Environmental Pollution and Biodiversity: Light Pollution and Sea Turtles in the Caribbean\(^{a}\)

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Abstract

We examine the impact of pollution on biodiversity by studying the effect of coastal light pollution on the sea turtle population in the Caribbean. To this end we assemble a panel data set of sea turtle nesting activity and satellite-derived measures of nighttime light. Controlling for the surveyor effort, the local economic infrastructure, and spatial spillovers, we find that nighttime light significantly reduces the number of sea turtle nests. According to data on replacement costs for sea turtles raised in captivity, our result suggests that the increase in lighting over the last two decades has resulted in the loss of close to 1,800 sea turtles in the Caribbean, worth up to $288 million. Incorporating our empirical estimates into a stage-structured population model, we discover that the dynamic effect of nighttime light on future generations of sea turtles is likely to be much larger, with a cost of approximately $2.8 billion for Guadeloupe alone. More generally, our study provides a new approach to valuing the cost of environmental pollution associated

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with species extinction.

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**JEL:** Q57
1 Introduction

Over the last few decades, coastal areas have witnessed considerable growth in economic activity (UNEP, 2008). Inevitably, such growth has also been accompanied by significant increases in environmental pollution that potentially threatens the rich biodiversity that is characteristic of the world’s coastlines (Jackson et al., 2001; Myers and Worm, 2003). One important aspect of the biodiversity debate is the protection of species from extinction, since any disappearance of species will reduce biodiversity (Polasky et al., 2005). More recently, the impact of increased lighting on biodiversity because of local economic development has been the focus of attention (Navara and Nelson, 2012; Gaston et al., 2013; Kyba and Holker, 2013). While a number of studies have already demonstrated that some marine species are particularly sensitive to light pollution (Bustard, 1967; Witherington and Martin, 1996; Bird et al., 2004), the impact of rising coastal illumination has gone largely unexplored (Hill, 2006; Rich and Longcore, 2006; USC, 2008). In this study, we investigate how light pollution in Caribbean coastal areas may have affected the critically endangered sea turtle population (IUCN, 2001).\textsuperscript{1} As Nicholas (2001) points out, light pollution in the Caribbean is already thought to be an important threat to the three indigenous turtle species. Hence, in this paper we provide a quantitative estimate of the impact of light pollution on Caribbean sea turtle populations in both the short and long term.

In the natural sciences, considerable attention is given to the preservation of biodiversity and species extinction. Economists are also concerned with similar issues but have tended to concentrate on the design and implementation of conservation policies subject to resource constraints. Examples of different studies on this broader topic include harvesting (Clarks, 1973; Costello et al., 2008), habitat change (Polasky et al., 2004; Hanley et al., 2009), and the general problem of measuring biodiversity (Solow et al., 1993; Weitzman, 1992, 1998). Important related research includes studies on natural capital and sustainability (see Helm and Hepburn, 2014, for a recent survey).\textsuperscript{2}

\textsuperscript{1}In this paper we consider three different species of turtle. Of those, both the green turtle (\textit{Chelonia mydas}) and the leatherback turtle (\textit{Dermochelys coriacea}) were classified as endangered in 1996, while the hawksbill turtle (\textit{Eretmochelys imbricata}) was listed as endangered in 1986 before being changed to critically endangered in 1996.

\textsuperscript{2}As observed above, species extinction is a key component of the biodiversity debate (Solow et al., 1993). Mace (2014) notes that conservation biologists, nature conservationists, and wildlife managers care explicitly about endangered species and extinction. Moreover, Polasky et al. (2005) distinguish between two categories of biodiversity measures: measures based on relative abundance and measures based on joint dissimilarity. It is the latter category that tends to be most frequently used in the economic literature when there is a focus on extinction (Weitzman, 1992).
terms of pollution more generally, Polasky et al. (2005), Spangenberg (2007), and UNEP (2012) emphasise the detrimental role that pollution may play in loss of biodiversity or species extinction. Indeed, pollution is widely recognised as one of the key threats to biodiversity. Moreover, biodiversity conservation is often the subject of public discourse in response to major pollution incidences such as the Deepwater Horizon oil spill. Polasky et al. (2005) argue that an understanding of how human actions impact biodiversity and how this relationship changes over time is a major remaining challenge for the economics of biodiversity.

A number of articles in the natural science literature note that the presence of nighttime light is likely to interfere with sea turtle behaviour in several ways. Artificial nighttime light tends to deter sea turtle adults from nesting (Raymond, 1984; Hirth and Samson, 1987; Witherington, 1992; Johnson et al., 1996). It also reduces the ability of sea turtle hatchlings to find their way from the beach where they hatch to the sea, thus resulting in higher mortality rates due to exhaustion, dehydration, and predation (Bustard, 1967; Tuxbury and Salmon, 2005; Lorne and Salmon, 2007). However, the quantitative effect of nighttime light on sea turtle nesting and population levels has not yet been investigated statistically or has been limited to case studies of particular beaches (Kaska et al., 2003; Witherington and Frazer, 2003). The only exception is the study by Mazor et al. (2013), who investigated the effects of satellite-measured nighttime light on sea turtle nesting in coastal areas of Israel. However, although their descriptive statistics suggest a negative correlation between nighttime light and nesting activity, the authors find that the relationship between nighttime light and nesting is positive according to regression analysis. Importantly, however, they did not control for either surveyor effort or potential spatial spillovers between beaches. Moreover, they did not, as we do here, interpret their quantitative estimates in terms of either the short- or long-term impact.

Our paper contributes to the existing literature in a number of ways. First, we provide a quantitative assessment of how a potentially important type of pollution affects an

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3 See the Convention on biological diversity at http://www.cbd.int for details.
4 The report of the Center for Biodiversity (April 2011) showed that more than 82,000 birds, 6,000 sea turtles, 26,000 marine mammals, and an unknown large number of fish and invertebrates may have been harmed by the oil spill and its aftermath.
5 See Figure 3 and Tables 2 and 3 of their paper. It is noteworthy that in an earlier study, Aubrecht et al. (2010) also found a positive relationship between nighttime light intensity and sea turtle nesting activity in Florida from a simple plot of their data. However, as the authors argue, this counterintuitive finding may have been a result of legislation in the mid-1980s that imposed regulations on beachfront lighting for protection of sea turtles on beaches that were more brightly lit.
endangered species. More specifically, we estimate the impact of nighttime light pollution on sea turtle populations in Guadeloupe by combining data for satellite-derived nighttime light images, the location of nesting sites, nesting activity, local economic activity, and surveyor effort. From a methodological perspective, we explicitly take into account the spatial effects of nighttime light pollution on sea turtle nesting in the context of a count data model. We then apply our estimates to a population model that enables us to capture the dynamic implications of nighttime light on the sea turtle population. To this end, we incorporate our estimates into a simulation of sea turtle population dynamics for Guadeloupe using a stage-structured population model first described by Crouse et al. (1987) and Crowder et al. (1994). Our approach follows Crowder et al. (1994), who investigated how turtle excluder devices in trawl fisheries affect the sea turtle population in the Southeastern United States. However, in contrast to Crowder et al. (1994), we estimate rather than assume the impact of our factor of interest on the population dynamics.

To briefly summarise our main findings, we show that after controlling for local economic activity and the effort made in nest counting in the econometric analysis, there is a significant negative impact of coastal nighttime light on the nesting activity of sea turtles in Guadeloupe. Other things being equal, we provide evidence that an increase of 1 unit in nighttime illumination reduces the number of nests by approximately 4. Extending our estimate of the marginal effect of nighttime light to the whole Caribbean, we benchmark against the cost of rearing sea turtles in captivity and find that the replacement cost for the nearly 1,800 sea turtles estimated as lost due to greater nighttime illumination since 1992 may be as high as $288 million. With respect to the impact of nighttime illumination on future generations of sea turtles, we conclude from our calibrated population model for Guadeloupe that the fertility drop caused by photopollution appears to substantially accelerate the extinction of sea turtles. For hawksbill and green turtles, coastal nighttime light decreases the time to extinction from 164 and 154 years to 130 and 139 years, respectively. This impact is even greater for leatherback turtles, which, under current light conditions, would disappear in 514 years, but without nighttime light would not become extinct. Finally, our estimates suggest that offsetting the future impact of nighttime light pollution could cost up to $2.8 billion.

The remainder of the paper is organised as follows. Section 2 reviews the literature on the potential effects of light pollution on sea turtles. In Section 3, we describe our database. The econometric methodology is introduced in Section 4 and the econometric
results are discussed in Section 5. In Section 6 we compute the replacement cost for lost turtles in the Caribbean, and in Section 7 we investigate the population dynamics and value the implications under different scenarios. Section 8 concludes.

2 Sea turtle nesting and nighttime light

It is now widely accepted that coastal nighttime light may deter sea turtles from nesting (Raymon, 1984; Witherington and Martin, 1996; Witherington and Frazer, 2003; Jones et al., 2011). Although sea turtles spend very little of their life on beaches, where females nest and hatchlings emerge, almost exclusively at night, these nocturnal activities are critical to the creation of future generations of sea turtles and may be significantly disturbed by nighttime illumination. Raymond (1984) and Witherington (1992) have shown that artificial lighting drastically alters the way in which adults choose their nesting sites, as they generally prefer unlit beaches. Nighttime illumination also increases the possibility of direct human disturbance of nesting activity (Carr and Giovannoli, 1957; Carr and Ogren, 1958), frequently causing turtles to abandon their nesting attempts (Hirth and Samson, 1987; Johnson et al., 1996) and to expedite the process of covering the eggs and camouflaging the nest site (Johnson et al., 1996). Moreover, Witherington and Martin (1996) found that sea turtles discard their eggs in the ocean without nesting when there is a lack of appropriate dark beaches. Photopollution may also affect the return of adult sea turtles to the ocean after nesting. A number of experimental studies have shown that adult turtles rely on brightness to locate the sea (Caldwell and Caldwell, 1962; Ehrenfeld and Carr, 1967; Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1975). However, this problem seems to be less severe for adults than for hatchlings (Witherington and Martin, 1996).

Hatchlings emerge from eggs beneath the sand mainly at night, and then crawl to the sea via the most direct route possible to increase their survival chances (Hendrickson, 1958; Bustard, 1967; Neville et al., 1988; Witherington et al., 1990). However, by creating unnatural stimuli, nighttime light can disrupt their instinctive sea-finding mechanism, often resulting in disorientation and causing hatchling death due to exhaustion, dehydration, and predation (Bustard, 1967; Witherington and Martin, 1996). It has also been observed that indirect lighting can act as a perturbing factor by reflecting off buildings or trees that are visible from the beach (Witherington and Martin, 1996). The difficulty in finding the sea for hatchlings, together with the possibility of adult disorientation, has led
in some cases to replacement of the common blue-light (shorter wavelength) beach illumination with red-light (longer wavelength) lamps, since it has been found that sea turtles are more sensitive to blue light. Nevertheless, such measures are frequently criticised because any illumination tends to encourage human activity on beaches (Witherington and Martin, 1996).

It is important to note that sea turtles exhibit natal philopatry, so females are likely to return to their natal beach for nesting. However, they may nest on neighbouring beaches if the original site is no longer suitable (Worth and Smith, 1976; Witherington and Martin, 1996). Nighttime light may therefore have spatial spillover effects: a beach may receive additional turtles because neighbouring nesting sites are brighter. Not taking this into account could thus lead to a biased estimation of the effect of nighttime illumination.

3 Data description

3.1 Turtles nests

The sea turtle nesting data were provided by the Guadeloupe Sea Turtles Recovery Action Plan. The survey identified a total of 156 beaches in Guadeloupe and their geolocation. Of these, 67 beaches are known nesting beaches and were regularly surveyed for nesting activity at night during the nesting season of 2008, 2010, and 2013. These 67 beaches thus constitute the basis of our analysis, including the identification of neighbouring nesting beaches. The data include the number of nests, the number of times the beach was surveyed, and the sea turtle species. The species indigenous to Guadeloupe are the green turtle (*Chelonia mydas*), the hawksbill turtle (*Eretmochelys imbricata*), and the leatherback turtle (*Dermochelys coriacea*). Summary statistics and definitions of the nesting data, as well as all other variables used in our analysis, are provided in Table 1. On average, each beach was surveyed 52 times, with a mean discovery of 31 nests, although there is considerable variation for both surveying effort and nest discovery across beaches. More than half of the nests found were for the hawksbill turtle.

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6For instance, low-pressure sodium vapour lamps seem to affect nesting less than light from other sources (Witherington, 1992).

3.2 Nighttime light

As a proxy for nighttime illumination at the local level, we use data derived from satellite images of nighttime light provided by the Defense Meteorological Satellite Program (DMSP). In terms of coverage, each DMSP satellite has a 101-minute near-polar orbit at an altitude of approximately 800 km above the surface of the earth, providing global coverage twice per day at the same local time each day. In the late 1990s, the National Oceanic and Atmospheric Administration (NOAA) developed a methodology to generate “stable, cloud-free night light data sets by filtering out transient light such as produced by forest fires, and other random noise events occurring in the same place less than three times” from these data (see Elvidge et al., 1997 for a comprehensive description). The resulting images denote the percentage of nighttime light occurrences for each pixel per year normalised across satellites to a scale ranging from 0 (no light) to 65 (maximum light). The spatial resolution of the original pictures is approximately 0.008 degrees on a cylindrical projection (i.e., with constant areas across latitudes) and has been converted to a polyconic projection, leading to squares of approximately 1 km² near the equator. To obtain yearly values, simple averages across daily (filtered) values for grids were generated. Data are publicly available on an annual basis over the period 1992–2013.8

Figure 1 shows a nighttime light image of Guadeloupe in 2013 and the location of nesting beaches. It is evident that there is an unequal distribution of nighttime light intensity across the islands. More importantly, a large part of the brightness is concentrated on or near the coast.

8Note that a number of studies have used nighttime light as a proxy for economic activity, such as Henderson et al. (2012). Here we use nighttime light as measure of local light intensity during the night, while controlling for economic activity in the area.
3.3 Other data

We gathered information on the location of hotels and their capacity from a number of sources, including www.guadeloupe-antilles.com, Google Maps, and the websites for the hotels. We identified 69 hotels near our nesting beaches as of 2013. The capacity of these ranges from 10 to 688 beds. We obtained information on ports and marinas from www.portbooker.com and general internet searches. Using this approach we identified the geolocation of the two main ports in Guadeloupe and calculated the distance to the nearest port for each beach. There were a total of 24 marinas, ranging in size from two to 224 docks. As a benchmark measure we summed the number of docks within 1 km of each beach. To generate a dummy variable indicating the presence of roads within 1 km of the beaches, we used the shape files available at www.diva-gis.org/gdata and the centroid for each beach.
Table 1: Descriptive statistics

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Obs. (n)</th>
<th>Mean</th>
<th>Std. dev.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>All species</td>
<td>No. of nests</td>
<td>201</td>
<td>30.57</td>
<td>83.01</td>
<td>0</td>
<td>830</td>
</tr>
<tr>
<td>Hawksbill</td>
<td>No. of nests</td>
<td>201</td>
<td>20.19</td>
<td>74.38</td>
<td>0</td>
<td>830</td>
</tr>
<tr>
<td>Green</td>
<td>No. of nests</td>
<td>201</td>
<td>9.05</td>
<td>36.41</td>
<td>0</td>
<td>358</td>
</tr>
<tr>
<td>Leatherback</td>
<td>No. of nests</td>
<td>201</td>
<td>1.32</td>
<td>3.96</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Nighttime light</td>
<td>Nighttime light intensity</td>
<td>201</td>
<td>14.50</td>
<td>10.83</td>
<td>0</td>
<td>53</td>
</tr>
<tr>
<td>Effort</td>
<td>No. of beach visits</td>
<td>201</td>
<td>52.44</td>
<td>50.86</td>
<td>0</td>
<td>237</td>
</tr>
<tr>
<td>Roads</td>
<td>Presence of roads</td>
<td>201</td>
<td>0.45</td>
<td>0.50</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Marinas</td>
<td>No. of docks</td>
<td>201</td>
<td>25.72</td>
<td>51.78</td>
<td>0</td>
<td>224</td>
</tr>
<tr>
<td>Hotels</td>
<td>No. of beds</td>
<td>201</td>
<td>23.72</td>
<td>108.54</td>
<td>0</td>
<td>688</td>
</tr>
<tr>
<td>Ports</td>
<td>Distance (km)</td>
<td>201</td>
<td>25.12</td>
<td>14.38</td>
<td>2.22</td>
<td>57.58</td>
</tr>
</tbody>
</table>

Note: The total number of observations is 67 beaches × 3 years = 201, with variations over time for nesting activity, nighttime light, and effort. For roads, marinas, hotels, and ports we use data from the end of 2013.

4 Econometric model

Given that our dependent variable is a count of the number of nests, standard linear regression techniques would not be appropriate. In choosing the relevant model for count data it is important to first consider whether the data are characterised by overdispersion. The summary statistics in Table 1 reveal that this is clearly the case, as the variance is substantially greater than the mean. When overdispersion exists, it is generally preferable to use a negative binomial rather than the more common Poisson count model. However, overdispersion may also be caused by a large proportion of zeros in the data, rendering traditional distributions insufficient to describe the data at hand. In our data, 27% of nesting beaches had no nesting activity. We therefore follow Famoye and Singh (2006) and experiment with the zero-inflated Poisson (ZIP) and the zero-inflated generalised Poisson (ZIGP) models. The generalised Poisson regression (GPR) model is given by

$$f(\mu_i, \alpha, y_i) = \left( \frac{\mu_i}{1 + \alpha \mu_i} \right)^{y_i} \frac{(1 + \alpha y_i)^y_{i-1}}{y_i!} \exp \left[ -\mu_i(1 + \alpha y_i) \frac{1}{1 + \alpha \mu_i} \right],$$ (1)

where $y_i = 0, 1, 2, \ldots$ indicates the number of nests, $\mu_i = \mu_i(x_i) = \exp(\sum_{j=1}^{k} x_{ij}\beta_j)$ is the mean of $y_i$, $x_i = (x_{i1}, x_{i2}, \ldots, x_{ik})$ is the $i$th row of the covariate matrix $X$, and $\beta = (\beta_1, \beta_2, \ldots, \beta_k)'$ is a $k$-dimensional column vector of parameters. Subscript $i$
denotes beach \( i = 1, \ldots, 67 \). The parameter \( \alpha \) is a measure of dispersion, where there is overdispersion if \( \alpha > 0 \), while the model reduces to a standard Poisson regression model if \( \alpha = 0 \). As noted, any overdispersion due to an excess of zeros can be accounted for using the ZIGP model:

\[
P(Y = y_i | x_i, z_i) = \varphi_i + (1 - \varphi_i) f(\mu_i, \alpha, 0), \quad y_i = 0
\]
\[
= (1 - \varphi_i) f(\mu_i, \alpha, 0), \quad y_i > 0,
\]

where \( 0 < \varphi_i < 1 \) and \( \mu_i = \mu_i(z_i) \) and \( \varphi_i = \varphi(z_i) \) satisfy \( \logit(\varphi_i) = \log(\varphi_i[1 - \varphi_i])^{-1} = \sum_{j=1}^{m} z_{ij} \delta_j \). \( z_i = (z_{i1}, z_{i2}, \ldots, z_{im}) \) is the \( i \)th row of covariate matrix \( Z \) and \( \delta = (\delta_1, \delta_2, \ldots, \delta_m) \) is a \( m \)-dimensional column vector of known parameters. We assume that \( X \) and \( Z \) contain the same covariates. Note that the distribution of \( y_i \) is characterised by overdispersion when \( \varphi_i > 0 \) and that this model reduces to the ZIP model when \( \alpha = 0 \). The mean and variance of the count variable \( y_i \) are given by

\[
E(y_i | x_i) = (1 - \varphi_i) \mu_i(x_i)
\]

and

\[
V(y_i | x_i) = (1 - \varphi_i)[\mu_i^2 + \mu_i(1 + \alpha \mu_i)^2] - (1 - \varphi_i)^2 \mu_i^2
\]
\[
= E(y | x_i)[(1 + \alpha \mu_i)^2 + \varphi_i \mu_i].
\]

As argued earlier, there is reason to believe that nesting behaviour may be correlated across space. One possibility for modelling this correlation is the spatial correlation in the error term. To this end, we follow Czado et al. (2007) and use a Gaussian conditional autoregressive (CAR) formulation, which allows modelling of spatial dependence and dependence between multivariate random variables for irregularly spaced regions. More specifically, for our set of \( J \) beaches \( \{1, 2, \ldots, J\} \) we let \( \gamma = (\gamma_1, \gamma_2, \ldots, \gamma_J)' \) be the vector of normally distributed spatial effects for each beach:

\[
\gamma \sim N_{J}(0, \sigma^2 Q^{-1})
\]

\[
Q_{ij} = \begin{cases} 
1 + |\Psi| \cdot N_i & i = j \\
-\Psi & i \approx j \\
0 & \text{otherwise}
\end{cases}
\]
where \( N_i \) is the number of beaches within area \( i \) and \( \approx \) indicates that \( i \) and \( j \) are neighbouring beaches. The conditional distribution of the spatial effects \( \gamma_i \) is then

\[
\gamma_i | \gamma_{-i} \sim N\left( \frac{\Psi}{1 + |\Psi| \cdot N_i} \sum_{j \approx i} \gamma_j, \sigma^2 \frac{1}{1 + |\Psi| \cdot N_i} \right),
\]

(7)

where \( \gamma_{-i} \) are all the other values of \( \gamma \) and the sum above includes all the spatial effects of neighbouring beaches. Importantly, \( \Psi \) determines the degree of spatial dependence: when \( \Psi = 0 \) there is no spatial dependence across the error term, but as spatial dependence increases the value of \( \Psi \) also increases. In other words, when \( \Psi > 0 \), then shocks to nesting activity on one beach will have an effect on neighbouring beaches.

5 Econometric results

The results for estimates of the determinants of nesting activity using the ZIGP model are given in Table 2. For all specifications we include year dummies. We used a Clarke (2003, 2007) test for all specifications to determine whether the model could be reduced to a ZIP model by setting the overdispersion parameter to \( \alpha = 0 \). The Clarke test statistic in Table 2 suggests that ZIGP is the preferred model for all specifications. In the baseline regression in column 1, we only include our time-varying nighttime light measure as an explanatory variable without any spatial effects. The results suggest that the nighttime light intensity has a significant negative effect on the number of sea turtle nests.
<table>
<thead>
<tr>
<th></th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
<th>(4)</th>
<th>(5)</th>
<th>(6)</th>
<th>(7)</th>
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<td>Nighttime light</td>
<td>-0.02247*</td>
<td>-0.02729*</td>
<td>-0.03149*</td>
<td>-0.00256*</td>
<td>-0.11807*</td>
<td>-0.12641*</td>
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<tr>
<td></td>
<td>(-0.04180, -0.01018)</td>
<td>(-0.04464, -0.00748)</td>
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<td>(-0.00272, -0.00245)</td>
<td>(-0.16132, -0.05002)</td>
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<td>(0.00017, 0.00019)</td>
<td>(0.00000, 0.00040)</td>
<td>(0.00000, 0.00037)</td>
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<td></td>
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<tr>
<td>Spatial parameter</td>
<td>2.09022*</td>
<td>1.76970*</td>
<td>5.78680*</td>
<td>4.80544*</td>
<td>10.26844*</td>
<td>1.76499*</td>
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</tr>
<tr>
<td></td>
<td>(0.76854, 4.73306)</td>
<td>(0.56410, 3.90416)</td>
<td>(2.56654, 9.77264)</td>
<td>(1.63450, 9.68552)</td>
<td>(2.54525, 22.11406)</td>
<td>(0.46203, 3.46992)</td>
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<tr>
<td>Observations</td>
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<td>Beach dummies</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Year dummies</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Clarke test:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ZIP</td>
<td>0.00000</td>
<td>0.00000</td>
<td>0.00000</td>
<td>0.09735</td>
<td>0.01467</td>
<td>0.07154</td>
<td>0.00000</td>
</tr>
<tr>
<td>No decision</td>
<td>0.00000</td>
<td>0.14671</td>
<td>0.00017</td>
<td>0.35916</td>
<td>0.02688</td>
<td>0.07132</td>
<td>0.00486</td>
</tr>
<tr>
<td>ZIGP</td>
<td>1.00000</td>
<td>0.85329</td>
<td>0.99983</td>
<td>0.54349</td>
<td>0.95845</td>
<td>0.85714</td>
<td>0.99514</td>
</tr>
</tbody>
</table>

Notes: (a) Specifications (1)–(5) refer to all species, while specifications (6) and (7) are for the hawksbill and green turtle, respectively. (b) The 5% and 95% confidence bands are given in parentheses. (c) The Clarke test reports the proportion of decisions in favour of the ZIP, ZIGP, or neither of these models. (d) * Statistically significant at the 5% level.
Since the ZIGP is a nonlinear model, the coefficients have no straightforward intuitive interpretation. Marginal effects on nesting activity for any explanatory variable $x_k$ with estimated coefficient $\beta_k$ are thus calculated as follows:

$$
\frac{\partial y}{\partial x_k} = \beta_k \exp \left( \beta_1 + \sum \beta_j \cdot x_j \right),
$$

where $\beta_1$ is the constant in the regression, $\bar{x}_j$ denotes the average of covariate $x_j$, and the terms to which the summation operator $\sum$ apply are the explanatory variables found to be significant. The marginal effects of the significant coefficients for each specification in Table 2 are shown in Table 3. Accordingly, the estimated coefficient for the first specification suggests that a 1-unit increase in nighttime light reduces the number of nests by 0.59. As noted earlier, one concern is that sea turtle nesting behaviour may be spatially correlated. This would potentially induce correlation between the error term and the covariates, resulting in a biased estimate, particularly if there is omitted variable bias (Pace and LeSage, 2010). In the second specification we thus allow for spatial correlation of the error term as outlined above. As a benchmark, we considered beaches within 5 km of each other as neighbours. The significant positive estimate of the spatial parameter $\Psi$ suggests that the data indeed exhibit spatial dependence across neighbouring beaches. The second specification reveals that the marginal effect is somewhat lower, at -0.48 nests, than without spatial correlation. We thus continue to allow for spatial effects in all remaining regressions.

<table>
<thead>
<tr>
<th>Specification:</th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
<th>(4)</th>
<th>(5)</th>
<th>(6)</th>
<th>(7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nighttime light</td>
<td>-0.58709</td>
<td>-0.47709</td>
<td>-0.63048</td>
<td>-3.31499</td>
<td>-3.86179</td>
<td>-2.46902</td>
<td>-2.04096</td>
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<tr>
<td>Effort</td>
<td>–</td>
<td>–</td>
<td>0.00938</td>
<td>0.24539</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Roads</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Marinas</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Hotels</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>-9.82565</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ports</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

To confidently conclude that the estimated marginal effect in Table 3 is the causal effect of beach lighting intensity on sea turtle nesting activity, we need to assume that there is no omitted variable bias. It can be argued that this is unlikely to be the case. For instance, the number of nests discovered on a beach is likely to depend on the effort made

\footnote{According to the results in Table 2, the spatial effects are always statistically significant.}
by those counting. In addition, it is possible that greater effort might be undertaken on those beaches that are better lit, with a potential bias that could reduce the negative effect of nighttime light. To investigate this potential endogeneity bias, we included a proxy for surveying effort in the third specification. As expected, greater effort increases the number of nests discovered. Comparison of the marginal effects of lighting between specifications without and with the effort variable shows that there is a downward bias, with a reduction per unit of nighttime light of nearly 40% for the latter. This suggests that beaches with more illumination could be subject to greater monitoring.

Nighttime light intensity may also be correlated with a number of other features of local economic activity that may affect sea turtle decisions to nest on a particular beach. For example, beaches are usually more brightly lit the closer they are to hotels, and a nearby hotel is also likely to increase the probability of tourist disturbance of nesting activity. To ensure that the estimated effect of nighttime light intensity does not capture these other local features, i.e., to further reduce any endogeneity bias, we included distance to the nearest port, the total number of hotel beds, the number of docks, and an indicator variable of the presence of roads within a 1-km radius of each beach. Column 4 in Table 2 shows that ports, roads, and marinas have no significant effect on nesting. By contrast, greater hotel capacity in the vicinity reduces the number of nests found on a beach. We find that the marginal effect increases multiple times: the estimated coefficients imply that 1 unit of nighttime light reduces the number of nests by 3.3.

In addition to the variables already controlled for, other location-specific variables could be correlated with nighttime light. For example, some parks, marine protection areas, and reserves on Guadeloupe are closed during the nesting season (Dow et al., 2007). If such closures result in reduced economic development in these areas but also increase the number of nests, then this would induce an upward bias in our coefficient for nighttime light. Fortunately the panel nature of our data set allows us to potentially control for all other such factors by assuming they are time-invariant and including a set of beach-specific dummy variables to capture the factors. Doing so, as shown in column 5 of Tables 2 and 3, produces a number of interesting findings. First, the marginal effect increases by approximately 17%, so that 1 unit of nighttime light intensity reduces the number of nests by 3.9. Thus, not controlling for beach-specific effects induces downward bias for our coefficient. Second, inclusion of beach dummies renders the effort proxy nonsignificant. Importantly, this suggests that even if we do not have information regarding the effort
intensity for beach monitoring, we may be able to control for this by using beach dummies, at least in a short panel.

Our analysis can also be performed by sea turtle species. Our sample consists of 66% hawksbill, 30% green, and 4% leatherback nests. Given the small sample size for leatherback nests, estimation of the spatial model was not feasible, and we only re-estimate specification 5 for hawksbill and green turtle nests (columns 6 and 7, respectively). Reassuringly, nighttime light significantly deters nesting for both species. The inferred marginal effects indicate that the impact of an additional unit of nighttime light intensity on nesting activity is greater for the hawksbill than for the green turtle.

Thus far we have controlled for spatial effects only via the error term. However, there may also be spatial effects in terms of the covariates. For instance, with regard to the main focus of this study, greater brightness on nearby beaches may have positive spillover effects on a local beach, as discouraged turtles may look for alternative nesting sites in the vicinity. To investigate this, we calculate the average nighttime light intensity for beaches within 5 km, excluding the value for the beach being considered. The results using beach dummies in Table A.1 indicate that there are no direct spatial spillover effects of the nighttime light intensity for nearby beaches. Similar conclusions are reached when we extend the proximity threshold to 10 km.

6 “Missing” sea turtles in the Caribbean

In the previous section, we provided a quantitative estimate of the negative impact of light pollution on sea turtle nesting, taking account of other potentially confounding factors and spatial correlation. Apart from the arguable interest in the actual number, we can also use its value to derive a monetary interpretation for the wider Caribbean. To this end we would have ideally liked to expand our econometric analysis to the entire region. However, we were not able to obtain nesting activity data for other territories. Instead, we assume that Guadeloupe is representative of the Caribbean and use our econometric estimates to infer the total costs for the reduction in sea turtle nests due to nighttime light pollution.

As a proxy for the monetary value of “missing” sea turtles due to nighttime light pollution, we use the known costs for rearing sea turtles in captivity, an approach used by Freeman (2003) and Troeng and Drew (2004), for instance, in the absence of specific
estimates for willingness to pay (WTP). Moreover, in stated preference studies of animal populations, the evidence seems to indicate that people have difficulty in valuing individual animals, and instead value situations in which the size of a population remains above some critical size to avoid extinction (Bandara and Tisdell, 2003). To identify nesting beaches in the entire Caribbean, we used information from SWOT/OBIS-SEAMAP, which provides a list of known nesting sites and their location.\textsuperscript{11} The 1,086 known nesting beaches and the nighttime light intensity during 2010 are depicted in Figure 2. It is evident that the location of nesting beaches and their nocturnal illumination vary widely across the Caribbean. Moreover, there has been an increase in nighttime light intensity on most nesting beaches over time, as can be seen from Figure 3, which plots the nighttime light intensity for 1992 versus 2013 for each nesting site.

Figure 2: Nesting sites in the Caribbean

![Nesting sites in the Caribbean](image)

Note: Green dots indicate known nesting sites.

\textsuperscript{10}Note that in our case we would need a WTP measure per individual turtle. To the best of our knowledge, the only WTP estimates for sea turtles are for particular conservation programmes; see, for example, Jin et al. (2010).

\textsuperscript{11}SWOT – the State of the World’s Sea Turtles – is a partnership led by the Sea Turtle Flagship Program at the Oceanic Society, Conservation International, IUCN Marine Turtle Specialist Group, and supported by the Marine Geospatial Ecology Lab at Duke University (SWOT, 2006, 2008, and 2009).
With the change in nighttime light intensity for each beach and our measurement of the marginal effect of nighttime light, we can estimate the number of missing turtles as follows:

\[
\sum_{i=1}^{1086} \Delta \text{Nighttime light}_i \times \frac{\partial \text{Nests}}{\partial \text{Nighttime light}} \times \frac{\text{Hatchlings}}{\text{Nest}} \times \text{survival rate to adulthood. (9)}
\]

The first term represents the overall change in nighttime light intensity for all nesting beaches over the period 1992–2013. For this we summed total net changes in illumination, which we found to be 3,895 units of light (i.e., a 42% increase over the 1992 intensity). For the marginal change in nests due to light pollution, we used the estimated marginal effect for all species as taken from specification 5 of Table 3, i.e., -3.86. These data together suggest that the number of missing nests over our sample period is 15,041. Although the number of eggs per nest varies across species and location, the average is approximately 120 (Marquez, 1990). Finally, we assume that the hatchling survival rate is 1/1000 (Frazer, 1986; Triessnig et al., 2012). Equation (9) then implies that there were 1,805 missing sea turtles due to increasing nighttime light intensity over our sample period.

To calculate the monetary value of these missing turtles, we use the costs for rearing sea turtles in captivity estimated in case studies of sea turtle farms and marine conser-
vation centres. We took information from three sources: Troeng and Drews (2004) for green and leatherback turtles, Webb et al. (2008) for hawksbill turtles, and a personal communication with the Cayman Turtle Farm in the Cayman Islands for green turtles. We summarise the replacement costs in Table 4 (Appendix B provides further details).

Table 4: Replacement costs per species (in US dollars)

<table>
<thead>
<tr>
<th>Farm</th>
<th>Species</th>
<th>Cost/15-year-old</th>
<th>Cost/adult</th>
<th>Total cost in millions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferme Corail</td>
<td>Green</td>
<td>1,672</td>
<td>3,455</td>
<td>6.2</td>
</tr>
<tr>
<td>Cayman Turtle Farm</td>
<td>Green</td>
<td>4,185</td>
<td>8,649</td>
<td>15.6</td>
</tr>
<tr>
<td>WMI Research facility</td>
<td>Hawksbill</td>
<td>18,045</td>
<td>26,466</td>
<td>47.8</td>
</tr>
<tr>
<td>TUMEC, Rantau Abang</td>
<td>Leatherback</td>
<td>112,128</td>
<td>159,504</td>
<td>287.9</td>
</tr>
</tbody>
</table>

The cost of raising a leatherback turtle in captivity to the age of 15 years or to adulthood is many times greater than for green and hawksbill turtles. This is not surprising since leatherback turtles are the largest of the three species, with a carapace length of 1.30–1.83 m and a weight of 300–500 kg. Green and hawksbill turtles are considerably smaller, with a carapace length of 83–114 and 71–89 cm and weight of 110–190 and 46–70 kg, respectively (Marquez, 1990).

Combining the cost per individual adult with our missing turtles estimate, we calculate the total replacement cost for missing sea turtles, which ranges from $6.2 to 287.9 million, depending on the relative importance of each species nesting in the Caribbean (Table 4). In other words, the cost of replacing the estimated number of missing sea turtles due to the increase in nighttime light with animals raised in captivity could be as much as $0.29 billion if these were all leatherback turtles. It is important to emphasise, as argued by Freeman (2003) and Troeng and Drews (2004), that the replacement cost as measured here should only be considered as a lower threshold of the true loss in ecosystem services, since it ignores the potential differences between sea turtles raised in captivity and those raised in their natural environment.

---

12 We assume that green turtles reach adulthood at 31 years (Cambell, 2003), leatherback turtles at 21 years (Martinez et al., 2007; Saba et al., 2012), and hawksbill turtles at 22 years (Crouse, 1999).

13 Unfortunately, there are no estimates of nesting activity by species available for the Caribbean.
7 Population dynamics

In the previous section, we quantified and valued the number of missing turtles due to nighttime illumination in the Caribbean. However, these results only take into account a single generation, and neglect any population dynamics. In this section, we incorporate generational effects by integrating our estimates in a population dynamics model using the case study for Guadeloupe.

In mathematical biology there are many different types of fairly sophisticated population models (Cushing, 2006; Wikan, 2012). However, calibration of these models is often constrained by data availability. Reproduction and survival rates, for instance, play a key role in these dynamic settings. For sea turtles it is well known that these data are age-dependent. It is thus argued that age-structured models, like the one introduced by Leslie (1945), would be an appropriate framework for studying the population dynamics of sea turtles. Unfortunately, there is little reliable age-specific information for long-lived iteroparous species such as sea turtles. However, the life cycle of sea turtles comprises a series of well-identified stages (Heppell et al., 2003) and information is available regarding the duration, survival, and reproduction rates for each stage. We thus follow the set-up introduced by Lefkovicth (1965), Crouse et al. (1987), and Crowder et al. (1994), in which individual animals are grouped by stage sharing the same reproduction and survival rates instead of age.

7.1 Stage-structured population model

As in Crowder et al. (1994), we consider five stages of development for sea turtles: (1) eggs/hatchlings, (2) small juveniles, (3) large juveniles, (4) subadults, and (5) adults. We thus define the stage distribution vector \( x_t \) at time \( t \) as

\[
x_t = (x_{1t}, x_{2t}, x_{3t}, x_{4t}, x_{5t}),
\]

where \( x_{it} \) is the number of female sea turtles in stage \( i \) at time \( t \) for \( i = 1, \ldots, 5 \). Let \( P_i \) denote the percentage of females in stage \( i \) that survive but remain in that stage, let \( G_i \) be the percentage of females in stage \( i \) that survive and progress to the next stage, and let \( F_i \) be the number of hatchlings per year produced by a sea turtle in stage \( i \) (annual fecundity). Therefore, the number of hatchlings produced by each stage class at time \( t \) is given by

\[
x_{1t} = F_1 x_{1t-1} + F_2 x_{2t-1} + F_3 x_{3t-1} + F_4 x_{4t-1} + F_5 x_{5t-1},
\]

(11)
while the number of females present in the subsequent stage \( j \), for \( j = 2, \ldots, 5 \), is

\[
x_{jt} = G_{j-1}x_{j-1t-1} + P_jx_{jt-1}.
\]

(12)

Taking (11) and (12), we can then rewrite the population model in matrix form:

\[
x_t' = Lx_{t-1}',
\]

(13)

where \( x' \) denotes the transpose of vector \( x \), and \( L \) is the five-stage population matrix

\[
L = \begin{bmatrix}
F_1 & F_2 & F_3 & F_4 & F_5 \\
G_1 & P_2 & 0 & 0 & 0 \\
0 & G_2 & P_3 & 0 & 0 \\
0 & 0 & G_3 & P_4 & 0 \\
0 & 0 & 0 & G_4 & P_5 \\
\end{bmatrix}.
\]

In general, the available stage-based life information comprises duration, and survival and reproduction rates. The fertility rates \( F_i \) are given by the fecundity data, while \( G_i \) and \( P_i \) need to be calculated. We follow the standard method of Crouse et al. (1987) and Crowder et al. (1994). If we denote the yearly survival rate and duration of stage \( i \) by \( \sigma_i \) and \( d_i \), respectively, we can determine the percentage of sea turtles from stage \( i \) that grow into stage \( i + 1 \) as

\[
\gamma_i = \begin{cases} 
\frac{(1-\sigma_i)\sigma_i^{d_i-1}}{1-\sigma_i^d} & \text{if } \sigma_i \neq 1 \\
\frac{1}{d_i} & \text{if } \sigma_i = 1.
\end{cases}
\]

(14)

Consequently, the percentage of turtles in stage \( i \) that remain in that stage is \( 1 - \sigma_i \). We can finally determine \( G_i \) and \( P_i \) as

\[
G_i = \gamma_i \sigma_i, \\
P_i = (1 - \gamma_i)\sigma_i.
\]

(15) (16)

7.2 Population dynamics and nighttime light pollution

As pointed out above, the usual stage-based life table for a specific type of sea turtle consists of information about the stage duration and the survival and reproduction rates for each stage. Appendix C provides stage-based life tables for each type of sea turtle in Guadeloupe. Considering (14)-(16), we can use these to compute the population matrix...
for each species. Taking (13) and an initial stage distribution vector \( x_0 \), we can then obtain the population dynamics for \( t > 0 \).

We now incorporate the effect of nighttime illumination into the population model. As we have shown earlier, nighttime light pollution significantly reduces the number of sea turtle nests, and consequently the annual fertility rate. Our objective is to adjust the parameter \( F_i \) to account for the marginal effect of nighttime light. Note that an additional negative consequence of nighttime light is the increasing difficulty in finding the sea after hatchlings emerge from their nest, resulting in a reduction in the annual survival rate \( \sigma_1 \) (Section 2). Our analysis should thus be interpreted as a lower bound for the negative effect of nighttime light pollution, although we later investigate how incorporation of this aspect would affect our results.

As a starting point we assume nighttime light intensity and nesting activity to be the average observed on Guadeloupe nesting beaches, denoted by \( NL_{\text{avg}} \) and \( NT_{\text{avg}} \), respectively. To modify the annual fertility, we need to estimate the reduction in hatchlings per year caused by nighttime light. Thus, the average percentage point reduction in nests \( \tau \) due to nighttime illumination is

\[
\tau(\beta_1) = \left| \frac{\beta_1NL_{\text{avg}}}{NT_{\text{avg}} + |\beta_1|NL_{\text{avg}}} \right| 100, \tag{17}
\]

where \( \beta_1 \) denotes the estimated marginal effect of light pollution.

With no empirical evidence available, we assume that the percentage reduction in nests will result in the same percentage reduction in eggs per sea turtle. Since we are working at the individual sea turtle level, we adjust the marginal effect of nighttime light to take account of the remigration interval. Following Doi et al. (1992), we assume that this interval is 2.6 years, implying that \( \tilde{\beta}_1 = \beta_1/2.6. \) The modified annual fertility rate can therefore be computed as \( \tilde{F}_i = [1 - \tau(\tilde{\beta}_1)/100]F_i \). Recall from Table 3 that the marginal effect for hawksbill and green turtles is -2.47 and -2.04, respectively. For leatherback turtles, we assume that the marginal effect is equal to that for the total population, i.e., -3.86. For example, for leatherback turtles the annual fertility rate would be reduced by 42%, changing the population matrix accordingly. Note that the analysis is based on the assumption of a constant level of nighttime light per beach, since

\[\text{\footnote{Other studies on remigration intervals include Carr and Carr (1970), Carr et al. (1978), Hays (2000), and Troeng and Chaloupka, (2007).}}\]
our objective is to evaluate the generational consequences of the current level of light pollution. However, this set-up could easily be applied to evaluate different scenarios for nighttime light changes.

7.3 Dynamic population response

We can now evaluate the population dynamics under scenarios with and without nighttime light pollution. We can obtain the population dynamics for each turtle type, starting from a given initial stage distribution, by recursively applying Equation (13) to the population matrix with and without nighttime light. Given that the number and stage distribution are highly uncertain because of difficulties in tracking sea turtles, we assume an initial number of turtles for each stage consistent with broad estimates for Guadeloupe (DREG, 2008; Delcroix et al., 2011). More precisely, we assume a population of 1,000 females per stage for each turtle species, although we verified that the qualitative population response was robust to alternative demographic configurations.\(^{15}\)

7.3.1 Population dynamics

In Figures 4–6 we plot the evolution of the stage population for each sea turtle species with and without nighttime light. Even without light pollution, hawksbill and green sea turtles eventually become extinct, while the leatherback population continues to grow over time. This difference in the long-term population dynamics across species is in line with existing studies (Evans et al., 2001) and is driven by the underlying survival and fertility parameters for the population matrix. The presence of nighttime light considerably accelerates the extinction of hawksbill and green turtles. For leatherback turtles the negative impact of nighttime light reverses the population growth, so that this species also becomes extinct in the long run.

\(^{15}\)Details are available from the authors on request.
Figure 4: Population per stage: hawksbill turtles

(a) No nighttime light

(b) Nighttime light

Figure 5: Population per stage: green turtles

(a) No nighttime light

(b) Nighttime light
Note that the qualitative population dynamics do not depend on the initial stage distribution. Indeed, the eigenvalues of the population matrix allow us to identify the dynamic properties regardless of the initial conditions. An intrinsic characteristic of our population model is that a population either increases or decreases in the long run, since the model consists of a system of first-order linear difference equations. We can easily verify that the absolute value of all eigenvalues for the population matrices for hawksbill and green turtles is less than one (Appendix D). Consequently, their populations will be asymptotically extinct, regardless of the presence of light pollution. For leatherback turtles, however, there is an eigenvalue ($\lambda_1$) greater than one if there is no nighttime light pollution, so that the population increases in the long run. As for hawksbill and green turtles, nighttime light results in all eigenvalues being lower than one, leading to eventual depletion of this species too. As pointed out earlier, there are more sophisticated frameworks that consider non-linearities that induce steady populations. This is usually the case for models that incorporate the effect of agglomeration by allowing, for instance, food and/or space competition among individuals. Even if the data required to estimate a model of this type were available, the existence of such agglomeration effects seems unlikely for endangered species such as sea turtles.

The eigenvalues also allow us to provide quantitative information regarding the long-run response of the population for each turtle type in terms of the growth rate and stage distribution. Since system (13) has constant coefficients and $|\lambda_1| > |\lambda_j|$ for $j = 2, \ldots, 5$
(Table A.6), the unique solution in the long run takes the form

\[ x_t' \simeq c_1 v_{\lambda_1} \lambda_1^t, \tag{18} \]

where \( v_{\lambda_1} \) is the eigenvector corresponding to the eigenvalue \( \lambda_1 \), and \( c_1 \) is a constant.\(^{16}\) Consequently, the long-run annual growth rate of the population (per stage and total) is equal to \( \lambda_1 - 1 \). Applying this result to our simulations, we observe that the population eventually decreases for both hawksbill and green turtles, while nighttime light increases the long-run annual depletion rate from 7.19% to 8.8% and from 7.9% to 8.56%, respectively. We also confirm that the leatherback population increases if there is no light pollution, with a long-run annual growth rate of 1.07%. However, the presence of nighttime illumination reverses this trend, resulting in an eventual decreasing population rate of 2.18% per year.

With respect to the stage distribution of each type of turtle, using Equation (18) the long-run proportion of the population in stage \( i \) is given by

\[ \xi_i = \frac{v_{\lambda_1 i}}{\sum_{k=1}^{5} v_{\lambda_1 k}}, \tag{19} \]

where \( v_{\lambda_1 k} \) is the \( k \)th coordinate of the eigenvector \( v_{\lambda_1} \). Considering the eigenvalues and eigenvectors of Tables A.6 and A.7 in Appendix D, we obtain the stage distribution for each type of turtle with and without nighttime light. A well-known feature of these types of population model is that the population reaches a stable stage distribution in the long run (Table A.8 and Figure A.2). It is evident from Table A.8 that the proportion of hatchlings is most severely affected by nighttime light pollution. The reduction is particularly apparent for leatherback turtles, for which the proportion of hatchlings falls by more than 2.6 percentage points. This is a major reason why the population reverses from its increasing long-run trend. These results are robust to the initial stage distribution and other population sizes because there are strong accumulative effects of the reduction in annual fertility.

The population model can also be applied to investigate how fast this extinction may occur. We define the time to extinction as the number of years it takes for less than one

\[^{16}\text{The solution of system (13) for all } t \text{ is } x_t' = \sum_{i=1}^{5} c_i v_{\lambda_i} \lambda_i^t, \text{ where } v_{\lambda_i} \text{ denotes the eigenvector corresponding to the eigenvalue } \lambda_i \text{ of the population matrix, and } c_i \text{ are constants determined by the initial population distribution.}\]
sea turtle to survive. Table 5 shows that for an assumed initial population of 1000 sea turtles per stage, nighttime illumination significantly accelerates the extinction of all three species. Without light pollution, hawksbill and green turtles will take 164 and 154 years, respectively, to become extinct, whereas there is no extinction for leatherback turtles and the population continues to increase. In the presence of nighttime light, all three species will eventually disappear. According to our simulations, the time to extinction would be 130 years for the hawksbill, 139 years for the green, and 514 years for the leatherback turtle. Thus, nighttime illumination of nesting sites has a clear accumulative effect in the long run by reducing fertility rates for adult females.\(^\text{17}\)

Table 5: Time to extinction (years)

<table>
<thead>
<tr>
<th></th>
<th>No light</th>
<th>Light</th>
<th>Light ((\tilde{\sigma}_1))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawksbill</td>
<td>164</td>
<td>130</td>
<td>101</td>
</tr>
<tr>
<td>Green</td>
<td>154</td>
<td>139</td>
<td>122</td>
</tr>
<tr>
<td>Leatherback</td>
<td>(\infty)</td>
<td>514</td>
<td>205</td>
</tr>
</tbody>
</table>

Our estimates of the impact of nighttime light are likely to be only lower bounds as we do not allow for the fact that lighting will also reduce the number of hatchlings that make it from the nesting site to the sea because of disorientation. Unfortunately, we do not have any information on the impact of nighttime light on the survival rate of hatchlings during this period of their life cycle. However, Peters and Verhoeven (1994) studied the survival of loggerhead hatchlings during the voyage from their nests to the sea. They examined two nesting sites on the Turkish Mediterranean coast and found that only 21% of hatchlings reached the sea on the site that was well lit, compared to 48% for an adjacent unlit area. To obtain a rough idea of how far our estimates are from the upper bound, we modify the hatchling survival probability to \(\tilde{\sigma}_1 = 0.56\sigma_1\).\(^\text{18}\) As expected, extinction accelerates. More precisely, the time to extinction is now 101, 122, and 205 years for hawksbill, green, and leatherback turtles, respectively (column 3 in Table 5).

Finally, Figures 4–6 reveal that the short-run population dynamics are cyclical. This property is explained by the fact that sea turtles spend several years in each stage of development, resulting in accumulation or reduction of the number of individuals in a

\(^{17}\)Note that the time to extinction depends on the distribution and size of the initial population; however, the qualitative results remain unchanged when we use alternative scenarios.

\(^{18}\)The value of 56% is the percentage reduction in survival rate observed by Peters and Verhoeven (1994).
specific stage. This result is confirmed by examining the eigenvalues of the population matrix (Table A.6).\textsuperscript{19} Moreover, the negative effect of light pollution does not seem to be strong enough to eliminate these cycles in the short term.

7.3.2 Compensation costs

One conservation management tool used to address diminishing sea turtle populations is headstarting, which broadly entails captive hatching and rearing of sea turtles during the early part of their life cycle (Bell \textit{et al.}, 2005). For instance, the Cayman Turtle Farm released 16,422 neonates, 14,282 yearlings, and 65 older (19-77 months) green sea turtles during 1980-2001.\textsuperscript{20} Using our results above, we can consider the costs of such a headstarting strategy to counteract the negative effect of nighttime light on sea turtles by calculating the number of headstarted turtles that would have to be released into the wild today to keep the extinction time the same as that without light pollution.\textsuperscript{21} We can then infer an estimate for the potential cost of such a conservation strategy using our information on the costs incurred in raising turtles in captivity. Note that focusing on the costs of reducing the time to extinction is probably much more in line with how people value animal species, as stated earlier.

As mentioned before, headstarted turtles have been released at various life stages, normally well before they reach the age of 7 years. Moreover, since we do not have information on the replacement costs for hatchlings, we limit our analysis to the release of headstarted 1-year-old juveniles. For the green turtle we find that 3.5 million juveniles would be needed to keep the time to extinction at the no-illumination level of 154 years in the absence of light pollution, with an associated cost of between $0.4 and 0.9 billion, depending on the source used for the yearly replacement cost. In the case of the hawksbill turtle, 10 million yearlings would have to be released to keep the time to extinction at the no-illumination level of 164 years, with an associated cost of between $1.1 and 2.8 billion.

At first sight, the costs for headstarting as a conservation management tool may seem remarkably high. However, it should be remembered that this involves counteracting the

\textsuperscript{19}The existence of complex and/or negative eigenvalues implies short-run cycles in different equation systems.

\textsuperscript{20}Other examples include the North Carolina Head Start Program (loggerhead turtles) and the National Marine Fisheries Service Program (Kemp’s ridley turtles).

\textsuperscript{21}Note that this exercise only considers a one-time release of sea turtles, but could of course be extended to yearly release programs.
negative effect of nighttime light for all the years until extinction. Moreover, in line with arguments made by Heppel et al. (1996) regarding the use of headstarting to compensate for reduced survival rates, these high costs are also related to the characteristics of sea turtles. First, for slow-maturing species such sea turtles, large increases in juveniles are needed to compensate for the reduction in nesting activity and hence hatchling production due to light pollution. Second, except for extremely small populations, it is not feasible to headstart enough juveniles to have an impact on the overall survival rate of a cohort.

There are other likely costs involved with headstarting, as reviewed by Bell et al. (2005). First, sea turtles raised in captivity may behave differently to their wild counterparts. For example, there is some evidence that headstarted sea turtles forage and nest outside of their natural range. Others have questioned the ability of headstarted sea turtles to survive as well as wild animals because of nutritional deficiencies and behavioural modifications resulting from insufficient exercise, a lack of or inappropriate stimuli, and the unavailability of natural food sources and feeding techniques during captivity. In addition, headstarted sea turtles may have negative spillover effects on wild sea turtles via transmission of diseases acquired during captivity and genetic pollution. Thus, the cost estimates provided here should only be viewed as a lower bound for the total costs of headstarting as a remedy for the detrimental effects of light pollution on sea turtle populations.

With the aforementioned replacement costs in mind, we can also consider the public WTP for such headstarting programs. To this end we need some measure of the WTP for sea turtles. Unfortunately, to the best of our knowledge there has been no study of WTP for sea turtles for Guadeloupe or even the rest of the Caribbean. However, a number of studies have been conducted for Asia and we use such results as a proxy for the WTP in Guadeloupe. Jin et al. (2010) calculated an average WTP of 0.19% of total household income for a 5-year sea turtle conservation programme for five major cities in four developing countries in Asia.\(^{22}\) Using this average WTP and considering the total number of households in Guadeloupe (166,317) and the average annual income per household ($16,598) in 2011,\(^{23}\) the present value of the total WTP for Guadeloupe using

\(^{22}\)The estimates as a percentage of household total income were 0.24 for Beijing (China), 0.19 for Davao City (Philippines), 0.17 for Bangkok (Thailand), and 0.14 for Ho Chi Minh/Hanoi (Vietnam).

\(^{23}\)Source: www.insee.fr/fr/bases-de-donnees, Nombre de ménages, and revenu net déclaré moyen par foyer fiscal, respectively.
a positive social discount rate of 10% would be approximately $21.5 million for a 5-year headstarting program. Using the replacement cost for 1-year-old juveniles (Appendix B), we calculate estimates for yearly release of the corresponding number of headstarted turtles over 5 years.\textsuperscript{24} Our population model suggests that such a conservation programme would reduce the years to extinction by between 1 and 2 additional years. This limited population response emphasises the small scale of public WTP contributions regarding conservations programmes such as headstarting of sea turtles, although Jin \textit{et al.} (2010) note that their WTP estimates are comparable to results from other studies for developed countries and endangered species such as the spotted owl (Loomis and Ekstrand, 1998) and grey and blue whales (Bulte and Van Kooten, 1999).\textsuperscript{25} However, Tisdell and Wilson (2002) point out that the pro-conservation attitude of individuals significantly affects their WTP. In this respect, further investigation of the factors that may affect and foster the public WTP for the protection of endangered species is warranted.

Finally, it is important to discuss the limitations of using the results of Jin \textit{et al.} (2010) in conjunction with data from Guadeloupe to infer the costs of a conservation program for the Caribbean, as we do here. First, in using average per household income we implicitly assume income elasticity of one with respect to WTP. However, this may not hold true for the valuation of biodiversity, as shown by Jacobson and Hanley (2009). Second, in using data from China for the Caribbean we are ignoring any cultural and institutional differences in the valuation of sea turtles. A meta-analysis by Lindhjem and Navrud (2008) showed that for valuation of non-timber benefits across three Scandinavian countries, WTP transfer errors due to differences in cultural and institutional environments across countries can be substantial.\textsuperscript{26} This was confirmed by Lindhjem and Tuan (2012). Finally, scaling up of our results from Guadeloupe to the entire Caribbean may also be questionable. As noted by Brander \textit{et al.} (2012), possible changes that occur across individual sites should ideally be taken into account when scaling up from one site to a greater region rather than using a simple aggregation or generalisation across sites, as we had to do here. Because of these weaknesses, our approach should be viewed only as a starting point for analysing the potential compensation costs of the negative effect of lighting intensity on sea turtle nesting. A substantial number of additional studies

\textsuperscript{24}Using these data, the conservation programme would imply yearly release of 18,471 (Cayman Turtle Farm) or 38,562 (Ferme Corail) 1-year-old green juveniles and 3,573 hawksbill turtles (WMI research facility).

\textsuperscript{25}According to IUCN (2001), the spotted owl is considered as “near threatened with a decreasing population trend”, and the blue and grey whales are, respectively, “endangered” and “critically endangered” species.

\textsuperscript{26}See Ready and Navrud (2006) for a general discussion of the issue of international benefit transfers.
of the issue are needed before methods such as those proposed by Ready and Navrud (2006) and Brander et al. (2012) can be used to assess the welfare effects of conservation programmes in a more reliable manner.

8 Concluding remarks

We examined loss of biodiversity due to environmental pollution by studying the impact of coastal light pollution on the sea turtle population in the Caribbean. To this end, we assembled a data set for sea turtle nesting activity and satellite-derived measures of nighttime light for Guadeloupe. Using a spatial count data model, we showed that after controlling for the surveyor effort and local economic infrastructure, nighttime light reduces the number of nests on beaches. Considering the growth of nighttime light over the last 20 years across beaches used for nesting in the Caribbean, our quantitative estimate suggests that if we consider the value of a sea turtle to be its replacement cost in captivity, then the increase in coastal lighting in the region has resulted in losses of up to $288 million. We combined our statistical estimate with a stage-structured population model for Guadeloupe to study the generational implications of light pollution. The results suggest that light pollution will substantially accelerate the extinction of sea turtles. Moreover, we found that compensating for the negative effect of the current nighttime light intensity by rearing sea turtles in captivity and then releasing them into the wild, which is part of some current conservation strategies, may be an expensive remedy according to studies of public willingness to pay. This suggests that exploration of the economic costs of reducing coastal illumination near sea turtle nesting beaches as an alternative or supplementary conservation management tool is warranted. To the best of our knowledge, no such estimates are currently available.

More generally, our paper arguably provides a new approach to valuing losses due to species extinction caused by environmental pollution. In particular, given data for a species of interest and some type of relevant pollution, our paper shows that statistical estimates of the short-term impact within a population model can provide helpful insights into the range of the likely long-term impacts and their costs. The reliability of such predictions will obviously depend on the quantity and quality of data available. For example, for the case studied here, data spanning a longer time period and greater geographical area in the Caribbean would give greater confidence in the results.
References


Caldwell M., and D. Caldwell (1962), “Factors in the ability of the northeastern Pacific green turtle to orient toward the sea from the land, a possible coordinate in long-range navigation”, Science, 60, 5-27.


and leatherback sea turtles of the western north Atlantic”, *NOAA Technical Memorandum, NMFS-SEFSC-455.*


The case of Rethymno coastal area in Greece”, *Ocean and Coastal Management*, 54, 577-584.


UNEP (United Nation Environment Programme) (2008), *Climate Change in the Caribbean and the Challenge of Adaptation*, UNEP Regional Office for Latin America and the Caribbean, Panama City, Panama.


Appendices

A Robustness checks

Table A.1: Direct spatial spillovers

<table>
<thead>
<tr>
<th></th>
<th>5 km</th>
<th>Marginal effect</th>
<th>10 km</th>
<th>Marginal effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nighttime light</td>
<td>-0.03000*</td>
<td>-3.14012</td>
<td>-0.04203*</td>
<td>-3.08470</td>
</tr>
<tr>
<td></td>
<td>(-0.05185, -0.01431)</td>
<td></td>
<td>(-0.06617, -0.01303)</td>
<td></td>
</tr>
<tr>
<td>Effort</td>
<td>0.00055</td>
<td>0.0020</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.00000, 0.00076)</td>
<td></td>
<td>(0.00000, 0.00036)</td>
<td></td>
</tr>
<tr>
<td>Neighbouring nighttime light</td>
<td>0.00020</td>
<td>0.00370</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.00000, 0.00028)</td>
<td></td>
<td>(0.00000, 0.000650)</td>
<td></td>
</tr>
<tr>
<td>Spatial parameter</td>
<td>10.13342*</td>
<td>8.03332*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.52779, 22.96918)</td>
<td></td>
<td>(0.71158, 18.66336)</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>5.08590*</td>
<td>4.90550*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(3.28418, 6.48527)</td>
<td></td>
<td>(3.12482, 6.09731)</td>
<td></td>
</tr>
<tr>
<td>Observations</td>
<td>201</td>
<td>201</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beach dummies</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year dummies</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clarke test:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ZIP</td>
<td>0.00000</td>
<td>0.00000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No decision</td>
<td>0.00000</td>
<td>0.00625</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ZIGP</td>
<td>1.00000</td>
<td>0.99375</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: (a) Nighttime light refers to nighttime light intensity within 1 km. Neighbouring nighttime light refers to nighttime light intensity for beaches within 1–5 km and 1–10 km in the first and second specifications, respectively. (b) The 5% and 95% confidence limits are given in parentheses. (c) The Clarke test reports the percentage of decisions in favour of the ZIP or ZIGP or neither of these models. (d) * Statistically significant at the 5% level.

B Replacement costs

We present here the information used in Section 6 to construct Table 4.

1. *Ferme Corail (Reunion):* Assuming an age at maturity of 15 years, the estimated cost of raising one green turtle is US$1672, corresponding to an annual cost of US$111.45 (Troeng and Drews, 2004).

2. *TUMEC, Rantau Abang (Malaysia):* This marine conservation centre mainly focuses on leatherback turtles. They estimate a monthly cost of US$132 per turtle
during the first year, and US$658 per month for each subsequent year (Troeng and Drews, 2004).

3. WMI research facility: This facility ran a prototype pen for captive breeding of farm-raised turtles for 18 hawksbill adults over 18 months and found that the total running cost was US$34,285, corresponding to US$1203 per turtle per year (Webb et al., 2008).

4. Cayman Turtle Farm: This farm specialises in green sea turtles. In a personal communication, Walter Mustin, Chief Research Officer of Cayman Turtle Farm, provided the following production cost estimates per turtle and year.

<table>
<thead>
<tr>
<th>Item</th>
<th>Cost/turtle/year (US$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Energy</td>
<td>106</td>
</tr>
<tr>
<td>Salaries and wages</td>
<td>56</td>
</tr>
<tr>
<td>Feed</td>
<td>53</td>
</tr>
<tr>
<td>Repairs and maintenance</td>
<td>25</td>
</tr>
<tr>
<td>Security</td>
<td>13</td>
</tr>
<tr>
<td>Depreciation</td>
<td>13</td>
</tr>
<tr>
<td>Chemicals</td>
<td>6</td>
</tr>
<tr>
<td>Waste removal</td>
<td>4</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>279</strong></td>
</tr>
</tbody>
</table>

C Stage-based life tables

Crouse (1999) provides the following table for the hawksbill sea turtle.
Table A.3: Hawksbill sea turtle

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Stage duration ($d_i$)</th>
<th>Annual survival ($\sigma_i$)</th>
<th>Annual fecundity ($F_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Eggs/hatchlings</td>
<td>1</td>
<td>0.6747</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Small juveniles</td>
<td>7</td>
<td>0.75</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>Large juveniles</td>
<td>8</td>
<td>0.6758</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>Subadults</td>
<td>6</td>
<td>0.7425</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>Adults</td>
<td>$&gt;32$</td>
<td>0.8091</td>
<td>76.5</td>
</tr>
</tbody>
</table>

For the green sea turtle, we take the five-stage life table from Cambell (2003).

Table A.4: Green sea turtle

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Stage duration ($d_i$)</th>
<th>Annual survival ($\sigma_i$)</th>
<th>Annual fecundity ($F_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Eggs/hatchlings</td>
<td>1</td>
<td>0.8</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Small juveniles</td>
<td>14</td>
<td>0.8</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>Large juveniles</td>
<td>15</td>
<td>0.76</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>Subadults</td>
<td>1</td>
<td>0.76</td>
<td>26.4</td>
</tr>
<tr>
<td>5</td>
<td>Adults</td>
<td>$&gt;32$</td>
<td>0.89</td>
<td>26.4</td>
</tr>
</tbody>
</table>

For the leatherback turtle, we refer to Saba et al. (2012) and Martinez et al. (2007) for annual fecundity data.

Table A.5: Leatherback sea turtle

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Stage duration ($d_i$)</th>
<th>Annual survival ($\sigma_i$)</th>
<th>Annual fecundity ($F_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Eggs/hatchlings</td>
<td>1</td>
<td>0.6747</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Small juveniles</td>
<td>7</td>
<td>0.727</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>Large juveniles</td>
<td>7</td>
<td>0.78</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>Subadults</td>
<td>6</td>
<td>0.78</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>Adults</td>
<td>$&gt;32$</td>
<td>0.78</td>
<td>91</td>
</tr>
</tbody>
</table>
### D Dynamic results

#### Table A.6: Eigenvalues

<table>
<thead>
<tr>
<th></th>
<th>( \lambda_1 )</th>
<th>( \lambda_2 )</th>
<th>( \lambda_3 )</th>
<th>( \lambda_4 )</th>
<th>( \lambda_5 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawksbill no light</td>
<td>0.9281</td>
<td>0.7318+0.2037i</td>
<td>0.7318-0.2037i</td>
<td>0.4744</td>
<td>0.0060</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.9120</td>
<td>0.7292+0.1849i</td>
<td>0.7292-0.1849i</td>
<td>0.4975</td>
</tr>
<tr>
<td>Green no light</td>
<td>0.9210</td>
<td>0.7569+0.0717i</td>
<td>0.7569-0.0717i</td>
<td>-0.0140</td>
<td>0.0132</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.9144</td>
<td>0.7601+0.0624i</td>
<td>0.7601-0.0624i</td>
<td>-0.0119</td>
</tr>
<tr>
<td>Leatherback no light</td>
<td>1.0107</td>
<td>0.7578+0.2908i</td>
<td>0.7578-0.2908i</td>
<td>0.3726</td>
<td>0.0243</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.9782</td>
<td>0.7520+0.2557i</td>
<td>0.7520-0.2557i</td>
<td>0.4275</td>
</tr>
</tbody>
</table>

#### Table A.7: Coordinates of the eigenvector \( v_{\lambda_1} \) corresponding to \( \lambda_1 \)

<table>
<thead>
<tr>
<th></th>
<th>( v_{\lambda_1 1} )</th>
<th>( v_{\lambda_1 2} )</th>
<th>( v_{\lambda_1 3} )</th>
<th>( v_{\lambda_1 4} )</th>
<th>( v_{\lambda_1 5} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawksbill no light</td>
<td>0.3028</td>
<td>0.9432</td>
<td>0.1360</td>
<td>0.0084</td>
<td>0.0037</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.2818</td>
<td>0.9483</td>
<td>0.1455</td>
<td>0.0097</td>
</tr>
<tr>
<td>Green no light</td>
<td>0.1604</td>
<td>0.9855</td>
<td>0.0550</td>
<td>0.0002</td>
<td>0.0054</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.1524</td>
<td>0.9866</td>
<td>0.0573</td>
<td>0.0002</td>
</tr>
<tr>
<td>Leatherback no light</td>
<td>0.4223</td>
<td>0.9000</td>
<td>0.1064</td>
<td>0.0169</td>
<td>0.0047</td>
</tr>
<tr>
<td></td>
<td>light</td>
<td>0.3851</td>
<td>0.9144</td>
<td>0.1224</td>
<td>0.0219</td>
</tr>
</tbody>
</table>

#### Table A.8: Long-run stage distribution (%)

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Hawksbill no light</th>
<th>Hawksbill light</th>
<th>Green no light</th>
<th>Green light</th>
<th>Leatherback no light</th>
<th>Leatherback light</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Eggs/hatchlings</td>
<td>21.72</td>
<td>20.27</td>
<td>13.29</td>
<td>12.66</td>
<td>29.12</td>
<td>26.54</td>
</tr>
<tr>
<td>2</td>
<td>Small juveniles</td>
<td>67.65</td>
<td>68.21</td>
<td>81.69</td>
<td>81.97</td>
<td>62.06</td>
<td>63.03</td>
</tr>
<tr>
<td>3</td>
<td>Large juveniles</td>
<td>9.76</td>
<td>10.47</td>
<td>4.56</td>
<td>4.76</td>
<td>7.34</td>
<td>8.44</td>
</tr>
<tr>
<td>4</td>
<td>Subadults</td>
<td>0.61</td>
<td>0.69</td>
<td>0.019</td>
<td>0.02</td>
<td>1.17</td>
<td>1.51</td>
</tr>
<tr>
<td>5</td>
<td>Adults</td>
<td>0.26</td>
<td>0.35</td>
<td>0.44</td>
<td>0.58</td>
<td>0.32</td>
<td>0.49</td>
</tr>
</tbody>
</table>
Figure A.1: Population difference per stage

(a) Hawksbill

(b) Green

(c) Leatherback
Figure A.2: Stage distribution

(a) Hawksbill turtles, no nighttime light  
(b) Hawksbill turtles, nighttime light  
(c) Green turtles, no nighttime light  
(d) Green turtles, nighttime light  
(e) Leatherback turtles, no nighttime light  
(f) Leatherback turtles, nighttime light