure can return [36,48].

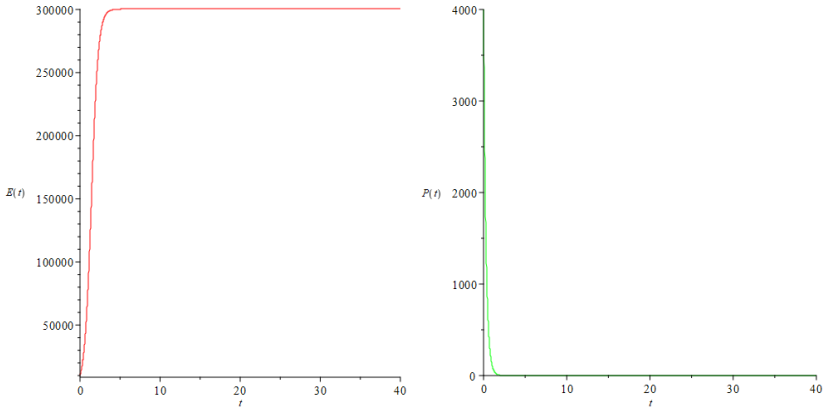

Figure 5. Time series for the predation-pressure-free initial condition, $E = K, P = 0$.

Figure 6 shows the phase portrait near the predation-pressure-free equilibrium at $(K, 0)$. The direction field indicates that trajectories starting from points with $P > 0$, even with very small positive predation pressure, move away from the $P = 0$ boundary rather than returning to it. This confirms the analytical finding that the predation-pressure-free equilibrium is unstable when predation pressure can be sustained in the system. The trajectory shown in the figure, starting from an initial condition near $(K, 0)$ but with a small positive P value, demonstrates that the system moves toward the coexistence equilibrium rather than remaining at or returning to the predation-pressure-free state. The arrows pointing away from the horizontal axis at $E = K$ show that any perturbation introducing predation pressure into a system at carrying capacity can lead to growth of P and eventual establishment of the coexistence state. This result emphasises that the predation-pressure-free equilibrium, while mathematically valid, is not a realistic long-term outcome for CHTS under natural conditions where predation events occur [10].

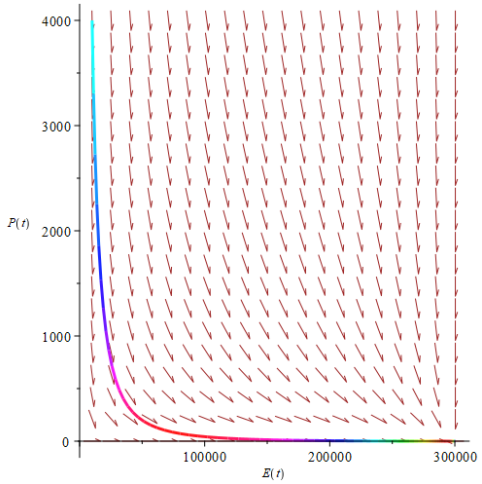

Figure 6. Phase portrait if $E = K, P = 0$.

Lastly, for the extinction equilibrium, $E_0 = (0,0)$, it is not illustrated numerically because the analytical results demonstrate that this equilibrium is always unstable. As shown in the stability analysis, the positive seasonal egg input coefficient ensures that any perturbation away from zero egg abundance leads to an increase in egg abundance, causing the system to move away from the extinction state. Consequently, trajectories initiated near E_0 do not converge to this point, making numerical simulation unnecessary for this case. From a biological perspective, this mathematical result is consistent with observations at CHTS, which functions as a major and persistent nesting site with continuous annual nesting activity. Under such conditions, complete extinction of both egg input and predation pressure is not a realistic long-term outcome, reinforcing the relevance of focusing on the predation-pressure-free and coexistence equilibria when assessing system dynamics and management implications.

The numerical simulations were not used as an independent validation procedure but instead used to examine whether the analytical stability results produced trajectories that are consistent with the estimated parameter values. Specifically, the time-series and phase-portrait outputs were checked to confirm convergence toward the analytically derived coexistence equilibrium, rather than divergence, extinction, or sustained oscillation. The convergence of trajectories toward approximately $(E*, P*) = (48133, 27277)$ provides an internal consistency check between the equilibrium calculation and the numerical solution of the model [28,30,31] and because the same 2013-2023 monitoring dataset was used for parameter estimation, the numerical simulations should not be interpreted as independently validated forecasts of future annual egg abundance or predation pressure. Rather, they represent theoretical projections under the estimated CHTS parameter values with lack of independent model validation is therefore acknowledged as a limitation and is addressed in the section on model limitations and future research directions. Despite this limitation, the model remains useful as a decision-support framework because it identifies which estimated coefficients most strongly influence the expected equilibrium state. In particular, the model highlights the roles of egg carrying capacity, the egg-predation pressure interaction coefficient and the predation pressure decline coefficient in determining whether the system tends toward a predation-pressure-free boundary state or a stable coexistence state. Therefore, the model is best interpreted as a theoretical and management-oriented tool for examining possible long-term tendencies at CHTS, rather than as a fully validated predictive forecasting model.

Characterization of system equilibria

The first objective of this study is to identify and characterise the steady states of the egg-predation-pressure system at CHTS. The mathematical analysis has successfully identified three distinct equilibrium points, each representing a fundamentally different long-term outcome for the nesting beach. The extinction equilibrium, $E_0 = (0, 0)$, represents the complete absence of egg abundance and predation pressure, a state that would occur only following catastrophic disturbance, permanent habitat loss, or total cessation of nesting activity [34]. The eigenvalue analysis revealed this equilibrium to be unstable, with $\lambda_1 = r > 0$ indicating that any seasonal input of eggs would initiate movement away from extinction. This mathematical finding aligns with empirical observations that sea turtles demonstrate strong natal homing behaviour and will persistently return to established nesting beaches across decades [12], making voluntary abandonment of CHTS unlikely.

The predation-pressure-free equilibrium, $E_1 = (K, 0)$, represents the theoretical maximum egg abundance in the complete absence of recorded predation pressure. At CHTS, this condition allows egg abundance to remain at the environmental carrying capacity of the nesting beach, which is determined by nest-site availability, nest environment, beach quality, and density-dependent constraints [10,14,24,25,33,35]. However, the stability analysis demonstrated that this equilibrium is unstable when $\beta K > m$ which is when predation pressure can increase in response to egg availability. Given the documented predation events at CHTS throughout the 2013-2023 study period, the condition $\beta K > m$ is ecologically realistic. The positive eigenvalue $\lambda_2 = \beta K - m > 0$ confirms mathematical instability, meaning that any reintroduction or recurrence of predation pressure would trigger departure from this equilibrium. This finding has critical management implications as complete predator exclusion or removal of predation pressure, even if temporarily achieved, does not represent a sustainable long-term state unless permanent exclusion measures were maintained indefinitely [36,48].

The coexistence equilibrium, $E_2 = \left(\frac{m}{\beta}, \frac{r}{\beta}\left(1 - \frac{m}{\beta K}\right)\right)$, emerged as the most ecologically realistic outcome. The analysis aligns with ecological models showing that stable coexistence can occur when prey availability and predator-related losses balance one another, but the present model adapts this idea to sea turtle egg abundance and observed predation pressure rather than direct predator abundance counts [10,15,28]. The stability analysis demonstrated negative real parts for both eigenvalues, indicating that this equilibrium is stable, and that the system returns to these state-variable levels following perturbations [28]. The damped oscillatory approach to equilibrium, as visualised in Figure 4, reflects time lagged feedback between egg availability and predation pressure [11,62-67]. This equilibrium represents a balance point where seasonal egg input and carrying capacity limitation are balanced by predation-related egg loss, while predation pressure is balanced by its decline coefficient. Importantly, both egg abundance and predation pressure remain positive at this equilibrium, demonstrating that moderate predation pressure does not necessarily threaten nesting-beach viability, a finding consistent with ecological theory on sustainable predation [15,37].

Predicted long-term dynamics at CHTS

The second objective is to determine which steady state is most likely to occur at CHTS given current ecological conditions. The stability analysis predicts that the coexistence equilibrium represents the expected long-term outcome. This prediction emerges from the mathematical properties of the equilibria rather than from assumptions about management interventions or environmental change. Under current conditions where predation events occur and eggs are available, the system naturally converges toward coexistence regardless of initial egg abundance and predation pressure levels, as demonstrated by the multiple trajectories in Figure 4. This finding provides both reassurance and realistic expectations for conservation managers. It shows that stable coexistence is possible within the model assumptions, but it also indicates that egg abundance at CHTS will remain below carrying capacity if predation pressure persists.

The predicted equilibrium egg abundance $\left(E^* = \frac{m}{\beta}\right)$ depends critically on two parameters which are the predation pressure decline coefficient (m) and the egg predation pressure interaction coefficient (β). Higher predation pressure decline coefficient shifts the coexistence equilibrium toward higher egg abundance, whereas a stronger egg predation pressure interaction coefficient shifts the equilibrium toward lower egg abundance [10,15,38] due to P defined as a predation pressure index rather than direct predator abundance, these parameters should be interpreted as coefficients of observed predation pressure rather than direct demographic rates of predator individuals. At CHTS, empirical estimation of these parameters through field studies would enable quantitative prediction of equilibrium values. However, even without precise parameter values, the qualitative prediction remains robust as under current management, where predators are neither intensively controlled nor protected, CHTS will maintain both egg abundance and predation pressure at intermediate densities determined by the interaction of biological rates and carrying capacity constraints [62-67].

The model also predicts that the equilibrium predation pressure $\left(P^* = \frac{r}{\beta}(1 - \frac{m}{\beta K})\right)$ increases with the seasonal egg input coefficient (r) and decreases with the egg predation pressure interaction coefficient (β). This prediction highlights an important ecological relationship where beaches with higher seasonal egg input can support higher predation pressure at equilibrium. For CHTS, where green turtles demonstrate relatively consistent annual nesting [20,39], the predation pressure is likely buffered against short-term fluctuations in nesting activity. However, long-term declines in nesting frequency, whether due to climate change impacts on adult survival [40], or degradation of offshore feeding grounds [41], would lower equilibrium predation pressure and potentially alter the egg-predation-pressure dynamics in

ways not captured by the current model.

Conservation implications for CHTS

The mathematical analysis provides several concrete insights for conservation management at CHTS. Although stable coexistence and instability of the extinction equilibrium are expected outcomes in many predator-prey type systems [10,15,28,30], the applied value of the present study is that these theoretical outcomes are interpreted using field-derived CHTS parameters. First, the finding that the coexistence equilibrium is stable suggests that moderate predation pressure represents a natural component of the system rather than a crisis requiring aggressive intervention. This does not imply that predation should be ignored, but rather that conservation efforts should focus on ensuring that equilibrium egg abundance remains sufficient to support viable sea turtle populations [42,43,55]. The key management question thus shifts from removing all predation pressure to determining whether equilibrium egg abundance and hatchling output are sufficiently high to meet conservation objectives. This reframing emphasises the need for empirical studies linking egg production to hatchling recruitment and ultimately to adult population size, relationships that extend beyond the scope of the current model but are essential for comprehensive conservation planning [43,55-57].

Second, the model identifies carrying capacity (K) as a critical leverage point for management intervention. Unlike the predation-pressure-free equilibrium, which requires ongoing predator exclusion or suppression of predation pressure, increasing carrying capacity offers a pathway to sustainably higher egg abundance even in the presence of predation pressure. At CHTS, carrying capacity could be increased through several mechanisms, such as physical expansion of available nesting habitat through beach nourishment or removal of erosion barriers [44], reduction of density dependent mortality through nest relocation programs that prevent overcrowding in preferred areas [45], and mitigation of anthropogenic disturbances that currently limit usable nesting space, such as artificial lighting that disorients hatchlings or coastal development that restricts beach access [46]. Each unit increase in (K) translates directly into higher equilibrium egg abundance at the coexistence state, providing lasting benefits that persist even when active management ceases.

Third, the model can be used as a management screening tool to compare broad conservation strategies. Actions that increase (K) improve the habitat-side capacity of the beach, whereas actions that reduce (β) lower the interaction between egg abundance and predation pressure. Short-term predator control campaigns may reduce predation pressure temporarily and improve hatchling output during critical years, but the model suggests that the system will return toward the coexistence equilibrium if the underlying parameters remain unchanged [36,48]. Therefore, the model supports an integrated strategy that combines habitat improvement, targeted nest protection, and monitoring of predation pressure records, rather than relying only on predator suppression.

Fourth, the stability properties of the coexistence equilibrium suggest that temporary management interventions can produce temporary benefits but will not fundamentally alter long-term dynamics unless they change the underlying system parameters. For example, a predator control campaign that temporarily reduces predation pressure for one or two seasons would allow egg abundance to increase toward carrying capacity, but predation pressure may eventually recover if predator activity resumes, and the system would return to the coexistence equilibrium [36,48]. This does not mean such interventions are futile, as the temporary increase in egg abundance and hatchling production during critical years could support population recovery following disturbance events [55,56]. However, managers should have realistic expectations about the duration of these benefits and should not expect predator control alone to produce permanent increases in egg abundance without complementary interventions that alter parameters such as (K) [48].

From an applied perspective, the model provides practical value by identifying measurable quantities that managers can monitor over time, such as egg abundance, predation pressure records, and effective nesting capacity. These quantities can be updated with future monitoring data to reassess equilibrium predictions and evaluate whether management actions are moving the system toward higher egg abundance or lower excessive predation pressure.

Model limitations and future research directions

While the model provides valuable theoretical and management insights, several limitations warrant discussion. First, the model parameters were estimated using data collected from 2013–2023, representing ecological conditions during this specific period. Future environmental changes could alter these parameter values over multi-decadal timescales. For example, climate change may alter nesting

phenology and hatching success rates [49], coastal development may progressively reduce carrying capacity [50], and predation pressure dynamics may be influenced by factors beyond egg availability, such as alternative prey, predator movement, or habitat changes [2,11,27,51]. Because the dataset did not include direct predator abundance, model predictions should also be interpreted with the caution normally required when demographic models are based on sparse or incomplete process observations [47,62-67]. Future modelling efforts should explore parameter sensitivity and incorporate scenarios of environmental change to assess the robustness of predictions under realistic conditions of temporal variability [52].

Second, the model treats egg abundance as spatially aggregated and does not account for spatial heterogeneity in either nesting distribution or predation risk. At CHTS, nests are not uniformly distributed, and predator activity may concentrate foraging in areas with high nest density [6,9,53,58-61]. Spatial structuring could lead to source-sink dynamics, where certain beach sections consistently produce more hatchlings than others or could create refuges where predation pressure is lower than average [13]. Future work incorporating spatial structure through reaction-diffusion models or individual-based simulations could reveal whether spatial heterogeneity fundamentally alters predictions about equilibrium egg abundance, predation pressure, and stability [54].

Third, the model intentionally combines ants, crabs, monitor lizards, and maggots into a single predation pressure index. This simplification was necessary because the monitoring records documented the number of eggs affected by predator groups rather than direct predator abundance or predator-specific encounter rates. As a result, the model does not distinguish predator-specific functional responses, seasonal activity, or differences in predation mechanisms among predator groups. Future studies should extend the model by separating dominant predator groups where sufficient data are available and by incorporating seasonal forcing to represent monthly changes in nesting intensity and predation pressure during the nesting season [6,7,58-61].

Fourth, although the parameters were estimated from the 2013–2023 field records, the present study did not conduct independent validation using a separate testing dataset. Therefore, the numerical simulations should be interpreted as internally consistent theoretical projections based on the estimated parameter values rather than as independently validated forecasts. This limitation does not invalidate the analytical results, but it means that the model should be used cautiously for prediction. Future studies could strengthen the applied contribution by withholding part of the monthly or annual dataset, comparing simulated and observed egg abundance or predation pressure trends, and reporting prediction errors such as RMSE or MAE [47,62-67].

Finally, the model focuses exclusively on the nesting beach phase and does not connect egg abundance to adult population dynamics. Sea turtles experience mortality across all life stages, and population viability depends on the recruitment of hatchlings to adulthood, not merely on egg production or nest abundance [55]. Future research should embed the nesting model within a full life cycle framework that tracks cohorts from eggs through hatchlings, juveniles, and adults, incorporating stage-specific survival rates and reproductive maturity schedules [56]. Such integrated models would enable assessment of whether the equilibrium egg abundance and hatchling production predicted by the current model are sufficient to maintain stable adult populations, which is the ultimate criterion for conservation success [57].

Conclusion

This study demonstrates that stable coexistence between sea turtle egg abundance and predation pressure represents the expected long-term outcome at CHTS under the estimated parameter values. Although predation-pressure-free scenarios theoretically allow egg abundance to approach the environmental carrying capacity, such states are dynamically unstable when predation pressure can re-enter the system. The main contribution of this study is the application and parameterisation of a modified Lotka-Volterra framework using eleven years of local monitoring data, allowing the model to be interpreted in relation to site-specific carrying capacity and observed predation pressure records. Consequently, long-term improvements in nesting success may be better supported by enhancing environmental carrying capacity and reducing excessive predation pressure than by relying solely on short-term predator suppression. By identifying carrying capacity and predation pressure interaction strength as key management levers, this model provides a quantitative basis for prioritising habitat-based conservation strategies while highlighting the need for future validation, spatial extensions, and seasonal modelling.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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