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A linked model of animal ecology and human behavior for the management of wildlife tourism

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ABSTRACT

Wildlife tourism attractions are characterized as having intricately coupled human–wildlife interactions. Accordingly, the ability to mitigate negative impacts of tourism on wildlife necessitates research into the ecology of the system and of the human dimensions, since plans aimed at optimizing wildlife fitness must also be acceptable to tourists. We developed an integrated systems dynamics model for the management of tourist–stingray interactions at 'Stingray City Sandbar' (SCS), Cayman Islands. The model predicts the state of the tourism attraction over time in relation to stingray population size, stingray life expectancy, and tourist visitation under various management scenarios. Stingray population data in the model comprised growth rates and survival estimates (from mark-and-recapture data) and mortality estimates. Inputted changes in their respective rates under different management scenarios were informed by previous research. Original research on the demand of heterogeneous tourist segments for management regulations via a stated choice model was used to calculate changes in the tourist population growth rate from data supplied by the Caymanian government. The management attributes to which tourists were responsive also have anticipated effects on stingray ecology (migration and mortality), and vice versa, thus linking the two components. We found that the model's predictions over a 25-year time span were sensitive to the stingray population growth rate and alternate management options. Under certain management scenarios, it was possible to maximize both the tourist segment in favor of no management and stingray numbers while reducing stingray health. However, the most effective relative strategy included a reduction in visitor density, restricted stingray interactions, and an imposition of a small fee. Over time, although fewer stingrays were predicted to remain at SCS, they would live longer and experience fewer stochastic disease events, and the desirable tourist segment was predicted to predominate. By understanding how management will affect tourist activities and their subsequent impacts on both wildlife health and visitor satisfaction, one can explore the management alternatives that would optimize both.

1. Introduction

In recent years, a growing worldwide demand to interact with wildlife has led to the emergence of a wide range of wildlife-tourism activities. In certain cases, wildlife tourism has resulted in unmitigated development that has compromised the ecological integrity of the system and even the fitness of focal organisms (Green and Higginbottom, 2000; Higginbottom et al., 2003). However, managers cannot simply ignore the needs of the tourist, since visitor satisfaction ensures continued economic returns, and contributes to local social welfare. Nevertheless, if tourist expectations and subsequent activities are left unchecked, they can eventually undermine and spoil the visitor experience through deterioration in the quality of the environment, less wildlife to observe or to interact with, concern over animal welfare and conservation, or a resistance to management. Further complicating this issue is the heterogeneous composition of the tourist population, given that wildlife tourists can differ by ethics, values, and motivations, and be diverse in their preferences for the intensity and type of management (Martin, 1997; Moscardo, 2000). Consequently, as wildlife tourism increases in popularity, optimizing the relationship between the tourism experience and the resource upon which it is based has become a crucial and challenging management goal. Research that integrates the ecological and social aspects of wildlife tourism can help to solve these complex situations, and stands to increase our understanding of the entire recreational system more completely than simply considering the ecological and human aspects separately (Newsome et al., 2005).

Ecological research has recently experienced a surge in integrated modelling of ecological and social systems that is partly theoretically and partly management motivated (Phillipson et al.,

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2009). Ecosystems such as agriculture, watersheds, rangelands, coastal zones, fisheries and farming have been investigated from both ecological and social perspectives simultaneously (Rouquette et al., 2009; Stave, 2003; Janssen et al., 2000; Chang et al., 2008; BenDor et al., 2009; Guzy et al., 2008, respectively). Social data incorporated into these models can be qualitative or quantitative, and are primarily based on human decisions – which in turn, are governed by people's utility (in the form of income or willingness to pay) or values (e.g., different behavioral roles; as reviewed in Cooke et al., 2009). Direct human–wildlife interactions have also been modelled, although to a much lesser extent, despite researchers calling for greater integration (see Higham et al., 2009 for a wildlife tourism example). Some examples include human–wildlife conflict (e.g., fowl and agricultural land use, Amano et al., 2007 and Beall and Zeoli, 2008; tiger and human forest use, Ahearn et al., 2001), and human–human conflict over wildlife (e.g., tour-operator behaviors in whale-watching enterprises, Anwar et al., 2007). To successfully manage wildlife tourism, one must consider the factors that make animal and tourist populations vulnerable, and explore the differential effects alternative management scenarios can have on their respective population dynamics. Our study is novel in that we employ an integrative framework that links a quantitative wildlife population model and a quantitative visitor behavior model dynamically to simultaneously predict the ecological and social outcomes for wildlife and visitors to the wildlife tourism attraction.

Our research presented here synthesizes ecological and social research for a wildlife-tourism activity – the feeding of stingrays at 'Stingray City Sandbar' (SCS) in the Cayman Islands – into a system dynamics model to explore the relative effectiveness of alternate management scenarios on the future state of the tourism attraction. SCS is a popular and valued marine tourism attraction in which tourists can hand-feed, touch, and hold wild Southern stingrays (*Dasyatis americana*). The stingrays have become permanent residents of the site, forming dense aggregations and relying on the provisioned squid (*Illex* and *Loligo* spp.) as their main diet, contrary to their biology. In 2003, Cayman Island stakeholders (government officials, tour operators and local citizens) convened a committee to agree upon a set of detailed rules for stingray protection and crowding alleviation. While each proposed regulation by itself would be expected to redress the known problems (e.g., limits on boat density would likely reduce the risk of boat-related injuries for stingrays and/or reduce congestion), individual stakeholders understandably raised concerns about unilateral changes to single portions of the system. It was therefore necessary to project the effects of proposed management scenarios on the integrated SCS system rather than on individual components (e.g., stingray-interaction rules could reduce stingray injuries but also dissuade visitors).

Given the complexity of this decision-making environment in which management directives will impact both wildlife fitness and the tourist experience, a system dynamics model – STELLA, was chosen for describing the interrelated system with its powerful yet simple causal-loop and stock-flow diagrams (Isee Systems, 2006). Dynamic models are particularly useful for testing the leverage of modelling assumptions, prioritizing variables for data collection, and for identifying the most sensitive attributes that require long-term monitoring (Faust et al., 2004). The assumptions of our model are informed by our previous ecological research on the stingray population's health and dynamics (Semeniuk et al., 2007, 2009; Semeniuk and Rothley, 2008), and by our social science research on the stated preferences of tourists for a range of management alternatives (Semeniuk et al., 2008). Because we have information and data on the main ecological and social drivers of the system (i.e., tourism impacts on stingrays, and tourist demand for SCS experiences), we are using the integrative systems dynamics model to explore and compare the relative effects of various management policies on stingray population size, stingray life-expectancy, and tourist population size and composition, after a 25-year time span. The overall goal for the SCS model is to identify meaningful management strategies that can sustain the wildlife tourism attraction through the protection of the wildlife resource and the enhancement of the tourist experience, rather than simply the maximization of stingray and/or tourist numbers.

2. Methods

2.1. Background information

Stingray City Sandbar is a warm, shallow water (1.6 m maximum depth) sandbar approximately 7740 m^2 area located roughly 300 m inland from the fringing reef in the North Sound in Grand Cayman Island. Stingray City Sandbar began in 1984 as a small attraction populated by only a few stingrays that were fed by a handful of locals. Due to the accessibility and quantity of provisioned food, the site became attractive to stingrays; and the positive feedback between the number of stingrays, amount of food, and tourists (who had then become the main food-providers) has resulted today in SCS being home to an estimated population of 150 stingrays and nearly 1 million tourist visits annually (CIMoT, 2002).

Although the Southern stingray inhabits all shallow bays around the Cayman Islands in a solitary manner, only in the vicinity of SCS can stingrays be found year-round in a dense mixed-sex aggregation of individuals. This amassment results from the unregulated quantity of provisioned squid (*Illex* and *Loligo* spp.), a non-natural diet item shipped in from the North Atlantic and North Pacific (Semeniuk pers. obs.; Gina Ebanks-Petrie Director, Cayman Islands Department of Environment pers. comm., 2004). The feeding routine (daily, except during the off-season, when weekends are excluded in summer) lasts from early morning until mid afternoon as tour boats continuously deliver tourists (mainly cruise line passengers) for an average 45-min visit to SCS.

2.1.1. Stingray ecology at SCS

The stingrays' non-natural diet has become the major source of food (Semeniuk et al., 2007), demonstrating stingrays have become attracted to the site due to the provisioning activities of tourists and tour operators. This diet, and its associated repercussions, have had a negative impact on the SCS stingrays. First, the diet does not provide the proper, balanced nutrition for proper health maintenance in terms of essential fatty acids (Semeniuk et al., 2007); secondly, the novel grouping behaviors of the tourist-fed stingrays, normally solitary foragers, has resulted in over-crowding conditions, and the stingrays are more likely to be in poorer body condition, injured by boats and predators, susceptible to ecto-dermal parasites, and engaged in intense interference competition, sustaining wounds from conspecifics, when compared to stingrays from control sites about the Island (Semeniuk and Rothley, 2008). As a result of the unnatural diet in combination with the physical stresses at SCS, tourist-fed stingrays display physiological responses indicative of sub-optimal health and attenuation of the defence system, including oxidative stress (Semeniuk et al., 2009). Over the long term, our results suggest that without management, the SCS stingray population is likely not sustainable without the addition of new recruits.

2.1.2. Human behavior at SCS

An investigation of the tourist component at SCS has equally provided invaluable insights. We wished to determine how tourist experiences would change under future alternative management scenarios, and used a stated preference model administered as part of a questionnaire survey of cruise line passengers at SCS to

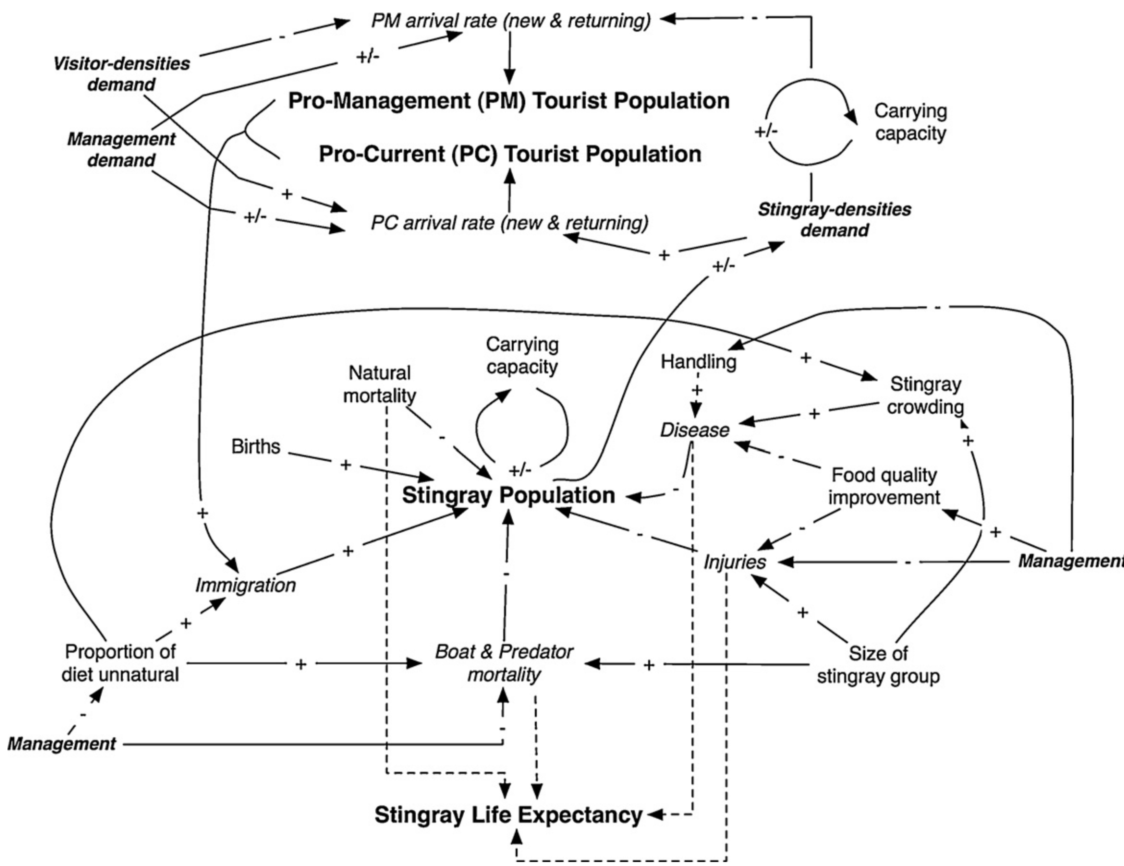

Fig. 1. Causal-loop diagram of the interlinked social (i.e., tourist) and ecological (i.e., stingray) population sub-models of SCS. Italicized terms represent main variables through which population dynamics are driven; italicized-bolded terms denote driver variables which link the two system components.

accomplish our objective (Semeniuk et al., 2008). This methodology involves the evaluation of hypothetical management scenarios, and possesses the unique advantage of being capable of analyzing the scenario components independently of one another (i.e., no colinearity), and of evaluating plausible future scenarios (Louviere et al., 2000). Our model was comprised of multiple sets of hypothetical scenarios as well as the status quo, or, 'business as usual' (no management), and asked respondents to repeatedly choose their preferred alternative. The scenarios were characterized by seven attributes of varying levels concerning animal-feeding and handling rules, resulting ecological outcomes (number of surrounding stingrays and their risk of injury), social crowding (number of people and boats), and a management cost. The choice model was analyzed using a mixed conditional logit as this statistical form represents an approximation to the economic principle of utility maximization (i.e., demand), and can also test for latent heterogeneity in the data (Greene and Hensher, 2003).

The latent class choice model revealed that current SCS tourists could be divided into two groups which differ dramatically in their response to proposed management: (1) a 'pro-management' group (PM = 68% of respondents), preferring actions that reduce congestion, impacts on stingrays, and the number of stingrays present, and being amenable to a management fee, but nonetheless still mildly preferring to directly interact with and feed the stingrays; and (2) a 'pro-current' group (PC) supporting a small management fee but strongly desirous to continue direct interactions with and be surrounded by numerous stingrays. Based on these findings, our results suggest the two segments would differentially and dynamically respond to management scenarios and associated stingray population over time.

2.2. Model overview

Our model has two main components, both of which are population sub-models: stingray and tourist population trajectories (Fig. 1). For stingrays, we are interested in two elements: how the stingray population will change over time, and what the average life expectancy will be for the stingrays over the course of this period. We use data derived from mark-and-recapture analyses to establish stingray population growth rate; and a detailed understanding of the wildlife system from our previous research (mentioned above) to anticipate and project how model regulations will influence changes in stingray recruitment and mortality. For tourists, we explore how their composition (PM versus PC; see Section 2.1.1) and number will change over time, and the factors that affect visitation rates, and hence population trajectory. To accomplish this latter task, we use our stated preference choice data to quantify demand for the SCS experience, which allows us to model the tourist population in terms of arrivals and departures, thus making the tourist demand model compatible with the STELLA modelling environment.

2.3. Model assumptions based on collected data

Our model is based on four main assumptions: (1) immigration is an important source of new recruits into the stingray population; (2) tourism-induced sources are the more relevant contributors to stingray mortality than natural sources; (3) tourist visitation is affected by demand which is a function of the quality (condition) and supply of the resource as well as the social experience; and (4) the two sub-models are directly linked via the relationship between tourist numbers and stingray population size. These assumptions are described in detail below.

2.3.1. Stingray immigration

We simulate a stingray population growth trajectory under three scenarios: a growth rate at which the population is (1) in decline (based on mark-and-recapture analyses – more below), (2) at a steady state, and (3) increasing. The latter two scenarios are included since a decreasing population growth rate calculated from a 4-year study period in such a long-lived animal (26 years; Henningsen, 2002) may not necessarily reflect the long-term trend. To be conservative, we assume births and immigration to equally contribute to recruitment in the first scenario; however, should the stingray population be actually steady or increasing, we consider immigration to be the main contributing factor, and not a simultaneous increase in births. Our previous work on SCS female stingray fitness metrics shows no evidence for increased gestational frequency despite the excess of provisioned food. In fact, provisioned females are on average lighter (i.e., not gravid) for a given structural size than their control counterparts (Semeniuk and Rothley, 2008). Therefore, if current population growth is in actuality at a steady state or increasing, these differences are likely to occur through immigration, and not through an increase in birth rate (nor a decrease in mortality rate).

2.3.2. Stingray mortality

As mentioned above, our research has demonstrated that habitat suitability of SCS is poor: the non-natural food, atypical grouping behaviors, over-crowding conditions and hazards from boats and predators have resulted in stingrays in poor health. Our findings suggest that tourism is the driving source of stingray mortality rather than natural sources of disease, predation and ageing, and further substantiated by the mark-and-recapture analyses (below); and will be represented as such in our model. Consequently, we reasonably assume tourist activities affect stingray survival both directly and indirectly, which are represented in the model by the following sources: immediate and direct mortality via predation (by sharks) and boat collisions (PB); indirect mortality from sustained injuries (I) incurred by boats, marine predators, and conspecific aggression; and indirect mortality via disease (D) from being excessively handled by tourists, from increased parasite transmission rates due to crowding, and from low quality food.

2.3.3. Tourist demand

A stated preference model is typically employed in situations where estimates of current and future human preferences need to be calculated to determine the level of customer demand for alternative 'service products' in non-monetary terms (Louviere et al., 2000). By asking respondents repeatedly to choose from pairs of hypothetical management scenarios the one they felt would maximize their experience over the others, our survey question elicited tourism demand for alternative management-regulated experiences over the status quo. Tourism demand is influenced by resource, social and regulatory environments (Manning, 1999), and factors significantly affecting demand in our model included the type of management plan enacted at the tourist site, the density of crowds, and the number of stingrays present. In the actual SCS system, the arrival of new tourists is mainly influenced either directly via word-of-mouth, or indirectly; i.e., if tourists are satisfied, they will report so back to the cruiseship company or travel agent, who will in turn continue selling the trip. Therefore, we assume that differences in demand for tourist experiences will affect visitation rates.

This relationship has an empirical basis, as a fundamental characteristic of the choice model is that the statistical method employed; namely, the mixed conditional logit, describes total utility as a linear addition or subtraction of the component utilities within the choice context (i.e., regression estimates of the attribute levels). These component utilities can then be summed to provide an overall utility for any scenario composition (including the six management scenarios investigated in this paper). The overall utility, or demand, can then be used to estimate changes in visitation rates over the status quo for the tourist population in our model.

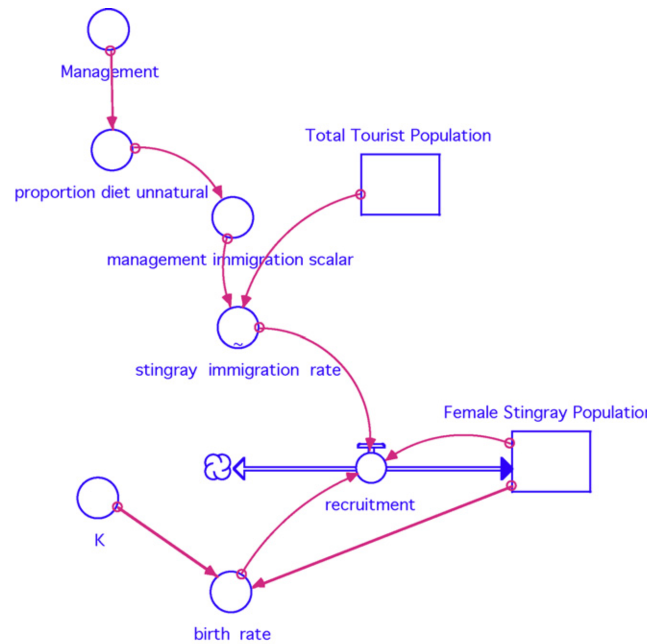

Fig. 2. Stock-flow diagram of the stingray recruitment sub-module of the 'Stingray City Sandbar' model.

2.3.4. Stingray–tourist functional relationship

Stingray City Sandbar is an artificial site; in other words, without the presence of tourists (and accompanying food), stingrays are typically solitary individuals, dispersed about Grand Cayman. Therefore, if tourists at the site begin to decline, there will be fewer feeding opportunities, and the ability to support a large population of stingrays will decline as stingrays permanently disperse in search of food. Equally, from the stated preference data, tourists (especially the pro-currents) prefer a higher density of stingrays over fewer, thus potentially initiating a negative feedback in tourist (PC) numbers. In our system dynamics model we model the functional relationship between stingray and tourist numbers via the effect tourist numbers have on the stingray immigration rate (see Section 3.1.3).

3. Model development

We used a systems dynamics approach to describe the linked relationships between the ecological and social components of SCS, and translated our flow diagrams (Figs. 2–4) to a set of difference equations with STELLA 9.03 (Isee Systems, Inc.). Our null model (NM) was contrasted against five management scenarios to predict the relative effects of management regulations on stingray fitness, and visitation rates for both tourist segments. The three state variables were 'Female Stingray Population', 'Pro-Management Tourist Population' (PM), and 'Pro-Current Tourist Population' (PC); auxiliary variables are listed in Table 1. The main variables through which population dynamics are driven are stingray immigration rate, stingray mortality rates, and tourist demand for the SCS experience (for each tourist segment). The driver variable which links

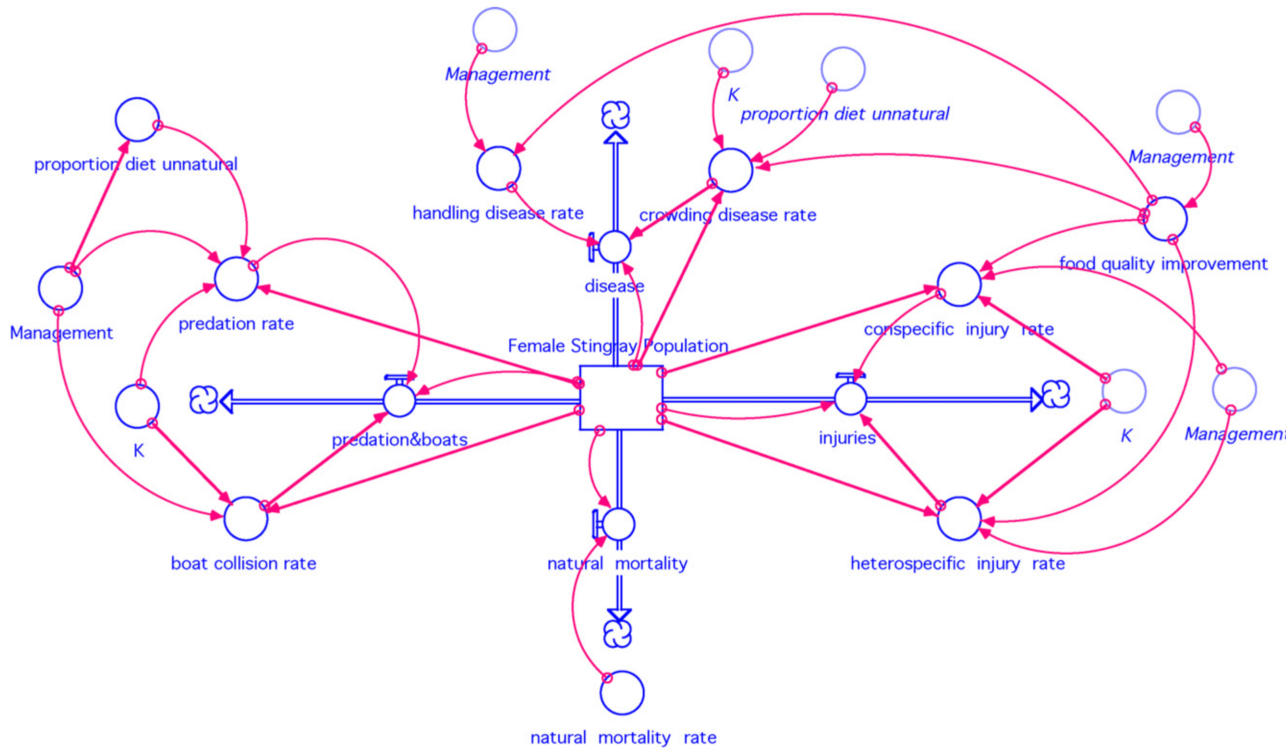

Fig. 3. Stock-flow diagram of the stingray mortality sub-module of the 'Stingray City Sandbar' model.

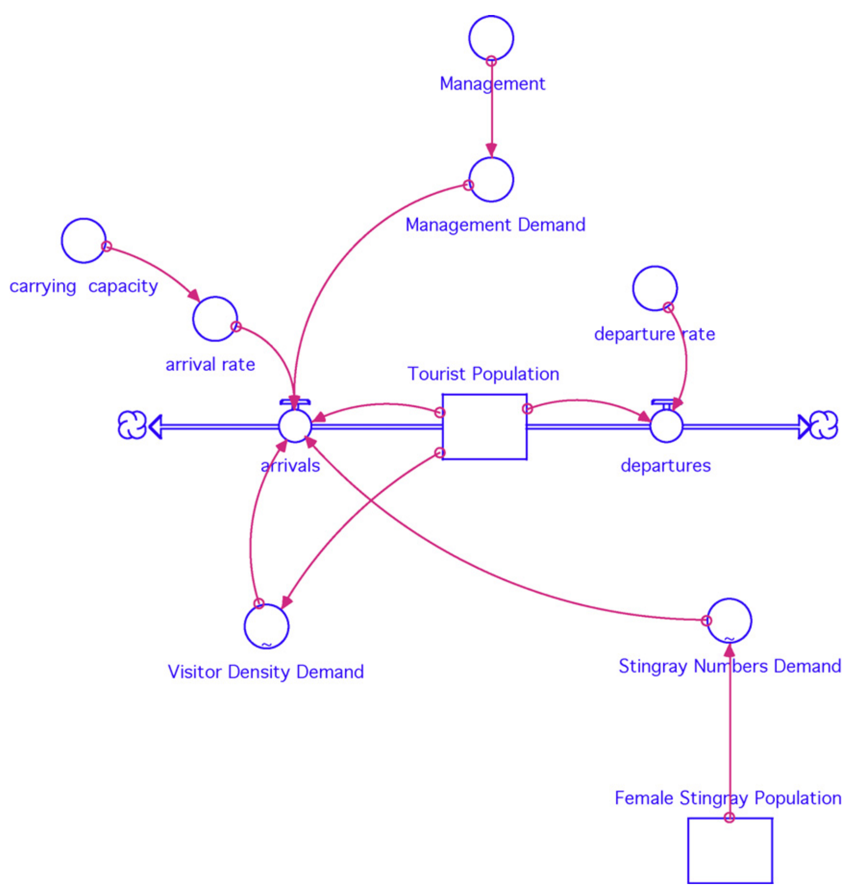

Fig. 4. Stock-flow diagram of the tourist module of the 'Stingray City Sandbar' model. The two tourist segments each had their own module with segment-specific inputs.

Table 1
Parameters and values used in Stingray City Sandbar management model.

Parameter	Value	Source
State variables		
Female stingray starting population	150 rays	Tour operator input and tagging study
Pro-management starting population	552,000 tourists	2006 Cayman Islands Port Authority (68% from Semeniuk et al., 2009)
Pro-current starting population	226,000 tourists	2006 Cayman Islands Port Authority (32% from Semeniuk et al., 2009)
Auxiliary variables		
Stingray		
Carrying capacity	250 rays	An estimate allowing stingray population to grow
Per capita rate of growth (R)	−0.12, 0, 0.15	Alternative values calculated from population growth rate ($\lambda = 0.88$ (from Pradel model), 1, and 1.5)
Overall mortality probability (d_{total})	(−) 0.15	Calculated as (1 − survival) from Pradel model
Birth rate (b)	0.015	One half the recruitment rate, calculated from (recruitment = $R - d$)
Management immigration scalar	0, −0.015, −0.020 (and scaled to accommodate alternate λ's)	Considers magnitude of immigration/emigration under different management plans
Immigration rate	See Eq. (3) (max: 0.031, min: 0)	Estimated positive decelerating curve
Natural mortality rate (d_{nm})	0.054	Based on average life-expectancy of 18 years using Eq. (6)
Mortality rate of predation and boat collision (d_{PB})	0.016	Mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Mortality rate of conspecific and heterospecific injury ($d_{Ic,Ih}$)	Same as above	Weighted values for indirect tourism-induced mortality; mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Mortality rate of handling- and crowding-disease	Same as above	Mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Tourists		
Carrying capacity	2,000,000 tourists	Estimated maximum cruise ship capacity via practical constraints
Per capita rate of growth (R_{now})	0.137	Calculated as value that minimized the sum of squares of the differences between the mean and actual population-size values over time
PM departure rate	(−) 0.9265	Calculated from the proportion of PM tourists in the population and proportion of returning visitors (from Semeniuk et al., 2009)
PC departure rate	(−) 0.8125	Calculated from the proportion of PC tourists in the population and proportion of returning visitors (from Semeniuk et al., 2009)
Density-dependent PM arrival rate	1.064	Calculated as PM departure rate subtracted from tourist population growth rate (R_{now})
Density-dependent PC arrival rate	0.950	Calculated as PC departure rate subtracted from tourist population growth rate (R_{now})
PM/PC management demand	See Table 3	Calculated as the percent relative change in support over status quo from a stated preference, discrete choice experiment
PM/PC visitor density demand	See Eq. (11)	Population-level estimate extrapolated from relationship of tourist preferences for number of immediate, surrounding rays per trip
PM/PC stingray numbers demand	See Eqs. (12) and (13)	Population-level estimate extrapolated from relationship of tourist preferences for number of people allowed per trip
Main driving variables		
Management regulations	See Tables 2 and 3	Projections of changes in stingray immigration and mortality rates are realistically based on previous ecological research; changes in visitor arrival and departure rates are calculated from stakeholder input via a stated preference choice model

the two system components (i.e., number of visitors and stingrays) is management regulations (Fig. 1).

3.1. Stingray population module

3.1.1. Stingray population trajectory

This sub-model is parameterized and calibrated with field data that were collected at SCS without any management enacted, and thus serves as the baseline (no management) scenario. The initial stock variable of Female Stingrays was set at 150 and carrying capacity at 250, based on the number of female stingrays tagged and identified at SCS and estimates from tour operator and marine research officer inputs. Only female stingrays are modelled in this paper since just 18% of the tagged stingrays at the tourist site are males; as such, females will be the major recipients of any management actions. Implications of this targeting are minor in that estimates are relative, and are likely conservative.

From 2002 to 2005, stingrays at SCS were captured, tagged (with a passive integrated transponder – PIT) or identified (if previously captured), and released and recaptured on subsequent sampling efforts. We used open-population Pradel models in the program MARK (White and Burnham, 1999; Cooch and White, 2002) to estimate realized population growth rate (λ) and apparent survival rates (φ). Model parameters also included capture probability (p).

The data supported models with variable λ over time, with two of the three final models with $\Delta AIC_c < 4.0$ (Burnham and Anderson, 1998) having λ decrease linearly over time. Model averaging produced a λ of 0.88 (95% CI = 0.682–0.977). Models of both time invariance and variance were supported for φ rate estimates, with a model average value of 0.85 (95% CI = 0.780–0.911). This estimate was fairly robust in the different models analyzed and was not subjected to sensitivity analysis. We used values obtained for λ and φ to create the stingray population module and to calibrate the model under alternative, simulated λ's (see below).

3.1.2. Stingray population recruitment

Stingray populations recruit via births and immigration (Fig. 2). We let realized λ (0.88) and apparent φ (0.85) parameters represent projected λ and annual survival rates, respectively. We used these values to estimate *R*, the net geometric per capita rate of growth to determine mortality (*d*) and recruitment rates (*f*).

$$\text{Since} \quad \lambda = (R+1), \tag{1}$$

R = −0.12. Because we wished to examine other population growth scenarios (as data based on a 4-year dataset may not accurately reflect long-term population trends), we also modelled the stingray population module using an *R* of 0 (λ = 1) and 0.15 (λ > 1).

Mortality (*d*) probability is simply calculated as $1-\varphi$, and therefore (−) 0.15 was used for *d*.

The recruitment rate (*f*) into the population by births (*b*) and immigration (*i*) was calculated as 0.03, 0.15, and 0.3 (for λ < 1, =1 and >1, respectively), using:

$$f = R - d. \tag{2}$$

We let *b* and *i* both equal 0.015 (i.e., for recruitment = 0.03) under λ < 1, but we varied *i* (0.135 and 0.285) and kept *b* at 0.015 (although density-dependent) for the alternate λ analyses (as explained above).

In sum, yearly recruitment into the stingray population ($N_{Stingray(t+1)}$) is calculated as the product of the current population estimate ($N_{Stingray(t)}$) with the sum of the stingray birth rate (*b*) and the immigration rate (*i*):

$$(N_{Stingray(t+1)})_{Recruitment} = (b + i^{\dagger}) \times N_{Stingray(t)}, \tag{3}$$

where immigration is influenced by the management scenario enacted and the tourist population size (†).

3.1.3. Stingray–tourist functional relationship

With increasing tourist numbers more feeding opportunities and food are available to stingrays, and hence their immigration rate into the SCS population will increase. Although actual data on this relationship are not available, we realistically assume this functional response between the stingray immigration rate and tourist population size to be a positive decelerating curve. We have ensured that equation parameters were constrained to reflect the actual immigration estimates (calculated from above) at the current tourist volume (circa 2006). We additionally ensured that the asymptotic yearly immigration rate would not produce a maximum stingray population size over the stingray carrying capacity. For instance, the relationship between stingray immigration rate and tourist density for λ < 1 is:

$$\text{stingray immigration rate } (i) = -3\text{E}-15(N_{PM+PC})^2 + 2\text{E}-08(N_{PM+PC}) - 0.0012, \tag{4}$$

where *N* is the total tourist population size.

Management regulations, however, can influence this relationship if there are actions to reduce the amount of provisioned food. For instance, food reduction is simulated to slow down the immigration rate and potentially cause it to become negative (i.e., emigration). This phenomenon is accomplished by adding a variable comprised of an ordinal range of negative values (including zero) to the calculated immigration-rate estimate, the values of which are dependant on the level to which feeding is restricted (e.g., for λ < 1: no restriction (0.0), mild (−0.015), and high restriction (−0.02)). However, an increasing tourist population can cancel out the food-restriction effects on immigration:

$$\text{stingray immigration rate } (i) = \text{Function(tourist population size)} + (-) \text{ management immigration scalar.} \tag{5}$$

3.1.4. Stingray population mortality

Stingray populations decline through emigration, natural mortality, and via tourism-induced mortality (Fig. 3). The emigration rate was incorporated into the 'recruitment' portion of the model (more below). Published longevity estimates for *D. americana* provide conflicting information for estimating natural mortality. García et al. (2008) cites a maximum lifespan of 18 years, while a captive study (Henningsen, 2002) suggests 26 years. We used the shorter, more conservative lifespan to represent the average, and back calculated a natural mortality estimate after Brownie et al. (1985):

$$\text{Lifespan} = \frac{1}{-\ln(\text{survival})}. \tag{6}$$

This natural mortality estimate (d_{nm} = 0.054) was held constant in the model, and represents natural sources of disease, predation and ageing.

Our mark-and-recapture analysis returned a mortality rate estimate almost three times as great (*d* = 0.15) as the one derived for natural mortality. Since we assume emigration at current conditions to be nil, the difference in mortality (0.096) is considered to be attributable to three tourism effects, each comprised of two related sources: predators and boats (PB), sustained injuries from conspecifics and heterospecifics (I), and disease from excessive handling and crowding (D). For simplification purposes, we assume each source contributes equally to the overall morality estimate (i.e., 0.016 each). In turn, each of these sources is differentially affected by the various management scenarios (Table 2 describes how the different management scenarios will be simulated in the model to affect stingray mortality rates). A series of if/then conditional statements is used to calculate the effect of different management scenarios on the six mortality-rate estimates. Additionally, a density-dependent function is factored into the mortality estimate calculation to denote that mortality severity lessens as stingray population size decreases (as our previous research revealed stingray crowding conditions affect health and predation risk). We therefore assume that with a remaining population of only 50 individuals at SCS, mortality rates caused by predators and boats, injuries, and disease (with the exception of disease caused by excessive handling), are nil. Lastly, for the disease mortality source, we also built in a random component (each year there is a small percent chance that a high mortality rate will occur) to reflect the stochasticity of outbreaks of disease-inducing events such as hurricanes, oil spills, and environmental perturbations (e.g., algal blooms, etc.). Specifically, we drew from a uniform distribution a 2–5% chance that for a specific year, in the absence of management, a population 'crash' would occur with a $d_{tourism\text{-}iduced\ mortality}$ of 0.25. With management, crashes could still occur, but with a reduced probability (1/10th).

In sum, yearly mortality of the stingray population ($N_{Stingray(t+1)}$) is calculated as the product of the current population estimate ($N_{Stingray(t)}$) with the sum of the stingray natural mortality rate (d_{nm}), direct mortality rate from boats (d_B) and predators (d_P), indirect mortality rate from injuries sustained from conspecifics (d_{Ic}) and heterospecifics (d_{Ih}), and indirect mortality rate from disease via handling (d_{Dh}), and stingray crowding conditions (d_{Dc}):

$$(N_{Stingray(t+1)})_{Mortality} = (d_{nm} + d_B^{\dagger} + d_P^{\dagger} + d_{Ic}^{\dagger} + d_{Ih}^{\dagger} + d_{Dh}^{\dagger} + d_{Dc}^{\dagger}) \times N_{Stingray(t)}, \tag{7}$$

where the tourism-induced mortality rates are influenced by the management scenario enacted (†).

3.2. Stingray life expectancy module

Of equal importance to modelling stingray population size is the stingray's estimated average life expectancy over the 25-year time

Table 2
The projected impact of management scenarios on the tourism-induced stingray mortality rate (0.096) in relation to the status quo of no management. CC = Crowd Control, AFP = Amount of Food Provisioned, FQC = Food Quality Control, HR = Handling Rules, IP = Inclusive Plan. Projections are realistically based on previous ecological research, and serve to determine relative changes inputted for the immigration and mortality rates in the model.

Mortality type (rate estimate under status quo)	Sources of tourism-induced mortality[a]	Mechanisms through which stingray fitness is negatively affected without management	Management plan and associated reduction in mortality rate estimate				
			CC	AFP	FQC	HR	IP
Direct (0.016 each)	Predators	Predator detection reduced by tourist crowds; food quantity promotes competition, reducing predator vigilance.	−0.008	−0.004	0	0	−0.008
	Boats	Boat-propeller detection reduced by tourist crowds; food quantity promotes competition, reducing boat detection.	−0.008	−0.004	0	0	−0.008
Indirect (0.016 each)	Injuries from conspecifics	Ability to recover affected by poor nutrition; food quantity promotes competition, increasing aggression-induced injury.	0	−0.010	−0.006	0	−0.012
	Injuries from heterospecifics	Ability to recover affected by poor nutrition; food quantity reduces vigilance (via food competition), increasing likelihood of sustaining injuries from predators and boats.	−0.004	−0.010	−0.006	0	−0.012
Indirect (0.016 each)	Disease from handling[b]	Susceptibility enhanced by interacting with crowds, dense aggregations (promoted by food quantity), poor nutrition, and explicit handling by tourists.	−0.004	−0.006	−0.006	−0.010	−0.012
	Disease from stingray crowding conditions[b]	Susceptibility enhanced by dense aggregations (promoted by food quantity) and poor nutrition.	0	−0.010	−0.006	0	−0.012
Estimated mortality rate at stingray N = 150 and no stochasticity			0.072	0.052	0.072	0.086	0.032

[a] The parameter calculation for each mortality source with the exception of 'disease from handling' has an associated stingray density-dependent function – see text for details.
[b] A random component variable was added to this mortality source to represent a percent chance that within a given year a high mortality rate will occur, thereby reflecting the stochasticity of outbreaks. Percent probability of outbreak (range: 2–5%) is reduced through targeted management plans.

series. Stingray life span (using Eq. (6)) was calculated at each time interval using the sum of mortality estimates for d_{nm}, d_{PB}, d_I and d_D, to deduce average life span over the course of the model run.

3.3. Tourist module

3.3.1. Tourist population trajectory

Initial state variable stocks of the PM and the PC tourist segments were set at 552,000 and 260,000, respectively, based on the total number of cruise-ship passengers docked at Grand Cayman in 2006 (unpubl. data, CI Director of Tourism – DoT). We chose the initial population sizes for these two segments based on the heterogeneous probability classification of these two groups from the latent class model of tourist preferences (i.e., 68% and 32%, respectively, of 812,000 visitors in 2006; Semeniuk et al., 2008). The tourist population is defined as tourists per year visiting SCS by boat for a day-trip/excursion only, and leaving Grand Cayman soon after their visit.

The annual tourist population growth rate was calculated from actual data supplied by DoT's Port Authority of cruise-ship tourist numbers for the period 1984–2006 and adjusted for the proportion visiting SCS. A carrying capacity (K) of 2 million visitors annually to SCS was chosen as the maximum the site could potentially accommodate should the Port Authority allow eight cruise ships to dock each day throughout the year; presently, a maximum of four boats are docked at any given time and for a maximum of 5 days/week during the off-season. Assuming a logistic discrete growth with a carrying capacity of 2 million visitors to SCS, R – the net discrete per capita rate of growth – was estimated using the solver tool in Microsoft Excel designed to find a numerical solution yielding the optimal population trajectory that minimizes the sum of squares error value (i.e., maximizes fit with actual data). With a chosen carrying capacity (K) of 2 million visitors annually to SCS, the calculated R value (0.231) was made density dependent and converted to R_{now} to reflect current conditions:

$$R_{now} = R\left(1 - \frac{N_{PM+PC}}{K}\right), \tag{8}$$

where N is the total tourist population size. R_{now} was calculated as 0.137.

From Semeniuk et al. (2008), only 11% of survey respondents were return visitors. Moreover, the authors' decision-tree analysis revealed that of the 11% returning, 5% were PM tourists while 6% were PC tourists. From these data, we assumed that PM tourists will not return at a rate of 0.9265 (PM-tourist 'mortality' = 0.05/0.68), and PC tourists will not return at a rate of 0.8125 (i.e., PC-tourist 'mortality' = 0.06/0.32). Knowing the per capita rate of growth of the tourist population as well as their departure rate allowed for the calculation of the rate of arrival (i.e., arrival rate + departure rate = R) as 1.064 and 0.950 for PM and PC segments, respectively.

3.3.2. Tourist arrivals

The above values for the tourist arrival and departures rates are for the status quo of no management. Under this scenario, both tourist population segments continue to increase at their respective current growth rate; however, their segment population growth rates will differentially change as a function of the following model variables: tourist demand for: (1) the management scenario (M), (2) the density of visitors (V), and (3) the number of stingrays in the population (SR; Fig. 4), the composite utilities for which were determined from the mixed conditional logit (Semeniuk et al., 2008). Specifically, we first calculated the overall utility for each management scenario (M) in our model for each of the two tourist segments using the following equation:

$$P(i|i \in M) = \frac{\exp(X_i, \beta)}{\sum_{j=M} \exp(X_j, \beta)}, \tag{9}$$

where the probability of choosing alternative i from all scenarios included (M) equals the exponent of all the measurable elements of alternative i (i.e., X, the attribute level and its associated composite utility, β) over the sum of the exponent of all measurable elements of all alternatives, j. We next calculated the percent relative change of the management scenario utility over that of the status quo option. We used the formula:

$$M = \left(\frac{P_2 - P_{NM}}{P_{NM}}\right) + 1, \tag{10}$$

where P_2 is the total composite utility of the management scenario, and P_{NM} is that for No Management (status quo). Because we then set No Management to a value of 1, the demand for other scenarios is expressed relative to this value. If the calculated adjusted proportion relative change was <1.0, it meant demand was less for this scenario than for status quo, and hence tourist population growth will slow as presumably the site would be less attractive to future visitors; whereas >1.0 implied a greater demand than for status quo, as the site would become more attractive (e.g., through word-of-mouth and number of trips sold), and thus the population growth rate will increase. Tourist arrival and departure rates (already calculated at status quo) were then scaled by the value derived from Eq. (10) (Table 3).

Given that tourist-crowding issues were a concern within the survey (Semeniuk et al., 2008), and that the population of tourists is increasing (as evidenced from R), the density of visitors is predicted to affect the tourist experience, and hence their demand for alternative scenarios. To reflect this issue, we scaled the number of tourists present at any given time (presented in the stated preference choice model as 500, 750 and 1000, all other attributes set to status quo) to an annual population of 812,000, 1,200,000, and 1,600,000, respectively, and used the corresponding composite utilities (using Eq. (9)) to derive an equation of the assumed relationship (Eq. (11)). This relationship constrains the value of 812,000 annual visitors (the current estimate) to a value of zero change in demand so as to maintain status quo. The relationship was identical for both tourist segments:

$$V_{PM+PC} = -3\text{E}-07 \times (N_{PM+PC}) + 0.244. \tag{11}$$

The tourist module is additionally linked to the ecological component via the number of stingrays in the population. Tourists responded to the number of surrounding stingrays in the choice experiment from Semeniuk et al. (2008), and therefore the population size of stingrays will independently influence the tourist experience, site appeal, and hence tourist demand. We therefore used the change in composite utilities for 10, 24, 40 and 55 (current) surrounding rays (from the stated preference choice model, all other attributes set to status quo) to equal the utilities for total stingray population sizes at SCS of 27, 68, 110 and 150 (current) stingrays, and extrapolated the functional relationship of change in demand for each tourist segment for the stingray population ranging in size from 20 to 250 individuals (Eqs. (12) and (13)). Note that at the current stingray population estimate of 150, the change in demand is set to 0, so as to maintain status quo:

$$SR_{PM} = -5\text{E}-05 \times (N_{Female\,stingray})^2 + 0.0093(N_{Female\,stingray}) - 0.27, \text{ and} \tag{12}$$

$$SR_{PC} = 0.2778 \times \ln(N_{Female\,stingray}) - 1.392. \tag{13}$$

Table 3
Management scenarios compared in the STELLA simulation model. Bolded levels represent changes from the current scenario of 'No Management'. Included are the adjusted relative change in demand over status quo (No Management) of pro-management (PM) and pro-current (PC) tourist segments for each scenario, used as input into the STELLA model.

Management attributes		Management plans					
		No Management (NM)	Congestion Control (CC)	Amount of Food (AFP)	Food Quality Control (FQC)	Handling Rules (HR)	Inclusive Plan (IP)
Number of boats		40	**20**	40	40	40	**20**
Number of surrounding people		1000	**500**	1000	1000	1000	**500**
Stingray feeding		Operator and Tourist	Operator and Tourist	**Operator only**	Operator and Tourist	Operator and Tourist	**Operator only**
Stingray handling		Operator and Tourist	Operator and Tourist	Operator and Tourist	Operator and Tourist	**Operator only**	**Operator only**
Number of surrounding rays		55	**40**	**40**	55	55	**40**
Stingray risk of injury		High	**Medium**	**Medium**	**Medium**	**Medium**	**Low**
Conservation access fee		None	**5$ USD**	None	**5$ USD**	None	**5$ USD**
Scenario utilities (χ_i, β_i)[a]	PM:	−1.46	1.44	0.007	−0.23	0.13	1.86
	PC:	1.93	2.81	0.67	2.30	1.72	0.49
Adjusted relative change in demand over status quo (NM)[b]	**PM**:	NA (1.0)	1.50	1.37	1.33	1.40	1.51
	PC:	NA (1.0)	1.40	0.45	1.18	0.90	0.39

[a] Scenario utilities were calculated from the sum of the component utilities for each management attribute – i.e., regression estimates of the mixed conditional logit model from Semeniuk et al. (2008). The utility for the sum of alternative scenarios (χ_j, β_j) for calculation of P (Eq. (9)) is: PM = −2.07; PC = 1.86.

[b] These values were derived using Eqs. (9) and (10), and then used – via scaling – to determine the changes in tourist population growth rates for each segment.

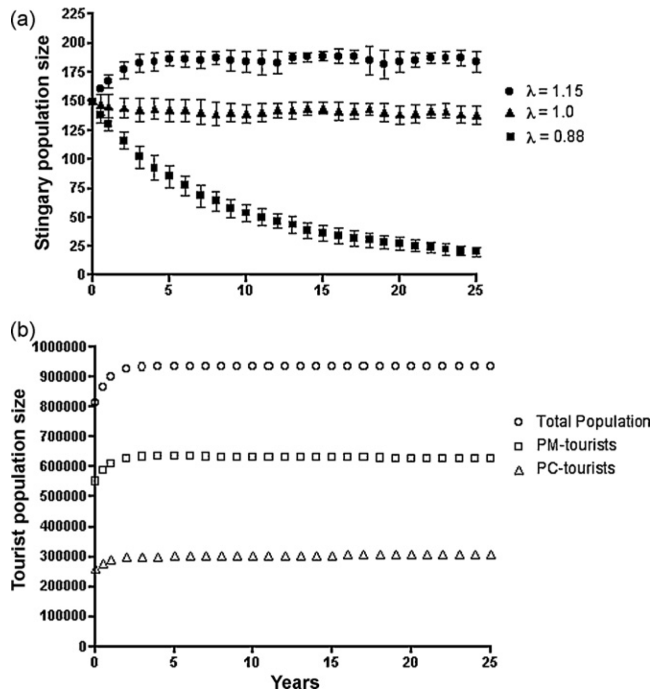

Fig. 5. Calibration results of each sub-model without the two components linked. (a) The density-dependent stingray population is run under three population growth scenarios (with λ = 0.88 calculated from mark-and-recapture data), and with stochasticity of disease built in. K = 250 individuals. (b) The density-dependent tourist segment population growths are derived from actual visitor landings data supplied by the Cayman Islands Port Authority. K = 2 million tourists.

In sum, yearly tourist arrivals into the population were calculated for each tourist segment as follows (without any interactions):

$$\text{Tourist arrivals } (N_{t+1}) = (\text{tourist population } (N_t) \times \text{arrival rate} \times (M + V + SR)). \quad (14)$$

3.3.3. Tourist departures

Tourist departures are composed of a large percentage of tourists who will not return (modelled as permanent 'mortality'), and a smaller percentage who will return to SCS (~11%; Semeniuk et al., 2008). These latter tourists are modelled as 'remaining' in the population. The calculation of tourist departures for each successive yearly time step is simply modelled as the current population size of the PM- and PC-segment multiplied by their respective departure rates:

$$\text{Tourist departures } (N_{t+1}) = \text{tourist population } (N_t) \times \text{departure rate}. \quad (15)$$

3.4. Drivers of the model: management regulations

The integrated management scenarios tested in our model (each comprised of seven attributes of varying levels) provide the key link between the stingray and tourist population components, since they are composed of regulations that can affect stingray ecology via immigration and mortality rates, and the tourist experience. Importantly, all the management attributes evaluated by tourists in the choice model have direct links to stingray ecology; and tourists (and tourist segments) are also (differentially) sensitive to each of these managerial attributes, and will have their tourist experiences affected. These links are explained both descriptively and quantitatively in Tables 2 and 3. It should be noted that although it is not possible to predict the exact amounts by which stingray mortality will be reduced by management, we are certain in our knowledge of the relative strengths each plan will have, and reflect this awareness (based on our ecological research) in the values chosen.

The six management scenarios tested in the model are as follows: (1) a status quo model of No Management (NM) which reflects current conditions at SCS, (2) Crowd Control (CC), 3) Amount of Food Provisioned (AFP), (4) Food Quality Control (FQC), (5) Handling Rules (HR), and (6) Inclusive Plan, which encompasses all of the above.

3.5. Model application

We began by calibrating the model to reproduce the measured data, and then ran each sub-population module separately to look for inconsistencies in behaviors (Fig. 5). We used a yearly time step over a period of 25 years to investigate the evolution of the tourist life-cycle model of SCS which currently appears to be approaching its 'consolidation' phase (Butler, 1980). Because the model is not used for precise quantification, but for an integrated complex system demonstration showing a reasonable long-term trend, structure assessment was used for validation (Sterman, 2000). The purpose is to determine whether the model is consistent with the real system, verifying model structure consistency with relevant system descriptive knowledge. The 'No Management' scenario in this case was configured to examine whether simulated results preserve ecological system relations. This scenario also serves as the baseline for later comparison with various management strategies. The 'No Management' plan assumes that no management strategies are adopted during the 25 year run. The six management scenarios were each simulated 50 times each for the three different stingray population growth rates. We were relatively unconcerned with adjusting our carrying capacity variables for both tourists and stingrays as we were more interested in exploring the relative differences between management scenarios than in determining absolute final output values. The final values for the stingray and the tourist populations, and the average stingray life expectancy along with its coefficient of variation (as a proxy for demographic stochasticity) were compared across management scenarios for each stingray λ. Tukey-Kramer HSD was used to statistically compare the outputs of the various scenarios while protecting the overall error rate (Table 4).

4. Results

Structural assessment of the models under different stingray population growth rates with No Management was sound (Fig. 7). Stingrays continued their projected trajectories, with the tourist population segments each responding differently. Both segments increased in numbers during the early part of the simulation (as dictated by the calculated R_{now}), but their growth rates were then influenced by the change in stingray numbers and/or visitor densities which affected their demand. With a decreasing stingray population, only PM-tourists preferred to visit SCS; at a stable population size, it took longer for the PC-tourist segment to 'out-compete' PM-tourists; whereas with an increasing stingray population size, both high stingray and visitor densities allowed PC-tourists to dominate more quickly, as expected. Regardless of the scenarios tested, the stingray and tourist systems converged to a stable equilibrium (except for when periodic stingray-disease outbreaks took place); and tourist populations mostly fluctuated in response to the stingray population variable. Predictions of final outputs differed according to the management scenario and stingray population growth rate (λ) used (Fig. 6).

Table 4
Model outputs (after 25 years) ±S.D. after 50 simulations.

		Management plans					
		No Management (NM)	Congestion Control (CC)	Amount of Food (AFP)	Food Quality Control (FQC)	Handling Rules (HR)	Inclusive Plan (IP)
Female ray							
Population	$\lambda = 0.88$	21 ± 6.0	32 ± 5.6	26 ± 9.5	41 ± 6.2	31 ± 4.0	53 ± 4.2
Size (current: 150 rays)	$\lambda = 1.0$	156 ± 4.5	178 ± 11.4	129 ± 2.1	177 ± 10.7	171 ± 7.2	130 ± 9.4
	$\lambda = 1.15$	203 ± 7.5	213 ± 4.2	166 ± 3.7	211 ± 4.7	200 ± 2.0	162 ± 6.2
Mean Ray							
Life expectancy	$\lambda = 0.88$	9.3 ± 0.29	9.5 ± 0.22	9.6 ± 0.15	11.3 ± 0.27	9.5 ± 0.23	14.4 ± 0.13
(years) + coefficient of variation	$\lambda = 1.0$	5.8 ± 0.19	5.9 ± 0.14	7.6 ± 0.09	6.3 ± 0.22	5.7 ± 0.14	12.4 ± 0.05
	$\lambda = 1.15$	5.0 ± 0.16	5.3 ± 0.17	6.8 ± 0.10	5.55 ± 0.19	5.2 ± 0.12	11.4 ± 0.05
PM Tourist							
Population	$\lambda = 0.88$	878,059 ± 17,232	1,244,663 ± 13,218	1,165,212 ± 7181	1,191,122 ± 17,822	1,189,132 ± 12,614	1,295,285 ± 6533
Size (current: 552,000)	$\lambda = 1.0$	437,925 ± 106,814	309,715 ± 126,252	1,240,450 ± 4396	590,130 ± 121,997	1,110,751 ± 26,599	1,297,289 ± 3408
	$\lambda = 1.15$	29 ± 9.8	313 ± 107	1,137,786 ± 23,627	414 ± 231	714,889 ± 80,816	1,225,488 ± 19,108
PC Tourist							
Population	$\lambda = 0.88$	228 ± 70	746 ± 146	0 ± 0	142 ± 39	0 ± 0	0 ± 0
Size (current: 260,000)	$\lambda = 1.0$	489,602 ± 104,152	892,761 ± 133,848	0 ± 0	489,874 ± 121,234	1046 ± 323	0 ± 0
	$\lambda = 1.15$	1,003,562 ± 3433	1,244,731 ± 5338	0 ± 0	1,125,201 ± 6904	207,454 ± 46,309	0 ± 0
Total Tourist							
Population	$\lambda = 0.88$	*878,287*	*1,245,409*	*1,165,212*	*1,191,254*	*1,189,132*	*1,295,285*
Size	$\lambda = 1.0$	*927,527*	*1,202,476*	*1,240,450*	*1,080,004*	*1,111,797*	*1,297,289*
	$\lambda = 1.15$	*1,003,591*	*1,245,044*	*1,137,786*	*1,125,432*	*922,343*	*1,225,488*

Different management scenarios had differential consequences, depending on stingray population growth. With $\lambda < 1.0$, the highest stingray population was achieved under a IP and the lowest with NM and AFP. Stingray longevity was relatively unaffected by management with the exception of FQC and IP which produced significantly longer lifespans (although demographic stochasticity was highest with FQC and NM). Likewise, tourist demand was differentially affected, with the PC segment no longer frequenting the site after a 25-year time span (as they had a high demand to interact with many stingrays), and with the PM segment in great numbers under CC and a IP.

With $\lambda = 1.0$, stingray numbers were maximized under CC and FQC, with IP (and AFP) resulting this time in the smallest stingray population. Stingrays under the HR scenario were predicted to have the shortest lifespan, and demographic stochasticity was significantly lower in IP and AFP than in the other scenarios. In this instance, among the tourist population a mix of tourist segments occurred under NM, CC, and FQC, with PC tourists mostly dominating, while the remaining scenarios (AFP, HR, and IP) produced the PM segment exclusively.

Lastly, assuming a $\lambda > 1.0$ produced results similar to when stingray population growth was at a steady state, with a few notable differences. Only in the IP scenario do stingrays live as long as they could and have the smallest demographic stochasticity. However, the PC segment dominated entirely under NM, CC and FQC, with only AFP and IP producing PM segment-only tourists. Regardless of λ, the IP management scenario consistently produced the healthiest stingrays, as well as the highest total tourist population size with PM-segment tourists dominating. HR consistently produced stingrays with the shortest lifespan; the FQC plan produced the most inconsistent results; and the current scenario of ‘No Management’ resulted in the lowest total tourist population size.

5. Discussion

In this paper we explored with hypothetical management scenarios ways in which the negative impacts of tourism visits on wildlife health and the tourist experience can be mitigated. While our previous ecological research into the system served as a guide and hence allowed us to predict the effects of different management regulations on stingray immigration and mortality rates, without the use of the model we would be unable to predict the relative magnitude of the different management-regulation effects, or, more importantly, how the simultaneous application of these regulations to consumer demand would affect both stingray and tourist segment population dynamics. Our findings indicate that in the absence of a sound management plan the actions of tourists and the resultant ecological outcome will cause the life expectancy of the stingray to be considerably lowered, and prevent tourists from maximizing their tourist experience – with the undesirable tourist segment predominating under certain conditions.

5.1. Evaluation of alternative management scenarios

The ‘Inclusive’ management scenario (Figs. 6 and 7) is the most robust and consistent management regulation as it addresses all sources of mortality and is drastically preferred by the PM-segment in comparison to PC-segment tourists. It was simultaneously capable of: reducing stingray populations to levels without detriment to the tourist experience, increasing the average lifespan of the stingray, ensuring visitor satisfaction is maximized, and promoting the arrival and return of PM-segment tourists. Although the Crowd Control (CC) scenario was agreeable for both tourist segments, it still had large negative impacts on stingrays since it simply serves to reduce the focal intensity of boats and tourists at a given

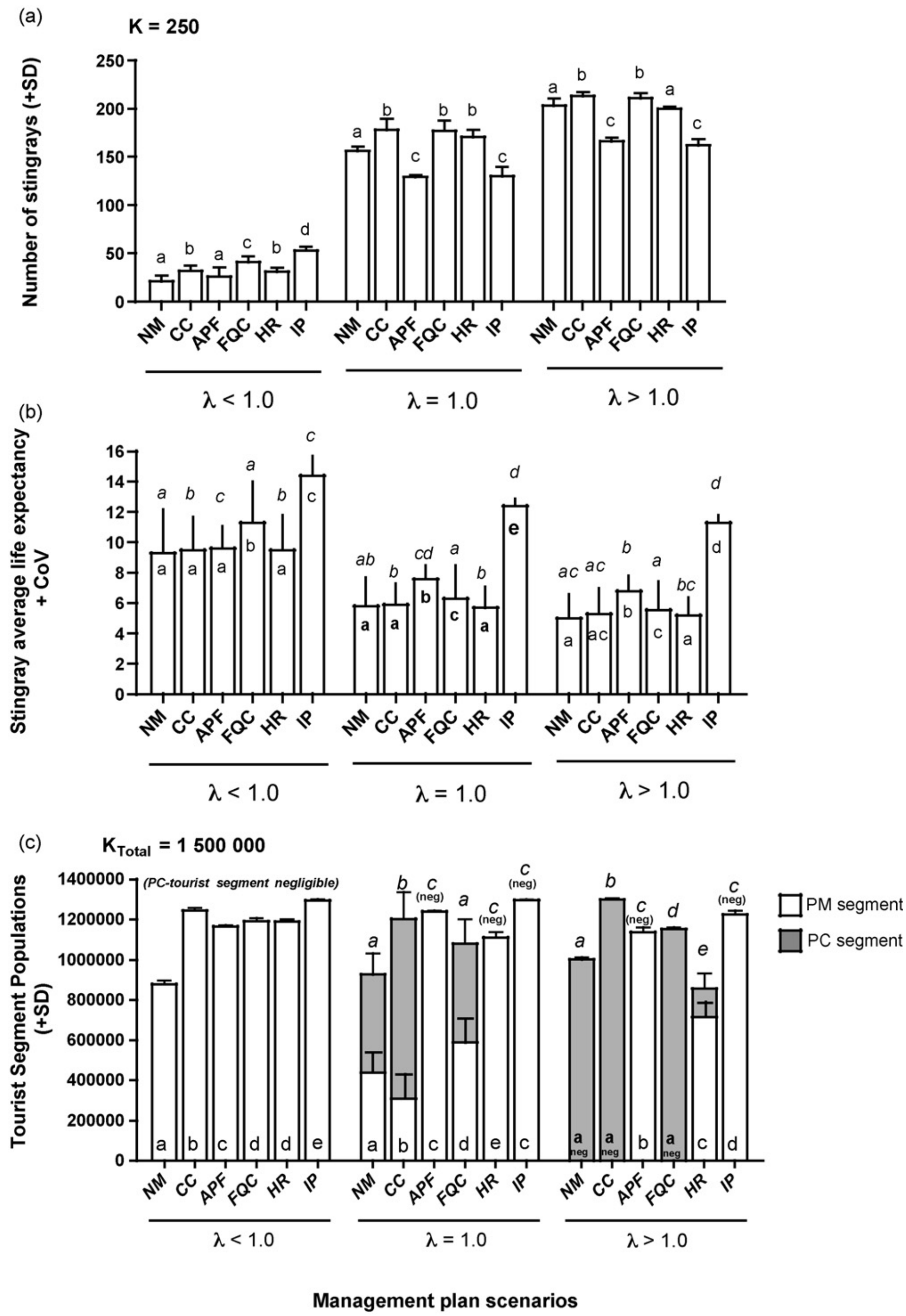

Fig. 6. Model output of (a) stingray population size (±S.D.), (b) stingray average life expectancy with accompanying coefficient of variation (CoV – as a proxy for demographic stochasticity), and (c) tourist population size (±S.D.) of each segment after a 25-year run, and for each stingray population-growth alternative (λ). Similar letters within each λ denote non-significance between management scenarios; for (b), similarly italicized letters represent non-significance for CoV independently from stingray life expectancy means, and for (c), italicized letters represent non-significance for the PC-segment of tourists between management scenarios. NM = No Management, CC = Crowd Control, AFP = Amount of Food Provisioned, FQC = Food Quality Control, HR = Handling Rules, IP = Inclusive Plan.

time and does not prevent the increased frequency of excursions per day/week. Although we gave the Food Quality Control (FQC) scenario the same reduction in stingray mortality as that for the CC-plan, it nevertheless produced better results since its interactions with the tourist component resulted in either fewer tourists overall, or fewer PC-segment tourists. However, unexpectedly, the FQC scenario proved a reasonable strategy in terms of stingray population size and lifespan with a stingray λ < 1, but did not perform as well with higher stingray population growth rates. Moreover, the coefficient of variation (CoV) was consistently high regardless of λ, denoting a vulnerability to demographic stochasticity. A likely explanation is that while the quality of food is improved, the plan still does not address mortality occurring from density-related issues at these higher stingray population sizes. Furthermore, in certain cases (particularly at λ ≥ 1), the PC-segment was predicted to out-compete the PM-segment of tourists under this management scenario. Controlling the amount of provisioned food (as in AFP) seemed a more robust management scenario under the differ-

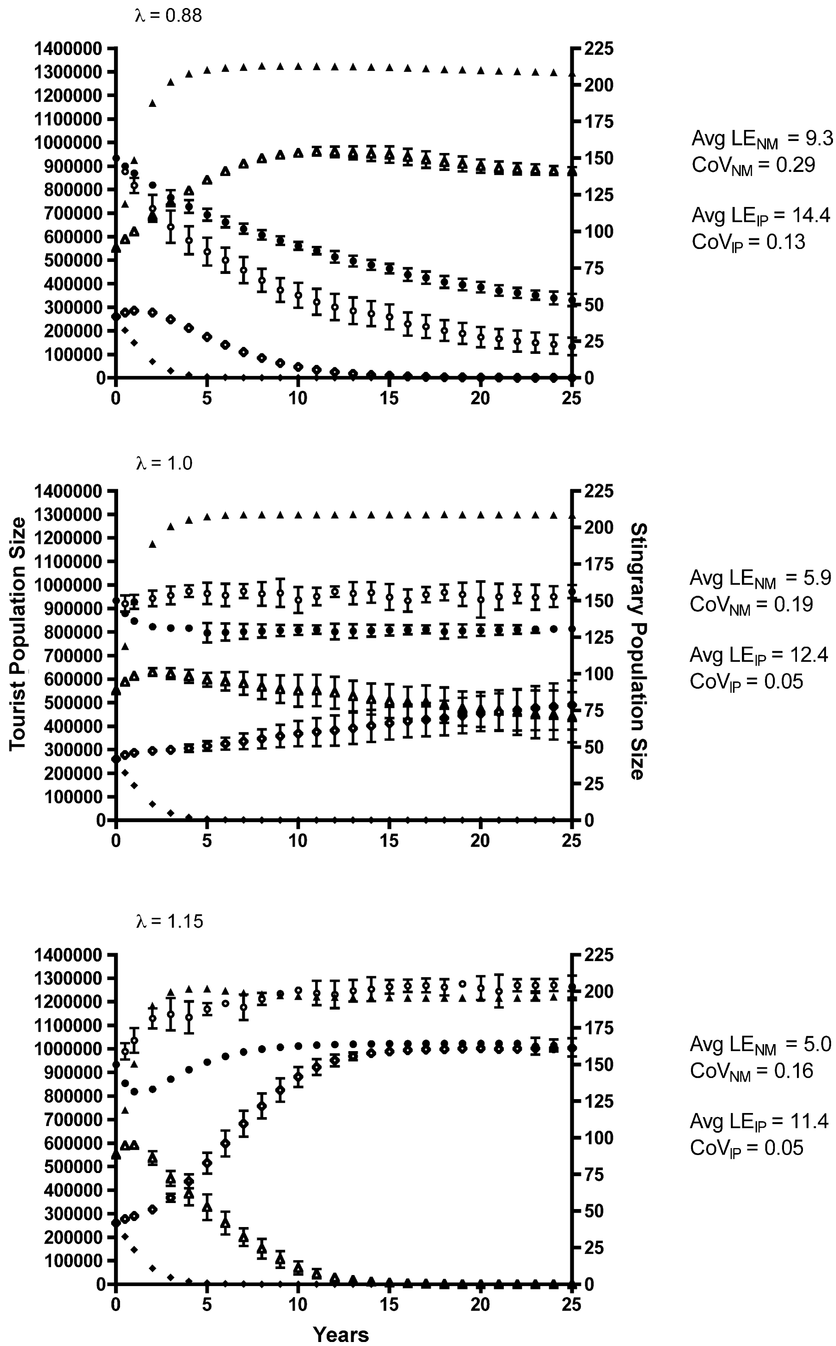

Fig. 7. Illustrative simulation outputs of population trajectories (±S.D.) of stingrays and of pro-management and pro-current segments of tourists as predicted after 25 years under alternate stingray population growth rate sensitivities and two management scenarios: no management (NM) and inclusive plan (IP). Accompanying each plot is the calculated stingray average life expectancy (Avg LE) and associated coefficient of variation (CoV) for each plan. Triangles = 'Pro-Management' segment, diamonds = 'Pro-Current' segment, and circles = stingray. Open symbols = NM, solid symbols = IP.

ing λ scenarios, as it consistently provided a second rank stingray lifespan and low associated CV. Furthermore, although it also predicts low stingray population sizes at λ's ≥1, this result is, in fact, favorable in alleviating the crowding conditions of stingrays at SCS, thus resulting in higher preferences for the PM-segment (who preferred fewer rays on average) and hence exclusivity at the site.

Without any site management, the model predicted that SCS tourist population numbers will fail to reach their potential maximum, suggesting that current behaviors of respondents are contributing to an experience which leaves room for significant improvement (Fig. 7). Visitor numbers are maximized under the IP, demonstrating how favorable this management regulation is (if a carrying capacity of 1 million tourists is imposed in the model for CC and IP, the total tourist population will stabilize at this equilibrium point). Indeed, in most wildlife tourism activities, the development goals should not be to increase numbers but rather to maximize the per unit value of each tourist, both fiscally and in terms of non-market values (Dearden et al., 2006).

How the two tourist segments differentially responded to the management scenarios was also influenced by the way the stingray population growth was modelled. Due to the strong preference of the PC segment for a large number of stingrays and of the PM segment for the opposite, a desirable management regulation for the PC segment could either be magnified or nullified by the number of animals (Fig. 7). Such an interplay between user groups has been suggested in the tourism and recreation literature before, i.e., the tourism life cycle model (Butler, 1980), which hypothesizes that the composition of the tourist population at a destination changes over time, but has rarely been tested empirically. Research in other areas of tourism and recreation has demonstrated heterogeneous visitor preferences for the management of recreation activities in parks; however, this is the first instance in which heterogeneous tourist segments, found endogenously from stated choice responses in a latent class model, were modelled to exploitatively compete with one another over time to determine their respective outcome in terms of visitor numbers.

Perhaps the most significant finding from our model is that without finer resolution of the sources of stingray health and condition, or of the typology of the tourists visiting the attraction, negative repercussions can unknowingly occur if a manager selects an inappropriate management plan. In particular, managers are indeed capable of acquiring sufficient stingray and visitor numbers at SCS after a 25-year time span without IP. For instance, with a stable or increasing stingray population trajectory, tourists are predicted to still be quite numerous, and many stingrays are predicted to be frequenting SCS under NM, CC, or FQC. What managers would be unaware of, though, is that these animals will mostly be new recruits and likely from a exhaustible resource, animal welfare will be reduced, and the characteristics of the majority of visitors will most likely be psychocentric and lack strong conservation values (from Semeniuk et al., 2008). The result is then an unsustainable tourism attraction over the longer term. This modelling exercise consequently demonstrates the need to collect and integrate information on wildlife fitness and tourist demand simultaneously to investigate population persistence. At the very least, in the absence of long-term population census datasets and better information on fitness metrics and tourist preferences, our findings suggest that in the immediate term, a precautionary approach – which encompasses appropriate marketing and promotional strategies – should be undertaken for wildlife management attractions, and must be coupled with continued research until this adaptive management method can confirm or refute the merit of an alternative approach.

5.2. Value of integrating ecological and social data

The various outcomes of our model could not have been predicted by an examination of each ecological and social component in isolation. Indeed, the examination of the ecological results of the model could not be discussed without placing them within the tourist context, and vice versa. This integrative model provides a valuable framework for the present synthesis of data and theories of alternative policies on both the ecological and social science front to explore the long-term viability of wildlife tourism attractions, as it is the attraction itself which is dependent on both tourists and wildlife. Such an activity is important for the economic and social-value returns of the host region, and therefore the goal is not to terminate such attractions, but to find a balance for sustainability. The point of our paper is to highlight that conservation of wildlife is as much about incorporating human values and behaviors as it is about optimizing wildlife fitness. The results of this integrative model are currently in use by the Caymanian government to explore more than one potential socio-ecological outcome in a transparent fashion for their management mandate, and represents an analysis of alternative management actions for policy makers to choose from (Noss, 2007; Scott et al., 2007).

Naturally, our model is not without its limitations. The sensitivity of our results to the various λ's highlights the need to accumulate long-term population census data sets. In addition, the continued collection of fitness metrics (parasite loads and injuries, physiological health parameters, etc.) will allow for the future partitioning of the overall mortality estimate into the proper disease- and injury-induced mortality and collision- and predator-induced components (we assumed equal contributions). This would help reduce the uncertainty in the model as to magnitude of the different sources of mortality which we were unable to accommodate, since different indicators were collected in different years. Furthermore, the absolute magnitudes by which we project stingray mortality rates to decrease with management cannot be known with certainty (although we are confident in the relative differences in reduction between management plans). However, our intent is to explore how modifications in management options would simultaneously affect both wildlife health and the tourist experience dynamically, since over time, changes in one component could precipitate changes in the other, in sometimes unexpected ways. Next, we use a stated-preference choice model to anticipate the changes in tourist visitations without explicitly incorporating a ‘no visit’ option. However, we do not feel this is detrimental to the model, since only 11% of respondents were repeat visitors (from the survey). What is more important is whether they would positively or negatively recommend the trip to others, their recommendation being contingent upon their experience. Chang et al. (2008) similarly used a willingness-to-pay (WTP) index in their system dynamics model to anticipate whether tourists will visit again, with the WTP variable serving as the bridge for connecting the key factors in all subsystems.

Finally, since our goal was to develop a model which adequately assesses different management practices at a broad, simplified scale, and to provide low-resolution data for interpretations of general trends, it is understandable that data gaps exist in our model (e.g., stage-based stingray population structure, individual optimization behaviors). However, the fundamental characteristic of this model is that it makes relative, rather than absolute, predictions by ranking different management options, a practice encouraged in simulation modelling (Grimm and Railsback, 2005). By taking this approach, we can simplify complex relationships and their effects on management decisions to provide resource managers with the tools to explore how key wildlife and tourist variables will interact to impact the ecological and social continuance of the tourism attraction.

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