

Exhibit R-013

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Environmental Pollution and Biodiversity: Light Pollution and Sea Turtles in the Caribbean^a

Michael Brei

University Paris Ouest & SALISES

Agustín Pérez-Barahona^b

INRA & École Polytechnique

Eric Strobl

École Polytechnique & IPAG

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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 data set of sea turtle nesting activity and satellite derived measures of nightlights. Controlling for surveyor effort, local economic infrastructure and spatial spillovers, we find that nightlights significantly reduce the number of sea turtle nests. Using data on replacement costs of turtles raised in captivity, our result suggests that the increase in lighting over the last 20 years has resulted in the loss of close to 2,000 sea turtles in the Caribbean, worth up to \$312 million. Incorporating our empirical estimate into a stage-structured population model we discover that the generational effects in the future are likely much larger. More generally, our study provides a new approach to valuing the cost of environmental pollution associated with species extinction.

Keywords: biodiversity, pollution, sea turtles.

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^bCorresponding author: Department of Economics, INRA and Ecole Polytechnique, Avenue Lucien Brétignière, 78850 Thiverval Grignon, France; e-mail: agperez@grignon.inra.fr.

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, thus potentially threatening the rich biodiversity that is characteristic of coasts (for instance, Jackson *et al.*, 2001; and Myers and Worm, 2003). One important component of biodiversity is of course the protection of species from extinction (Polasky *et al.*, 2005). A largely neglected aspect in this regard that has drawn recent attention is the role that increased lighting due to local economic development may play (Navara and Nelson, 2012; Gaston *et al.*, 2013; and Kyba and Holker, 2013). More specifically, while a number of studies in the natural sciences have already pointed out that some marine species are particularly sensitive to light pollution (see, among others, Bustard, 1967; Witherington and Martin, 1996; and Bird *et al.*, 2004), the impact of the rising degree of coastal illumination has gone largely unexplored (Hill, 2006; Rich and Longcore, 2006; and USC, 2008). In this paper we set out to study how light pollution in Caribbean coastal areas may have affected the critically endangered sea turtle population (IUCN, 2001).¹ In particular, light pollution in the Caribbean might be an important threat for these species (Nicholas, 2001). Our aim here is to derive a quantitative estimate of the impact of such pollution on sea turtle populations in the region both in the short and long term.

A number of papers in the natural science literature have emphasized that the presence of nightlights likely interferes with sea turtle behavior in several ways. On the one hand, artificial nightlight tends to deter sea turtle adults from nesting (Raymond, 1984; Hirth and Samson, 1987; Witherington, 1992; and Johnson *et al.*, 1996). At the same time, it 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; and Lorne and Salmon, 2007). Nevertheless, the quantitative effect of nightlight on sea turtle nesting and population has not yet been investigated statistically or limited to case studies of particular beaches (Kaska *et al.*, 2003; and Witherington and Frazer, 2003). The only exception in this regard is the study by Mazor *et al.* (2013), which investigates the effect of satellite-derived nightlights on sea turtle nesting in the coastal areas of Israel. However, although their descriptive statistics suggest a negative correlation between nightlights and nesting activity², the authors find in the regression analysis that, peculiarly, the relationship between nightlights and nesting is positive.³ Importantly though, they neither control for surveyors' effort nor for potential spatial spillovers between beaches, which as

¹In terms of the three turtle species examine here, both the green turtle (*Chelonia mydas*) and the leatherback turtle (*Dermochelys coriacea*) were classified as endangered in 1996, while the hawksbill turtle (*Eretmochelys imbricata*) was listed as endangered in 1986 but then upgraded to critically endangered in 1996.

²See Figure 3 and Table 2 of their paper.

³See Table 3 of their paper. It is noteworthy that in an earlier study Aubrecht *et al.* (2010) also noticed a positive relationship between nightlight intensity and the sea turtle nesting activity in Florida in a simple plot of their data. However, as the authors argue, this counter-intuitive finding was likely due to legislation in the mid-1980s which imposed regulation of beachfront lighting for the protection of sea turtles in those beaches that were more lit.

we show can bias the estimated impact. Moreover, they do not, as we do here, interpret their quantitative estimates either in terms of the short or long term impact.

More generally speaking, there is a surprising paucity of solid statistical evidence of the detrimental role that pollution may play in the loss of biodiversity or species extinction, despite the fact that it is widely recognized as one of the key threats to biodiversity⁴ and that it often enters public discourse in response to major pollution incidences such as the Deepwater Horizon oil spill.⁵ The few papers that have examined this aspect have been largely limited to the biology literature where the focus has been more generally on how human population density may result in losses in biodiversity.⁶ The only exception in the economics literature is the study by Conrad (1989) who concludes that the increased harvest of bowhead whales by Alaskan Eskimos threatened their existence.

Our paper contributes to the existing literature in a number of ways. First, we provide a quantitative measure of how a potentially important type of pollution affects an endangered species. More specifically, we estimate the impact of nightlight pollution on turtle populations in Guadeloupe by combining data on satellite-derived nightlight images, the location of sea turtle nesting sites, nesting activity, and local economic activity, as well as surveyor effort. From a methodological point of view, we explicitly take into account the spatial effects of nightlight pollution on sea turtle nesting in the context of count data models. We then apply our estimates to a population model so as to capture the dynamic implications of nightlights on the sea turtle population. To this end we incorporate our estimates into a simulation of the sea turtle population dynamics for Guadeloupe using a stage-structured population model as in Crouse *et al.* (1987) and Crowder *et al.* (1994). Our approach follows Crowder *et al.* (1994) who investigate 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.

After controlling for local economic activity and the effort made in nest counting in the econometric analysis, we find a significant negative impact of coastal nightlights on the nesting activity of sea turtles in Guadeloupe. Other things being equal, we provide evidence that a 1% increase of night illumination reduces the number of nests by around 6%. Moreover, we observe that the presence of marinas and hotels significantly deter sea turtle nesting, while the proximity of roads and ports does not appear to be important in our data. Extending our estimate of the marginal effect of nightlights to the whole Caribbean, we find, as gauged from the cost of rearing sea turtles in captivity, that the replacement of the nearly 2,000 “missing” sea turtles due to the greater night illumination since 1992 is up to 312 million US dollars. With respect to the impact of night illumination on the future generations of turtles, we conclude from the calibrated population model that the fertility drop caused by photopollution substantially accelerates

⁴See the Convention on Biological diversity at <http://www.cbd.int>.

⁵The 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 spill and its aftermath.

⁶See, for instance, Luck (2007).

the extinction of sea turtles. For hawksbill and green turtles, coastal nightlights decrease the time of extinction from 164 and 154 years to 120 and 135 years, respectively. This impact is even stronger for leatherback turtles, which under current light conditions will eventually become extinct in 403 years. In contrast, if there was no light pollution then the leatherback population would continuously increase in the long run.

The remainder of the paper is organized 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 of the missing turtles in the Caribbean, and in Section 7 investigate the population dynamics and value its implications under different scenarios. Finally, Section 8 concludes.

2 Sea turtle nesting and nightlights

It is now widely accepted that coastal nightlights may deter sea turtles from nesting (see, amongst others, Raymon, 1984; Witherington and Martin, 1996; Witherington and Frazer, 2003; and Jones *et al.*, 2011). More specifically, while sea turtles spend very little of their life on beaches and almost exclusively at night, where females nest and hatchlings emerge, these nocturnal activities are critical to the creation of future generations of turtles and may be significantly disturbed by the presence of night illumination. Indeed, artificial lighting drastically alters the way adults choose their nesting sites as they generally prefer unlit beaches (Raymond, 1984; and Witherington, 1992). Night illumination also increases the possibility of direct human disturbance of nesting activity (Carr and Giovannoli, 1957, and Carr and Ogren, 1960), frequently causing turtles to abandon their nesting attempts (Hirth and Samson, 1987; and Johnson *et al.*, 1996), or to expedite the process of covering the eggs and camouflaging the nest site (Johnson *et al.*, 1996). Moreover, Witherington and Martin (1996) found turtles discarding their eggs in the sea without nesting due to the lack of appropriate dark beaches. Photopollution may also affect adult turtles' return to the sea after nesting. Indeed, many experimental studies show that adult turtles rely on brightness to spot the sea (Caldwell and Caldwell, 1962; Ehrenfeld and Carr, 1967; Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1975). However, this problem seems to be less severe than it is for the hatchlings (Witherington and Martin, 1996).

Hatchlings emerge from eggs beneath the sand mainly at night and directly crawl to the sea in order to increase their survival chances (Hendrickson, 1958; Bustard, 1967; Neville *et al.*, 1988; Witherington *et al.*, 1990). However, by creating unnatural stimuli light illumination can disrupt their instinctive sea-finding mechanisms, often resulting in hatchling death due to exhaustion, dehydration, and predation. (see, for instance, Bustard, 1967; and Witherington and Martin, 1996). It has been additionally 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 sea-finding difficulties of hatchlings together with the possibility of adult disorientation has led in some cases to the replacement of the common blue light (shorter-wavelength) beach illumination with

red light (longer-wavelength) lighting, since sea turtles are more sensitive to blue light.⁷ Nevertheless, such measures are frequently criticized because any luminary tends to encourage human activity on beaches (Witherington and Martin, 1996).

It is important to also point out that sea turtles exhibit natal philopatry which means that females are likely to return to their natal beach for nesting. However, they may nest in neighboring beaches if the original site is no longer suitable (e.g., Worth and Smith, 1976; Witherington and Martin, 1996). Nightlights may therefore have spatial spillover effects: an illuminated beach may receive additional turtles because the neighboring nesting sites are brighter. Not taking this into account could thus lead to an underestimation of any negative influence of light illumination.

3 Data description

3.1 Turtles nests

The sea turtle nesting data were provided by the *Guadeloupe Sea Turtles Recovery Action Plan*.⁸ The survey identified a total of 156 nesting beaches in Guadeloupe, together with their geolocation, of which 67 beaches were regularly surveyed for nesting activity at night during the nesting season of 2008. The data consists of the number of nests, the number of nights the beach was surveyed, and the sea turtle species of the nest. The species indigenous to Guadeloupe are the green (*Chelonia mydas*), the hawksbill (*Eretmochelys imbricata*), and the leatherback (*Dermochelys coriacea*) turtles. Summary statistics of the nesting data, as well as all other variables used in our analysis, are provided in Table A.1 of the Appendix. As can be seen, on average each beach was surveyed 40 times, with a mean discovery of 26 nests, although there is considerable variation for both surveying effort and nest discovery across beaches. One may also note that over half of the nests found were for the hawksbill turtle.

3.2 Nightlights

In order to proxy nighttime illumination at the local level we resort to data derived from satellite images of nightlights. More specifically, we use nightlight imagery provided by the Defense Meteorological Satellite Program (DMSP) satellites. In terms of coverage each DMSP satellite has a 101 minute near-polar orbit at an altitude of about 800km 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 nightlight 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). Resulting images are percentages of nightlight occurrences for each pixel per year normalized across satellites to a scale ranging from 0 (no light) to 65 (maximum light). The spatial resolution of the original pictures is

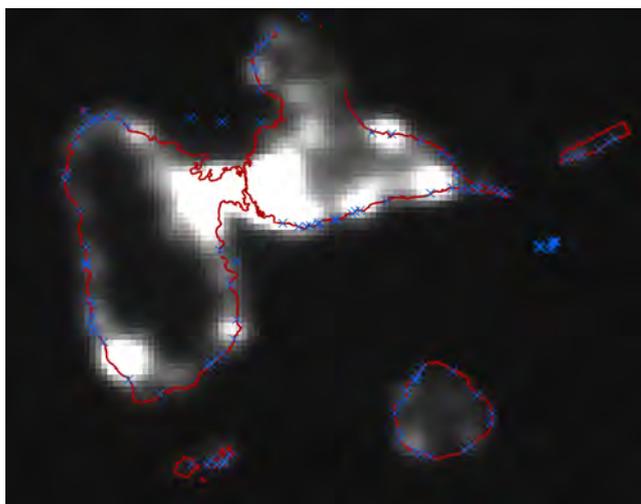
⁷For instance, the low-pressure sodium-vapor luminaries seem to affect nesting less than light from other sources (Witherington, 1992).

⁸See <http://www.tortuesmarinesguadeloupe.org> and Santelli *et al.* (2010) for further details.

about 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 about 1 km² near the equator. In order to get yearly values, simple averages across daily (filtered) values of grids were generated. Data are publicly available on an annual basis over the period 1992-2010.⁹

The nightlight image of Guadeloupe in 2008 is depicted in Figure 1. As can be seen, there is an unequal distribution of nightlight intensity across the islands. More importantly, a large part of the brightness is concentrated near or on the coast.

Figure 1: Nightlights and nesting sites in Guadeloupe



3.3 Other data

We gathered information on the location of hotels and their capacity from a number of sources, including <http://www.guadeloupe-antilles.com>, Google Maps and the individual internet pages of the hotels. This resulted in a total of 69 hotels. The number of beds of these range from 10 at Hostellerie des Chateaux to 1,316 at Club Mediterranee Caravelle. In terms of ports and marinas we resorted to information at <http://www.portbooker.com> and general internet searches. In this regard we identified and geo-localised the two main ports of Guadeloupe and calculated the distance to the nearest port for each beach. With respect to marinas there were a total of 24, ranging in size from 2 to 1,000 docks. As a benchmark measure we summed the number of docks within 1 km of each beach. To calculate out the distance to roads for our beaches we used the shape-files available at <http://www.diva-gis.org/gdata> and the centroid of each beach.

⁹One should note that a number of papers now use nightlights as a proxy for economic activity; see, for instance, Henderson *et al.* (2012). Here we use nightlights for what they are, namely a measure of local light intensity during the night, while controlling for economic activity in the area.

4 Econometric model

Given that our dependent variable is a count of the number of turtle nests, standard linear regression techniques would not be appropriate. In terms of choosing the relevant count data model one first needs to consider whether the data are characterized by over-dispersion. Examining the summary statistics in Table A.1 this is clearly the case, as the variance is substantially higher than the mean. When over-dispersion exists it is generally preferable to use a negative binomial rather than the more common poisson count model. However, importantly over-dispersion may also be caused by a large proportion of zeros in the data, rendering traditional distributions insufficient to describe the data at hand. Indeed in our data 27% per cent of nesting beaches were found to have no nesting activity. We therefore follow Czado *et al.* (2007) and experiment with using the Zero-Inflated Poisson and Zero-Inflated Generalized model. More specifically, the generalized Poisson regression (GPR) model is given by:

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

for $y_i = 0, 1, 2, \dots$; where $\mu_i = \mu_i(x_i) = \exp(\sum x_{ij}\beta_j)$, $x_i = (x_{i1}, x_{i2}, \dots, x_{ik})$ is the i -th row of covariate matrix X, and $\beta = (\beta_1, \beta_2, \dots, \beta_k)$ is a k -dimensional column vector of parameters. The mean of y_i is given by $\mu_i(x_i)$. One should note that in equation (1), the parameter α is a measures of dispersion, where if $\alpha > 0$ then there is over-dispersion, while if $\alpha = 0$ the model reduces to a standard Poisson regression model. As just noted, any over-dispersion due to an excess of zeros can be accounted for by using the Zero-Inflated Poisson model:

$$\begin{aligned} P(Y = y_i | x_i, z_i) &= \varphi_i + (1 - \varphi_i)f(\mu_i, \alpha, y_i), & y_i = 0 \\ &= (1 - \varphi_i)f(\mu_i, \alpha, y_i), & y_i > 0 \end{aligned} \quad (2)$$

where $f(\mu_i, \alpha, y_i)$, $y_i = 0, 1, 2, \dots$ is the GPR model in (1), $0 < \varphi_i < 1$ and $\varphi(x_i)$. One should note that the distribution of y_i is characterized by over-dispersion when $\varphi_i > 0$ and that this model reduces to the zero-inflated Poisson model when $\alpha = 0$. The mean and variance of the count variable y_i are given by:

$$E(y_i | x_i) = (1 - \varphi_i)\mu_i(x_i) \quad (3)$$

and

$$\begin{aligned} V(y_i | x_i) &= (1 - \varphi_i)[\mu_i^2 + \mu_i(1 + \alpha\mu_i)^2] - (1 - \varphi_i)^2\mu_i^2 \\ &= E(y | x_i)[(1 + \alpha\mu_i)^2 + \varphi_i\mu_i]. \end{aligned} \quad (4)$$

As argued earlier, there is reason to believe that nesting behavior may be correlated across space. One manner through which this can be modeled is the spatial correlation in the error term. In doing so we follow Czado *et al.* (2007) and use a Gaussian Conditional Autoregressive (CAR) formulation, which allows the modeling of spatial dependence, and dependence between multivariate random variables at irregular spaced regions. More specifically, for our set of J beaches $\{1, 2, \dots, J\}$ we let $\gamma = (\gamma_1, \gamma_2, \dots, \gamma_J)^t$ be the vector of normally distributed spatial effects for each beach:

$$\gamma \sim N_J(0, \sigma^2 Q^{-1}) \quad (5)$$

$$Q_{ij} = \begin{cases} 1 + |\Psi| \cdot N_i & i = j \\ -\Psi & i \sim j \\ 0 & \text{otherwise,} \end{cases} \quad (6)$$

where N_i is the number of beaches within area i and \sim indicates that i and j are neighboring beaches. The conditional distribution of γ_i is then:

$$\gamma_i | \gamma_{-i} \sim N \left(\frac{\Psi}{1 + |\Psi| \cdot N_i} \sum_{j \sim i} \gamma_j, \sigma^2 \frac{1}{1 + |\Psi| \cdot N_i} \right) \quad (7)$$

where γ_{-i} are all the other values of γ_i . Importantly Ψ determines the degree of spatial dependence, in that when $\Psi = 0$ there is no spatial dependence, but as spatial dependence increases the value of Ψ will also be larger.

5 Econometric results

The results of estimating the determinants of nesting using the Zero-Inflated Generalized Poisson model (ZIGP) are given in Table 1. One should note in this regard that we used a Clarke test for all specifications to determine whether the model could be reduced to a zero-inflated Poisson model by setting the over-dispersion parameter α equal to zero. As can be seen in Table 1, the resultant test statistic suggested that the ZIGP was the preferred model in all specifications. In the baseline regression, shown in the first column, we only include nightlights as an explanatory variable without any spatial effects. The results suggest that the intensity of nightlights has a significant and negative effect on the number of sea turtle nests. Since the ZIGP is a non-linear model, the coefficients have no straightforward intuitive interpretation. Marginal effects for any explanatory variable x_k with estimated coefficient β_k are thus calculated as follows:

$$\frac{\partial \text{Nests}}{\partial x_k} = \beta_k \exp \left(\beta_1 + \sum \beta_j \cdot \bar{x}_j \right), \quad (8)$$

where β_1 is the constant coefficient in our regression, \bar{x}_j denotes the average of x_j , and the terms inside the summation operator \sum refer to the explanatory variables found to be significant. The marginal effects of the significant coefficients are given in Table 2. Accordingly, the estimated coefficient in our base specification suggests that a one unit increase in nightlights reduces the number of nests by 3.8. As noted earlier, one concern is that sea turtle nesting behavior may be spatially correlated. In the second column of Table we thus allow for spatial correlation of the error term as outlined above. In this regard, we as a benchmark considered beaches within 5km of each other as neighbors. As can be seen, the positive and significant estimate of Ψ suggests that the data does indeed exhibit spatial dependence across neighbors. The marginal effect, as gauged from the second column in Table 2, is now somewhat lower, standing at -2.2 nests, than without spatial correlation. We thus continue allowing for spatial effects in the remaining specifications.¹⁰

¹⁰As can be seen throughout Table 1, the spatial effects are always found to be statistically significant.

Table 1: Determinants of sea turtle nesting activity

	(1)	(2)	(3)	(4)	(5)	(6)
Nightlights	-0.0735 (-0.1281, -0.0259)	-0.0909 (-0.1517, -0.0210)	-0.0894 (-0.1658, -0.0110)	-0.0869 (-0.1379, -0.0284)	-0.0868 (-0.1489, -0.0134)	-0.0924 (-0.1704, -0.0059=)
Effort			19,3983 (12.4168, 32.4372)	14.3023 (8.6860, 23.6536)	24.7793 (10.5916, 33.5149)	17.7003 (1.8344, 28.4067)
Roads				-0.3405 (-0.9545, 0.3221)	-0.1121 (-0.7751, 0.8339)	-0.4351 (-3.4642, 0.8692)
Marinas				-0.0237 (-0.0377, -0.0060)	-0.0282 (-0.0402, -0.0035)	-0.0368 (-0.0663, -0.0002)
Hotels				-0.0053 (-0.0060, -0.0042)	-0.0057 (-0.0067, -0.0024)	-0.0227 (-0.0263, -0.0053)
Distance to port				-0.0004 (-0.0008, 0.0000)	-0.0041 (-0.0048, -0.0000)	-0.0069 (-0.0091, 0.0029)
Spatial parameter		1.3654 (0.1604, 4.6391)	7.0969 (1.6764, 15.8881)	3.8690 (1.2483, 8.7586)	2.6935 (0.6313, 6.7299)	1.5540 (0.1100, 4.3290)
Constant	4.7348 (3.2526, 5.9300)	4.1349 (3.2008, 4.7707)	4.4418 (2.8292, 5,8064)	5.3409 (3.1082, 7.2999)	4.5363 (2.1336, 6.2304)	5.4483 (2.7065, 7.9775)
Observations	67	67	67	67	67	67
Clarke test:						
ZIP	0.1623	0.0055	0.0524	0.0070	0.0524	0.0020
No decision	0.0874	0.1568	0.1688	0.2088	0.1329	0.2143
ZIGP	0.7318	0.8272	0.7567	0.7687	0.7952	0.7537

Notes: (1) The 5th and 95th confidence interval are given in parentheses; (2) The Clarke test reports the proportion of decisions in favour of each model.

Table 2: Marginal effects for significant coefficients

Specification:	(1)	(2)	(3)	(4)	(5)	(7)
Nightlights	-3.8331	-2.1627	-5.9272	-5.7968	-6.9318	-3.4624
Effort	–	–	1.2857	0.9542	1.9787	6.6306
Roads	–	–	–	–	–	–
Marinas	–	–	–	-1.5824	-2.2517	-1.3778
Hotels	–	–	–	-0.3521	-0.4223	-0.8497
Ports	–	–	–	–	–	–

Importantly the number of nests discovered on a beach is likely to depend on the effort made by those counting. Moreover, one could very well imagine that perhaps greater effort is undertaken in those beaches that are better lit, thus potentially biasing the negative effect of nightlights downward. We thus in the third column include our effort intensity measure.¹¹ Unsurprisingly, greater surveying effort increases the number of nests being discovered, where the marginal impact of one unit greater monitoring intensity is associated with the discovery of one additional nest. Comparing the marginal effects of lighting from the specification without to that with the effort dummy, shows that there is indeed a downward bias, where for the latter the reduction per unit of night-light is nearly three times larger.

Nightlight intensity itself may be correlated with a number of other features of local economic activity that may affect a sea turtle’s decision to nest at a particular beach. For example, beaches are usually more lit the closer they are to hotels, but having hotels nearby will likely also increase the probability of nesting activity being disturbed by tourists. Similarly, local shipping activity might disturb nesting near beaches, and such activity tends to be higher at ports which are also more lit than, *ceteris paribus*, those without ports nearby. To ensure that the estimated effect of nightlight intensity is not capturing these other local features, we included the total number of hotel beds, the number of docks, and the number of ports within a 1km radius of the beach, as well as the distance to the nearest road. As can be seen in the fourth column of Table 2, ports and roads have no significant effect on nesting. In contrast, one finds that both the greater number of docks and the greater number of hotel beds nearby reduce the number of nests found on a beach. In terms of their marginal effects our coefficients imply that, for example, 10 additional beds in nearby hotels decrease the number of nests by 3.5, whereas a dock present within 1km of the nesting beach reduces nests by 1.58.

Our analysis can also be done by sea turtle species. More specifically our sample consists of 59% hawksbill, 38% green, and 3% leatherback nests. Given the small sample size of leatherback nests, the estimation of the spatial model was not feasible for these, and we only re-estimate the full specification of column (4) for hawksbill and green turtle nests; see columns (5) and (6), respectively. Reassuringly nightlights significantly deter

¹¹Note that, for ease of presentation, our variable effort \tilde{e} is in per thousand units of the original one e (*i.e.*, $\tilde{e} = e/1000$). Therefore, the marginal effect of the original effort variable is $\partial\text{Nests}/\partial e = \partial\text{Nests}/\partial\tilde{e} \cdot d\tilde{e}/de$, where $\partial\text{Nests}/\partial\tilde{e}$ is provided by (8) and $d\tilde{e}/de = 1/1000$.

nesting for both species. The inferred marginal effects indicate that the impact of an additional unit of nightlight on nesting activity is larger for the hawksbill than for the green turtle.

Thus far we have controlled for spatial effects only via the error term. Feasibly, however, there also may be spatial effects in terms of the covariates. For instance, with regard to the main focus of this study, a greater brightness of nearby beaches may have positive spillover effects on a local beach, as discouraged turtles look for alternative nesting sites nearby. To investigate this we calculate the average nightlight intensity of beaches within 5km, excluding a beach's own value. Similar measures were defined for the distance to road, docks, ports and hotel bed variables. The results, see Table A.2 in the Appendix, indicated that there are no direct spatial spillover effects of the nightlight intensity of nearby beaches. Similar conclusions were reached when we extended the proximity threshold to 10km.

6 The “missing” sea turtles in the Caribbean

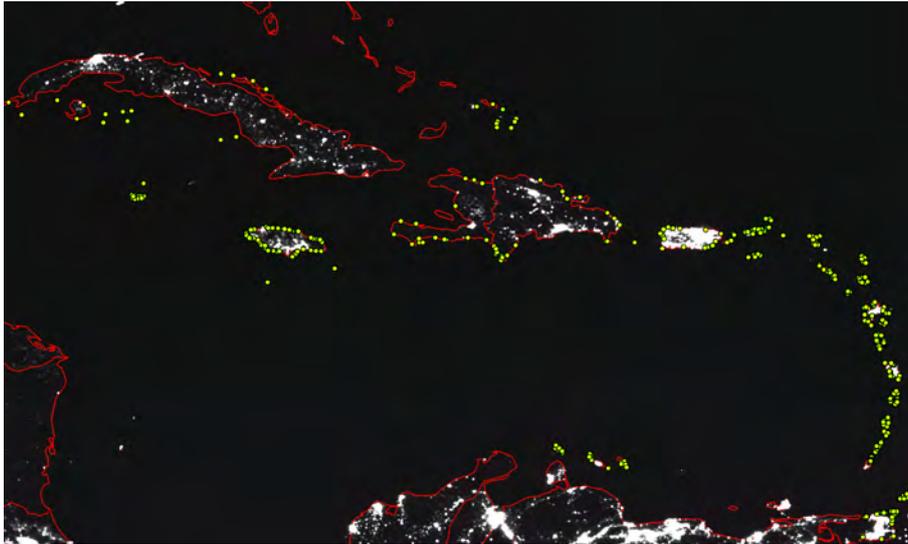
In the previous section we provided a quantitative estimate of the negative impact of light pollution on sea turtle nesting, taking account of other potentially confounding factors and spatial correlation. Apart from the arguable interest in the actual number itself, one can also use it to derive a monetary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

As a proxy of the monetary value of “missing” sea turtles due to nightlight pollution we use known costs of rearing sea turtles in captivity, an approach that has been used to infer the minimum value of the ecological services provided by sea turtles (see, for instance, Freeman, 2003; and Troeng and Drew, 2004), particularly if there are no specific estimates for willingness to pay available.¹² To identify the nesting beaches in the entire Caribbean we used information from SWOT/OBIS-SEAMAP, which provides a list of known nesting sites and their location.¹³ The 1,086 known nesting beaches along with nightlight intensity during 2010 are depicted in Figure 2.

¹²One should note that in our case we would need a willingness to pay (WTP) measure per individual turtle. As far as we are aware, the only WTP for sea turtles are those that refer to particular conservation programs - see, for example, Jin *et al.* (2010) -, and are not individual specific.

¹³SWOT - 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. See SWOT (2006, 2008, and 2009).

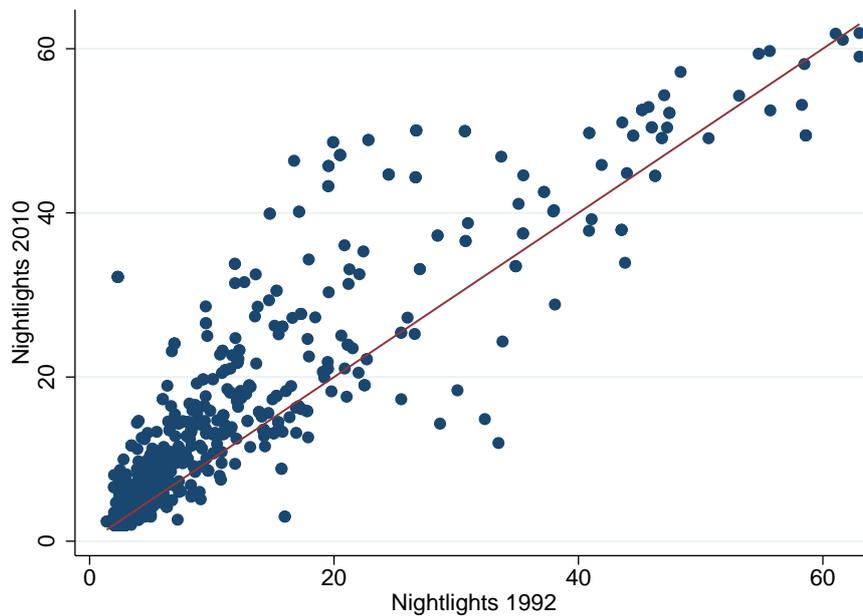
Figure 2: Nesting sites in the Caribbean



Note: Green dots indicate known nesting sites.

Accordingly, the location of nesting beaches and their nocturnal illumination varies widely across the Caribbean. Moreover, there has been an increase in nightlight intensity in most nesting beaches over time, as can be seen from Figure 3 which plots 1992 against 2010 nightlight intensity for each nesting site.

Figure 3: Light pollution at nesting sites in the Caribbean: 1992 *vs.* 2009



With the change in nightlight intensity for each beach and our measurement of the marginal effect of nightlights in hand, one can estimate the number of missing turtles as

follows:

$$\sum_{i=1}^{1086} \Delta \text{Nightlights}_i \times \frac{\partial \text{Nests}}{\partial \text{Nightlights}} \times \frac{\text{Hatchlings}}{\text{Nest}} \times \text{survival rate to adulthood.} \quad (9)$$

The first term represents the overall change in nightlight intensity on the nesting beaches over the period 1992-2010. For this we summed total net changes in illumination for all nesting beaches, which we found to be 2,811 units of light (*i.e.*, a 16% increase of 1992 intensity). For the marginal change in nests due to light pollution we used the estimated marginal effect for all turtles from our econometric analysis, *i.e.*, -5.8. These two figures together suggest that the number of missing nests over our sample period is 16,304. With regard to the average number of eggs per nest, while this varies across species and location, it is about 120. Finally we assume that the survival rate of hatchlings is equal to 1/1000; see, for instance, Frazer (1986). Equation 9 then implies that there were 1,957 missing sea turtles due to nightlight intensity over our sample period.

Regarding the monetary valuation of the missing turtles, we need the cost of rearing sea turtles in captivity. For this we resort to estimates derived from case studies of turtle farms and marine conservation centers. In this regard, we took information from three sources: Troeng and Drews (2004) for green and leatherback turtles, Webb *et al.* (2008) for hawksbill turtles, and, from a personal communication with the Cayman Turtle Farm in the Cayman Islands, for green turtles. We summarize the replacement costs in Table 3 (see Appendix B for further details):¹⁴

Table 3: Replacement costs per species (in US dollars)

Farm	Species	Cost/15-years old	Cost/adult	Replacement costs in millions
Ferme Corail	green	1,672	3,455	6.7
Cayman Turtle Farm	green	4,185	8,649	16.9
WMI Research facility	hawksbill	18,045	26,466	51.8
TUMEC, Rantau Abang	leatherback	112,128	159,504	312.1

Source: own calculations.

One striking aspect of these figures is that the costs of raising a leatherback turtle in captivity until 15 years of age and adulthood are multiple times larger than the equivalent figures for green and hawksbill turtles. However, the leatherback is also the largest of the three, with a carapace length between 1.30 and 1.83m and a weight between 300 and 500kg. In contrast, green sea and hawksbill turtles are considerably smaller with, respectively, a carapace length of 83-114cm and 71-89cm and normally weighing 110-190kg and 46-70kg (Marquez, 1990).

¹⁴We assume that green sea turtles reach adulthood at the age of 31 (Cambell, 2003), while the equivalent is 21 for the leatherback type (Martinez *et al.*, 2007; and Saba *et al.*, 2012) and 22 for the hawksbill turtles (Crouse, 1999).

Combining the cost per individual adult with our estimate of missing turtles we then calculate the total replacement cost of missing turtles. According to our estimates, shown in the last column of Table 3, this ranges from 6.7 million to 312.1 million US dollars, depending on the relative importance of each species nesting in the Caribbean.¹⁵ In other words, the cost of replacing the implied number of missing turtles with animals raised in captivity could be as much as 0.3 billion US dollars if these were mostly leatherback turtles. It is important to emphasize, 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 externalities arising from sea turtles being raised in their natural environment.

7 Population dynamics

In the previous section, making use of our econometric estimate of the negative impact of light pollution on sea turtle nesting, we have quantified and valued the number of “missing turtles” due to nighttime illumination in the Caribbean. These results however only take into account a single generation of turtles, neglecting any population dynamics. The aim of this section is to incorporate the generational effects by means of integrating our estimate into a population dynamics model.

Mathematical biology is plentiful of sophisticated population models (see, amongst others, Cushing, 2006; and Wikan, 2012). Nevertheless, the calibration of these models is often constrained by the availability of data. The reproduction and survival rates, for instance, play a key role in these dynamical settings. In the context of sea turtles it is well-known that these figures are age-dependent. It is thus argued that age-structured models, like the one introduced by Leslie (1945), would be an appropriate framework to study the population dynamics of sea turtles. Unfortunately, there is little reliable age-specific information for long-lived iteroparous species, such as the sea turtles. Still, since the life cycle of sea turtles is composed of a series of well-identified stages (see Heppell *et al.*, 2003, for an introduction to the ecology of sea turtle population), more information is available regarding the duration, survival, and reproduction rates of each stage. We thus follow the setup introduced by Lefkovicth (1965), Crouse *et al.* (1987), and Crowder *et al.* (1994), where individuals are grouped by stage instead of age, sharing the same reproduction and survival rates.

7.1 Stage-structured population model

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

$$x_t = (x_{1t}, x_{2t}, x_{3t}, x_{4t}, x_{5t}), \quad (10)$$

¹⁵Unfortunately there are no available estimates of nesting activity by species available for the Caribbean.

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

$$x_{1t} = F_1x_{1t-1} + F_2x_{2t-1} + F_3x_{3t-1} + F_4x_{4t-1} + F_5x_{5t-1}, \quad (11)$$

while the number of females present in the subsequent j -th stage, for $j = 2, \dots, 5$, is:

$$x_{jt} = G_{j-1}x_{j-1t-1} + P_jx_{jt-1}. \quad (12)$$

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

$$x_t' = Lx_{t-1}', \quad (13)$$

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 for sea turtles is comprised of 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. In this regard, we follow the standard method of Crouse *et al.* (1987) and Crowder *et al.* (1994). If we denote the yearly survival rate of sea turtles in stage i and the duration of the i -th stage by σ_i and d_i , respectively, one can then determine the percentage of sea turtles from stage i that grow into stage $i + 1$ (γ_i) as:

$$\gamma_i = \begin{cases} \frac{(1-\sigma_i)\sigma_i^{d_i-1}}{1-\sigma_i^{d_i}} & \text{if } \sigma_i \neq 1 \\ \frac{1}{d_i} & \text{if } \sigma_i = 1. \end{cases} \quad (14)$$

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

$$G_i = \gamma_i\sigma_i \quad (15)$$

$$P_i = (1 - \gamma_i)\sigma_i. \quad (16)$$

7.2 Population dynamics and nightlight pollution

As pointed out above, the usual stage-based life table for a specific type of sea turtle consists of information about the duration, survival and reproduction rates of each stage.

We provide in Appendix C the corresponding stage-based life tables for the nesting types of sea turtles in Guadeloupe. Considering (14)-(16), we can then compute the population matrix L for each species. With this matrix in hand, taking (13) and an initial stage distribution vector x_0 , we obtain the population dynamics for $t \geq 0$.

Let us now incorporate the effect of night illumination into the population model. As we have shown earlier, nightlight pollution significantly reduces the number of sea turtle nests and, consequently, the annual fertility per turtle. The objective then is to adjust the parameter F_i to account for the marginal effect of nightlights. One should note that an additional negative consequence of nightlights is the increasing difficulty of hatchlings to find the sea after emerging from their nest, resulting in a reduction of their annual survival σ_1 (see Section 2). Our analysis should thus be interpreted as a lower bound of the negative effect of nightlight pollution, although we do later investigate how incorporating this aspect would affect our results.

As a starting point we assume nightlight intensity and nesting activity to be the average observed on Guadeloupe nesting beaches, and denote these as NL_{avg} and NT_{avg} , respectively. In order to modify the annual fertility we essentially need to estimate the reduction of hatchlings per year caused by nightlights. Thus, the average percentage reduction in the nests τ due to the night illumination is:

$$\tau(\beta_1) = \frac{|\beta_1|NL_{avg}}{NT_{avg} + |\beta_1|NL_{avg}}100, \quad (17)$$

where β_1 denotes the estimated marginal negative effect of light pollution.

With no available empirical evidence to resort to, 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 marine turtle level, we will adjust the marginal effect of nightlights to take account of the remigration interval, which we, following Doi *et al.* (1992), assume to be 2.6 years implying that $\tilde{\beta}_1 = \beta_1/2.6$.¹⁶ The modified annual fertility can therefore be computed as $\tilde{F}_i = [1 - \tau(\beta_1)/100]F_i$. Recall that the marginal effect for the hawksbill and green turtles is -6.93 and -3.46, respectively. For the leatherback turtle we assume that the marginal effect is simply equally to the sample average of -5.8. Thus for the leatherback turtle the annual fertility would reduce by 47%, changing the population matrix accordingly. Note that our analysis is based on a constant level of nightlights per beach since our objective is to evaluate the generational consequences of the current level of light pollution. The set-up, however, could be easily applied to evaluate different scenarios of nightlight changes.

7.3 Dynamic population response

We can now evaluate the population dynamics under a scenario with and one without night pollution. One can obtain the population dynamics for each turtle type, starting

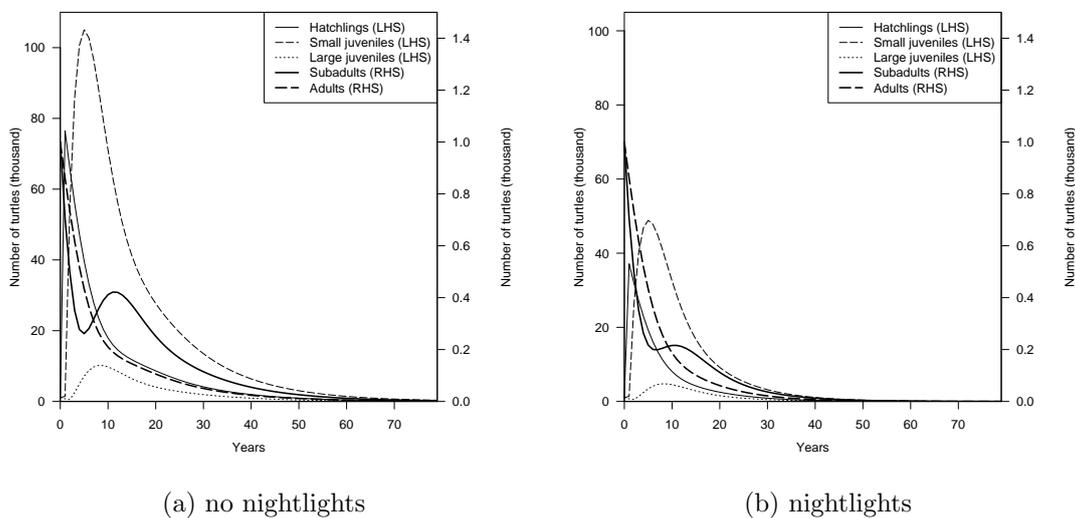
¹⁶Other studies on remigration intervals include Carr and Carr, 1970; Carr *et al.*, 1978; Hays, 2000; and Troeng and Chaloupka, 2007).

from a given initial stage distribution by recursively applying equation (13) to the population matrix with and without nightlights. Given that the data on the number and stage distribution of sea turtles is very uncertain due to the difficulties in tracking sea turtles, we assume an initial number of turtles for each stage which is consistent with broad estimates for Guadeloupe (see, amongst others, DREG (2008) and Delcroix *et al.* (2011)). More precisely, we assume for each type of turtle a population of 1,000 females per stage. Nevertheless, we verified that the qualitative population response is robust to alternative demographic configurations.¹⁷

7.3.1 Population dynamics

In Figures 4-6 we plot the evolution of the stage population for each type of sea turtle, with and without nightlights. As can be seen, even without light pollution both the hawksbill and the green sea turtle eventually become extinct, while the population of the leatherback continues to grow over time. One should note that this difference in the long-term population dynamics across species is in line with existing studies¹⁸ and is driven by the underlying survival and fertility parameters of the population matrix. However, as is also clear from the figures, the presence of nightlights considerably accelerates the process of extinction for hawksbill and green turtles. For the leatherback turtle the negative impact of nightlights reverses population growth so that these also become extinct in the long run.

Figure 4: Population per stage – hawksbill turtle



¹⁷Details are available from the authors upon request.

¹⁸For instance, Evans *et al.* (2001).

Figure 5: Population per stage – green turtle

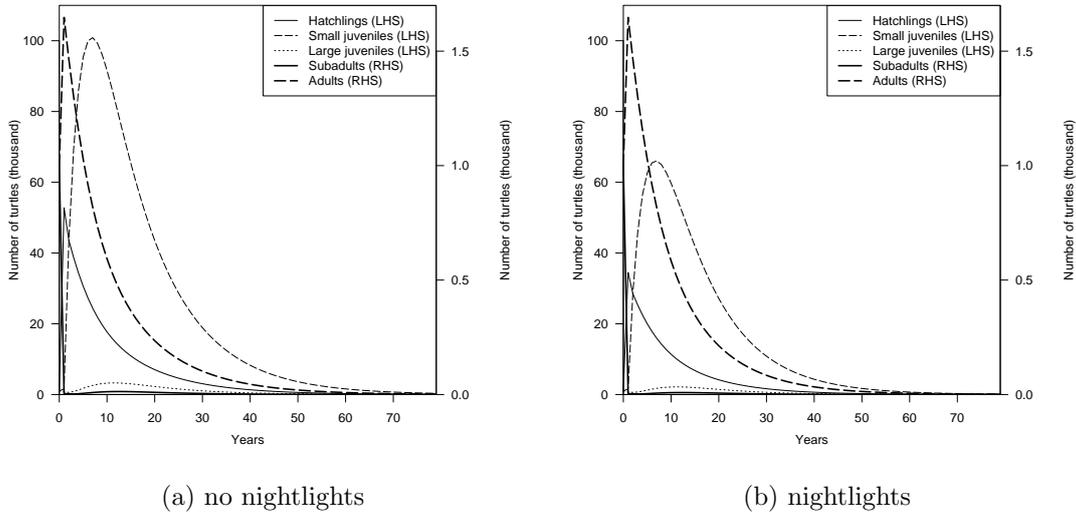
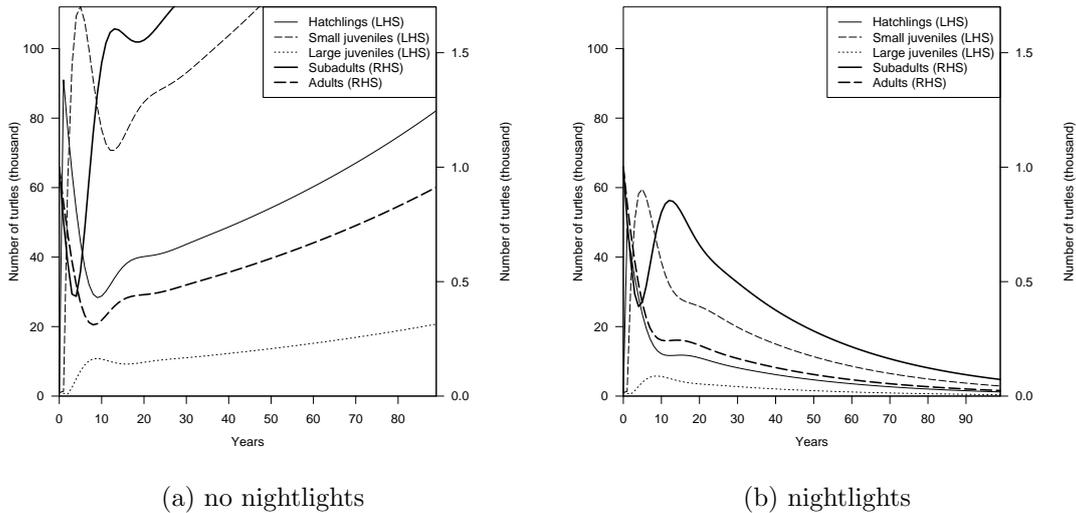


Figure 6: Population per stage – leatherback turtle



Figures 4 and 5 clearly show that the population of hawksbill and green turtles is always greater without nightlights than under night illumination. Moreover, one should also note from Figure 6 that the negative effect is more pronounced for the leatherback type. As a matter of fact without light pollution the population of leatherback turtles would increase in the long-run.

One should 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

the population model here is that population either increases or decreases in the long run, since the model consists of a system of first-order linear difference equations. One can easily verify, see Appendix D, that the absolute value of all eigenvalues of the population matrices for hawksbill and green turtles are lower than one. Consequently, their population will be asymptotically extinct regardless of the presence of light pollution. For the leatherback type, however, there is an eigenvalue (λ_1) greater than one if there is no nightlight pollution, so that its population increases in the long-run. As for hawksbill and green turtles, nightlights result in all eigenvalues being lower than one, leading to the eventual depletion of this species too. As pointed out earlier, there are of course more sophisticated frameworks that consider non-linearities which induce steady populations. This is usually the case of models that incorporate the effect of agglomeration by allowing, for instance, for 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 like the sea turtle.

The eigenvalues also allow us to provide quantitative information regarding the long-run response of the population of each type of turtle and, in particular, its growth rate and stage distribution. Since the system (13) has constant coefficients and $|\lambda_1| > |\lambda_j|$ for $j = 2, \dots, 5$ (see Table A.7), the unique solution in the long-run takes the form:

$$x_t' \approx c_1 \lambda_1^t v_{\lambda_1}, \quad (18)$$

where v_{λ_1} is the eigenvector corresponding to the eigenvalue λ_1 , and c_1 is a constant.¹⁹ 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, but that nightlights increase the long-run annual depletion from 7.19 to 10.18 % and from 7.9 to 8.76 %, respectively. We also confirm that the population of the leatherback type increases if there is no light pollution, with a long-run annual growth rate of 1.07%. However, the presence of night illumination reverses this trend, resulting in an eventual decreasing population at a rate of 2.75% per year.

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

$$\xi_i = \frac{v_{\lambda_1 i}}{\sum_{k=1}^5 v_{\lambda_1 k}}, \quad (19)$$

where $v_{\lambda_1 k}$ is the k -th coordinate of the eigenvector v_{λ_1} . Considering the eigenvalues and eigenvectors of tables A.7 and A.8 in Appendix D, we obtain the stage distribution for each type of turtle with and without nightlights. A well-known feature of these kinds of population models is that the population reaches a stable stage distribution in the long-run – see Table A.9 and Figures A.2 in Appendix D. As is evident from Table A.9, the proportion of hatchlings is most severely affected by nightlight pollution. The

¹⁹The solution of the system (13) for all t is $x_t' = \sum_{i=1}^5 c_i \lambda_i^t v_{\lambda_i}$, where v_{λ_i} denotes the eigenvector corresponding to the eigenvalue λ_i of the population matrix, and c_i are constants determined by the initial population distribution.

reduction is particularly apparent for the leatherback where the proportion of hatchlings falls by more than 3 percentage points, and it is a major reason for 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 be applied to study how fast this extinction may occur. More specifically, let us define the time to extinction t_e as the number of years it takes for less than one turtle to remain. Table 4 shows for our initial population of $p_0 = 5,000$ turtles that night illumination significantly accelerates the extinction of all three species. Without nightlight pollution the hawksbill and green turtles will take 164 and 154 years to become extinct, respectively. In the case of leatherback there is in contrast no extinction but rather an ever increasing population size. In the presence of nightlights eventually all three species will disappear. According to our simulations, the years of extinction now are 110 years for the hawksbill, 135 years for the green and 403 years for the leatherback. Thus night illumination on nesting sites has a clear accumulative effect in the long-run driven by the reduction in fertility rates of adult females.²⁰

Table 4: Time of extinction (in years)

	<i>no light</i>	<i>light</i>	<i>light</i> ($\tilde{\sigma}_1$)
Hawksbill	164	110	90
Green	154	135	119
Leatherback	–	403	186

Our estimates of the impact of nightlights are likely to be only lower bounds as we do not allow for the fact that, due to disorientation, lighting will also reduce the number of hatchlings that make it from the nesting site to the sea. Unfortunately we do not have any information of the impact of nightlights on the survival rate of hatchlings during this period of their life cycle in our data. However, Peters and Verhoeven (1994) studied loggerhead hatchling survival from their nests to the sea. More specifically, they examine two nesting sites on the Turkish Mediterranean coast and found that on the one that was well lit only 21% of hatchlings reached the sea, as compared to an adjacent unlit area where the success rate was 48%. In order to get a rough feel of how far our estimates are from the upper bound, we modify our hatchling survival probability as $\tilde{\sigma}_1 = 0.56\sigma_1$.²¹ As expected, extinction accelerates. More precisely, the time to extinction for hawksbill and green turtles is now 90 and 119 years, respectively, while for the leatherback it would take 186 years to extinction, see Table 4.

Finally, Figures 4-6 shown above reveal that the short-run population dynamics are cyclical. This property is explained by the fact that sea turtles spend several years in each

²⁰Note that the time of extinction depends on the distribution and size of the initial population, however, the qualitative results remain unchanged when we use alternative scenarios.

²¹The 56% is just the percentage reduction in the survival rates as found by Peters and Verhoeven (1994).

stage of development, resulting in the accumulation or reduction of number of individuals in a specific stage. This result is confirmed by examining the eigenvalues of the population matrix (see Table A.7).²² 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 a diminishing species' population that has been employed in the case of sea turtles is that of headstarting, where headstarting broadly entails the captive hatching and rearing of sea turtles through an early part of their life cycle.²³ For instance, the Cayman Turtle Farm has over the period 1980 to 2001 released a total of 16,422 neonates, 14,282 yearling and 65 older (19-77 months) green sea turtles.²⁴ As a simple thought experiment we can use our results above to consider the costs of using such a headstarting strategy to counteract the negative effect of nightlights on sea turtles.

We can use our results above to consider the costs involved in using headstarting to compensate for the accelerating effect of nightlights on sea turtle extinction. Our thought experiment in this regard consists of calculating the number of headstarted turtles that would have to be released into the wild today to keep the time of extinction the same as without nightlight pollution.²⁵ 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. As mentioned before, headstarted turtle have been release 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 of hatchlings, we here limit our analysis to the release of headstarted, one year old small juveniles. For the green turtle, we find that 5.5 million small juveniles would be needed to keep the time to extinction at the no nightlights level of 154 years with an associated cost between 0.6 and 1.5 billion dollars, depending on which source we use for the yearly replacement cost. In the case of the hawksbill, 130 million yearlings would have to released in order to keep the time to extinction at the no nightlight level of 164 years, with an associated cost of 156 billion dollars.

At first sight the compensating costs involved with using headstarting as a conservation management tool may seem remarkably high. However, one needs to remember that we are considering counteracting the negative effect of nightlights over all the years until extinction. Moreover, in line with arguments made by Heppel *et al.* (1996) in terms of using headstarting to compensate for reduced survival rates, these large figures are also due to the characteristics of the sea turtle itself. First, for a slow maturing species like sea turtles, large increases of juveniles are needed to compensate for the reduction in

²²The existence of complex and/or negative eigenvalues implies short-run cycles in difference equation systems.

²³See, amongst others, Bell *et al.* (2005).

²⁴Other examples include the North Carolina Head Start program (loggerhead turtles) and National Marine Fisheries Service Program (kemp's ridley turtles).

²⁵One should note that we are considering here only a one-time injection of sea turtles, however, the exercise could of course be extended to yearly release programs.

nesting activity and hence hatchling production due to light pollution. Secondly, except for extremely small populations, it is unfeasible to headstart enough juveniles to have an impact on the overall survival rate of a cohort.

Finally, it is important to also point out that there are other likely costs involved with headstarting; see Bell *et al.* (2005) for a review. Firstly, turtles raised in captivity may behave differently than those from the wild. For example, there is some evidence that headstarted turtles forage and nest outside of their natural range. Others have also questioned the ability of headstarted sea turtles to survive as well as wild ones due to nutritional deficiencies and behavioural modifications as a consequence of insufficient exercise, lack or inappropriate stimuli, and unavailability of natural food sources and feeding techniques during captivity. Additionally, headstarted sea turtles may have negative spillovers on wild sea turtles via the transmission of diseases acquired during captivity and genetic pollution. Thus, as large as they are, in actuality the cost estimates that we provide here should only be viewed as a lower bound of the total costs of using headstarting as a remedy for the detrimental sea turtle population effects of nightlight pollution.

8 Concluding remarks

We examine the loss of biodiversity due to environmental pollution by studying the impact of coastal light pollution on the sea turtle population in the Caribbean. To do so we assembled a data set of sea turtle nesting activity and satellite derived measures of nightlights for Guadeloupe. Using a spatial count data model we show that, after controlling for surveyor effort and local economic infrastructure, nightlights reduced the number of nests on beaches. Considering the growth of nightlights over the last 20 years across beaches known to be used for nesting in the Caribbean, our quantitative estimate suggests that if we consider the value of a sea turtle to be that of its replacement cost in captivity, then the increase in coastal lighting in the region has resulted in losses of up to 520 million US dollars. We then combine our statistical estimate within a stage-structured population model for Guadeloupe to study the generational implications of light pollution. The results suggest that light pollution substantially accelerates the extinction of sea turtles. Moreover, we find that compensating the negative effect of the current nightlight intensity by means of rearing sea turtles in captivity and then releasing them into the wild, as is part of some current conservation strategies, may be an expensive remedy. This suggests that one should explore what the economic costs of reducing coastal illumination near sea turtle nesting beaches as an alternative or supplementary conservation management tool would be.

More generally, our paper arguably provides a new approach to valuing the loss in species extinction due to environmental pollution. In particular, given data on a species of interest and some type of relevant pollution, our paper shows that using statistical estimates of the short-term impact within a population model can provide helpful insight into at least the range of the likely long-term impacts and their costs. Obviously how reliable such predictions might be will depend on the quantity and quality of data avail-

able. For example, for the case studied here, clearly data spanning a longer time period and greater geographical area in the Caribbean would provide greater confidence in our results.

References

- Abegunde D., and A. Stanciole (2006) *An estimation of the economic impact of chronic noncommunicable disease in selected countries*. World Health Organization Department of Chronic Diseases and Health Promotion (CHP). <http://www.who.int/chp>
- Bell C., J. Parsons, T. J. Austin, A. C. Broderick, G. Ebanks-Petrie and B. J. Godley (2005), "Some of them came home: the Cayman Turtle Farm headstarting project for the green turtle *Chelonia mydas*", *Oryx*, 19(2), 137-148.
- Bird B., L. Branch, and D. Miller (2004), "Effects of coastal lighting on foraging behaviour of beach mice", *Conservation Biology*, 18, 1435-1439.
- Bustard H. (1967), "Mechanism of nocturnal emergence from the nest in green turtle hatchlings", *Nature*, 244-317.
- 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.
- Campbell C. (2003), *Population assessment and management needs of a green turtle, Chelonia mydas, population in the Western Caribbean*, Ph.D. Dissertation, University of Florida, Gainesville.
- Carr A., and M. Carr (1970), "Modulated reproductive periodicity in *Chelonia*", *Ecology*, 335-337.
- Carr A., M. Carr, and A. Meylan (1978), "The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony.", *Bulletin of the American Museum of Natural History*, 162, 1-146.
- Carr A., and L. Giovannoli (1957), "The ecology and migrations of sea turtles. 2. Results of field work in Costa Rica, 1955", *American Museum Novitates*, 1835, 1-32.
- Carr A., and L. Ogren (1959), "The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica", *American Museum Novitates*, 1958, 1-29.
- Clarke A. (2003), "Nonparametric model discrimination in international relations", *Journal of Conflict Resolution*, 47, 72-93.
- Clarke A. (2007), "A simple distribution-free test for nonnested model selection", *Political Analysis*, 15(3), 347-363.
- Conrad J. (1989), "Bioeconomics and the bowhead whale", *Journal of Political Economy*, 97(4), 974-987.
- Crouse D. (1999), "Population modelling and implications for Caribbean hawksbill sea turtle management", *Chelonian Conservation and Biology*, 3 (2), 185-188.
- Crouse D., L. Crowder, and H. Caswell (1987), "A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation", *Ecology*, 68 (5), 1412-1423.

- Crowder L., D. Crouse, S. Heppell, and T. Martin (1994), "Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Population", *Ecological Application*, 3 (4), 437-445.
- Cushing J. (2006), "Nonlinear Semelparous Leslie Models", *Mathematical Biosciences*, 1(3), 17-36.
- Czado C., V. Erhardt, A. Min, S. Wagner (2007), "Zero-inflated generalized Poisson models with regression effects on the mean, dispersion and zero-inflation level applied to patent outsourcing rates". *Statistical Modelling*, 7(2), 125-153.
- Delcroix E., F. Guiougou, S. Bedel, G. Santelli, A. Goyeau, L. Malglaive, T. Guthmuller, J. Boyer, S. Guilloux-Glorieux, F. Creantor, P. Malterre, F. Le Quellec, R. Dumont, Alain Saint-Auret, J. Coudret, J. Flereau, M. Valentin, G. Berry, P. De Proft, S. Mege, R. Rinaldi, F. Mazeas, B. Marcel, A. Fabregoul, and M. Girondot (2011), "Le programme Tortues marines Guadeloupe: bilan de 10 années de travail partenarial", *Bulletin de la Société Herpétologique de France*, 139-140, 21-35.
- DREG (Direction Régionale de l'Environnement de Guadeloupe) (2006), *Plan de Restauration des Tortues Marines des Antilles Françaises*, Ministère de l'Ecologie, du Développement et de l'Aménagement Durables, Direction régionale de l'environnement, Guadeloupe.
- Doi T., R. Marquez, H. Kimoto, and N. Azeno (1992), "Diagnosis and conservation of the hawksbill turtle population in the Cuban Archipelago", Technical Report: The Bekko Industries, Japan.
- Ehrenfeld D. (1968), "The role of vision in the sea-finding orientation of the green turtle (*Chelonia mydas*). II. Orientation mechanism and range of spectral sensitivity", *Animal Behaviour*, 16, 281-287.
- Ehrenfeld D., and A. Carr (1967), "The role of vision in the sea-finding orientation of the green turtle (*Chelonia mydas*)", *Animal Behaviour*, 15, 25-36.
- Evans D., S. Gudes, and W. Hogarth (2001), "Stock assessment of loggerhead and leather back sea turtles, and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the western north atlantic", *NOAA Technical Memorandum*, NMFS-SEFSC-455.
- Freeman A. (2003), *The Measurement of Environmental and Resource Values*. Resources for the Future, Washington D.C.
- Gaston K., J. Bennie, T. Davies and J. Hopkins (2013), "The ecological impacts of nighttime light pollution: a mechanistic appraisal", *Biological Reviews*, 88, 912-927.
- Hays G. (2000), "The Implications of Variable Remigration Intervals for the Assessment of Population Size in Marine Turtles", *Journal of Theoretical Biology*, 206, 221-227.
- Henderson J., A. Storeygard, and D. Weil (2012), "Measuring Economic Growth from Outer Space", *American Economic Review*, 102(2), 994-1028.
- Hendrickson J. (1958), "The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak", *Proceedings of the Zoological Society of London*, 130, 455-535.
- Heppell S., M. Snover, and L. Crowder (2003), "Sea Turtle Population Ecology", in Lutz P., J. Musick, and J. Wyneken, Eds, *The biology of sea turtles*, CRC marine science series, Boca Raton, Florida.
- Hill D. (2006), "The Dark Side of Night Lighting", *Sciences*, 312, 56.

- Hirth H. and D. Samson (1987), "Nesting behavior of green turtles (*Chelonia mydas*) at Tortuguero, Costa Rica", *Caribbean Journal of Science*, 23, 374-379.
- IUCN (International Union for Conservation of Nature) (2001), *IUCN Red List categories and criteria. Version 3.1*, IUCN Species Survival Commission, IUCN, Gland, Switzerland.
- Jackson J., M. Kirby, W. Berger, K. Bjorndal, L. Botsford, B. Bourque, R. Bradbury, R. Cooke, J. Erlandson, J. Estes, T. Hughes, S. Kidwell, C. Lange, H. Lenihan, J. Pandolfi, C. Peterson, R. Steneck, M. Tegner, R. Warner (2001), "Historical overfishing and the recent collapse of coastal ecosystems", *Science*, 293, 629-638.
- Jina J., A. Indabb, O. Nabangchang, T. Thuyd, D. Harderb, and R. Subadee (2010), "Valuing marine turtle conservation: A cross-country study in Asian cities", *Ecological Economics*, 69(10), 2020-2026.
- Jones N., K. Panagiotidou, I. Spilanis, K. Evangelinos, and P. Dimitrakopoulos (2011), "Visitors' perceptions on the management of an important nesting site for loggerhead sea turtle (*Caretta caretta* L.): The case of Rethymno coastal area in Greece", *Ocean and Coastal Management*, 54, 577-584.
- Johnson S., K. Bjorndal, and A. Bolten (1996), "Effects of organized turtle watches on loggerhead (*Caretta caretta*) nesting behavior and hatchling production in Florida", *Conservation Biology*, 10, 570-577.
- Kaska Y., E. Baskale, R. Urhan, Y. Katilmis, M. Gidis, F. Sari, D. Sozbilen, F. Canbolat, F. Yilmaz, M. Barlas, N. Ozdemir, and M. Ozkul (2003), "Natural and anthropogenic factors affecting the nest-site selection of Loggerhead Turtles, *Caretta caretta*, on Dalaman-Sarigerme beach in South-West Turkey", *Zoology in the Middle East*, 50, 47-58.
- Kyba C. and F. Holker (2013), "Do artificially illuminated skies affect biodiversity in nocturnal landscapes?", *Landscape Ecology*, 28(9), 1637-1640.
- Lefkovitch L. (1965), "The study of population growth in organisms grouped by stages", *Biometrics*, 21, 1-18.
- Leslie P. (1945), "On the use of matrices in certain population mathematics", *Biometrika*, 33, 183-212.
- Lorne K. and K. Salmon (2007), "Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the ocean", *Endangered Species Research*, 3, 23-30.
- Luck G. (2007), "A Review of the Relationships between Human Population Density and Biodiversity", *Biological Reviews*, 82, 607-645.
- Marquez M. (1990), *FAO species catalogue. Vol.11: Sea turtles of the world.*, FAO Fisheries Synopsis 125, FAO, Rome.
- Martinez L., A. Barragan, D. Garcia, N. Garcia, P. Huerta, and F. Vargas (2007), "Conservation and Biology of the Leatherback Turtle in the Mexican Pacific", *Chelonian Conservation and Biology*, 6 (1), 70-78.
- Myers R., B. Worm (2003), "Rapid worldwide depletion of predatory fish communities", *Nature*, 423, 280-283.
- Mazor T., N. Levin, H. Possingham, Y. Levy, D. Rocchini, A. Richardson, and S. Kark (2013), "Can satellite-based night lights be used for conservation? The case of nesting sea turtles in the Mediterranean", *Biological Conservation*, 159, 63-72.

- Mrosovsky N. and S. Shettleworth (1975), "On the orientation circle of the leatherback turtle, *Dermochelys coriacea*", *Animal Behaviour*, 23, 568-591.
- Navara K. and R. Nelson (2012), "The dark side of light at night: physiological, epidemiological, and ecological consequences", *Journal of Pineal Research*, 43, 215-224.
- Neville A., W. Webster, J. Gouveia, E. Hendricks, I. Hendricks, G. Marvin, and W. Marvin (1988), "The effects of nest temperature on hatchling emergence in the loggerhead sea turtle (*Caretta caretta*)", *Proceedings of the Eighth Annual Workshop on Sea Turtle Biology and Conservation*, 214, 71-73.
- Nicholas M. (2001), "Light Pollution and Marine Turtle Hatchlings: The Straw that Breaks the Camel's Back?", *The George Wright Forum*, 18, 77-82.
- Ohnson S., A. Bjorndal, and A. Bolten (1996), "Effects of organized turtle watches on loggerhead (*Caretta caretta*) nesting behavior and hatchling production in Florida". *Conservation Biology*, 10, 570-577.
- Peters A. and K. Verhoeven (1994), "Impact of Artificial Lighting on the Seaward Orientation of Hatchling Loggerhead Turtles", *Journal of Herpetology*, 28, 112-114.
- Polasky S., C. Costello, and A. Solow (2005), "The economics of biodiversity", in K.-G. Muller and J.R. Vincent, Eds, *Handbook of Environmental Economics*, Elsevier B.V., Amsterdam, The Netherlands.
- Raymond P. (1984), *Sea turtle hatchling disorientation and artificial beachfront lighting*, Center for Environmental Education, Washington, DC, USA.
- Rich C. and T. Longcore (2006), *Ecological Consequences of Artificial Night Lighting*, Islands Press, Washington DC, USA.
- Saba V., C. Stock, J. Spotila, F. Paladino, and P. Tomillo (2012), "Projected response of an endangered marine turtle population to climate change", *Nature Climate Change*, 2, 814-820.
- Santelli G., E. Delcroix, S. Bedel, J. Mailloux, A. Burgan, C. Arlaud, and C. Baboulene (2010), *Atlas des sites de pontes des tortues marines de l'archipel guadeloupéen - Années 2000 à 2008*, Rapport technique Réseau Tortues Marines Guadeloupe, Kap'Natirel et Office National de la Chasse et de la Faune Sauvage.
- SWOT (2006), *SWOT Report - State of the World's Sea Turtles, vol. I and II*, OBIS-SEAMAP.
- SWOT (2008), *SWOT Report - State of the World's Sea Turtles, vol. III*, OBIS-SEAMAP.
- SWOT (2009), *SWOT Report - State of the World's Sea Turtles, vol. IV*, OBIS-SEAMAP.
- Troeng S. and M. Chaloupka (2007), "Variation in adult annual survival probability and remigration intervals of sea turtles", *Marine Biology*, 151, 1721-1730.
- Troeng S. and C. Drews (2004), *Money Talks: Economic Aspects of Marine Turtle Use and Conservation*, WWF-International, Gland, Switzerland, www.panda.org
- Tuxbury S. and M. Salmon (2005), "Competitive interactions between artificial lighting and natural cues during sea finding by hatchling marine turtles", *Biological Conservation*, 121, 311-316.
- USC (University of Southern California) (2008), "Light Pollution Offers New Global Measure Of Coral Reef Health", *ScienceDaily*, 26.

- 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.
- Webb G., C. Manolis, and M. Gray (2008), *Captive Breeding and Marketing of Turtles*, Australian Government Rural Industries Research and Development Corporation, RIRDC Publication 08/012, Kingston, Australia.
- Witherington B. (1992), “Behavioral responses of nesting sea turtles to artificial lighting”, *Herpetologica*, 48, 31-39.
- Witherington B., K. Bjorndal, and C. McCabe (1990), “Temporal pattern of nocturnal emergence of loggerhead turtle hatchlings from natural nests”, *Copeia*, 1990(4), 1165-1168.
- Witherington B. and N. Frazer (2003), “Social and Economic Aspects of Sea Turtle Conservation”, in P. Lutz, J. Musick, and J. Wyneken, Eds, *The Biology of Sea Turtles*, CRC marine science series, Boca Raton, Florida.
- Witherington B. and R. Martin (1996), “Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches”, *Florida Marine Research Institute Technical Report*, TR-2.
- Wikan A. (2012), “On Nonlinear Age- and Stage-Structured Population Models”, *Journal of Mathematics and Statistics*, 8(2), 311-322.
- Worth D. and J. Smith (1976), “Marine turtle nesting on Hutchinson Island, Florida, in 1973”, *Florida Marine Research Publication*, 18, 1-17.

Appendices

A Tables

Table A.1: Descriptive statistics

Variable	Mean	Standard deviation	Min.	Max.
Nests: <i>total</i>	26.72	70.42	0	394
Nests: <i>hawksbill</i>	15.76	51.65	0	392
Nests: <i>green</i>	10.03	45.43	0	358
Nests: <i>leatherback</i>	0.93	2.57	0	12
Nightlights	10.62	8.72	0	41.50
Effort	0.04	0.03	0.01	0.14
Roads	0.45	0.50	0	1
Marinas	25.71	52.04	0	224
Hotels	23.72	109.09	0	688
Distance to port	25.12	14.45	2.22	57.58

Table A.2: Robustness checks: spatial spillovers

	(5Km)	(10Km)
Nightlights	-0.0735 (-0.1281, -0.0259)	-0.0768 (-0.1152, -0.0192)
Effort	24.8148 (17.7977, 30.9772)	19.2240 (5.9266, 28.6271)
Roads	0.2760 (0.0000, 0.4103)	-0.8292 (-1.8791, 0.4407)
Neighboring roads	-0.2307 (-0.3269, 0.0000)	3.7197 (-0.2053, 7.8509)
Marinas	-0.0274 (-0.0293, -0.0097)	-0.0269 (-0.0440, -0.0034)
Neighboring marinas	0.0015 (-0.0003, 0.0023)	-0.0032 (-0.0058, 0.0000)
Hotels	-0.0019 (-0.0023, -0.0010)	-0.0015 (-0.0026, -0.0005)
Neighboring hotels	-0.0001 (-0.0001, 0.0000)	-0.0001 (-0.0002, 0.0000)
Distance to port	0.0000 (0.0000, 0.0000)	-0.0004 (-0.0012, 0.0000)
Distance to neighboring port	0.4271 (0.0000, 0.6488)	0.0088 (-0.0128, 0.0441)
Average nightlights	-0.0012 (-0.0018, -0.0000)	0.0031 (0.0000, 0.0064)
Spatial parameter	4.2332 (1.4054, 8.8414)	2.8201 (0.1997, 6.7729)
Constant	4.8870 (2.9939, 5.8284)	5.6342 (2.7403, 7.6911)
Observations	67	67
Clarke test:		
ZIP	0.0809	0.0005
no decision	0.1394	0.1329
ZIGP	0.7587	0.8536

Notes: (1) Column 1 refers to when neighboring is defined as between 1-5 km and column 2 to 1-10 km; (2) The 5th and 95th confidence interval are given in parentheses; (3) The Clarke test reports the proportion of decisions in favour of each model.

B Replacement cost

We present here the information which we use in Section 6 to build Table 3:

1. *Ferme Corail (Reunion)*: assuming the age of maturity at 15 years, they estimate that the cost of raising one green turtle amounts to US\$1672. This figure would imply 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 per turtle of US\$132 during the first year, and US\$658 per month for each subsequent years (Troeng and Drews, 2004).
3. *WMI Research facility*: they ran a prototype pen for captive breeding of farm-raised for 18 adult hawksbill turtles over 18 months and found that the total cost of running this was about US\$34285, which comes to about US\$1203 per turtle per year (Webb *et al.*, 2008).
4. *Cayman Turtle Farm*: this farm is specialized in green sea turtles. From a personal communication with Walter Mustin, Ph.D., Chief Research Officer of Cayman Turtle Farm, we obtained the following production cost estimates per turtle and year:

Table A.3: Annual production cost per turtle (US\$)

Item	Cost/turtle/year
Energy	106
Salaries and wages	56
Feed	53
Repairs & Maintenance	25
Security	13
Depreciation	13
Chemicals	6
Waste removal	4
Other	3
Total	279

C Stage-based life tables

Crouse (1999) provides the following table for the hawksbill sea turtle:

Table A.4: Hawksbill sea turtle

Stage	Description	Stage duration (d_i)	Annual survival (σ_i)	Annual fecundity (F_i)
1	Eggs/hatchlings	1	0.6747	0
2	Small juveniles	7	0.75	0
3	Large juveniles	8	0.6758	0
4	Subadults	6	0.7425	0
5	Adults	>32	0.8091	76.5

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

Table A.5: Green sea turtle

Stage	Description	Stage duration (d_i)	Annual survival (σ_i)	Annual fecundity (F_i)
1	Eggs/Hatchlings	1	0.8	0
2	Small juveniles	14	0.8	0
3	Large juveniles	15	0.76	0
4	Subadults	1	0.76	26.4
5	Adults	>32	0.89	26.4

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

Table A.6: Leatherback sea turtle

Stage	Description	Stage duration (d_i)	Annual survival (σ_i)	Annual fecundity (F_i)
1	Eggs/Hatchlings	1	0.6747	0
2	Small juveniles	7	0.727	0
3	Large juveniles	7	0.78	0
4	Subadults	6	0.78	0
5	Adults	>32	0.78	91

D Dynamic results

Table A.7: Eigenvalues

		λ_1	λ_2	λ_3	λ_4	λ_5
Hawksbill:	<i>no light</i>	0.9281	$0.7318+0.2037i$	$0.7318-0.2037i$	0.4744	0.006
	<i>light</i>	0.8982	$0.7271+0.1685i$	$0.7271-0.1685i$	0.5168	0.0029
Green:	<i>no light</i>	0.921	$0.7569+0.0717i$	$0.7569-0.0717i$	-0.014	0.0132
	<i>light</i>	0.9124	$0.7611+0.0593i$	$0.7611-0.0593i$	-0.0113	0.0107
Leatherback:	<i>no light</i>	1.0107	$0.7578+0.2908i$	$0.7578-0.2908i$	0.3726	0.0243
	<i>light</i>	0.9725	$0.7511+0.2494i$	$0.7511-0.2494i$	0.4365	0.012

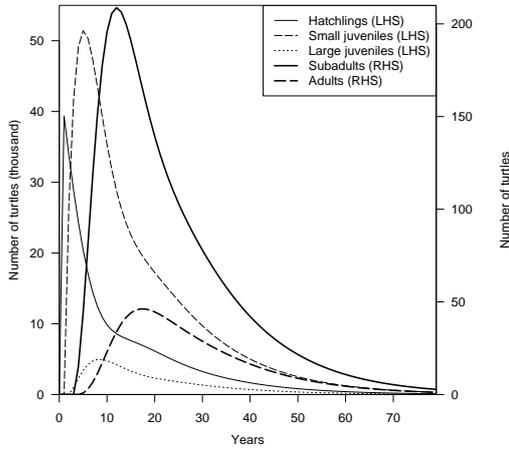
Table A.8: Coordinates of eigenvector v_{λ_1} corresponding to λ_1

		$v_{\lambda_{11}}$	$v_{\lambda_{12}}$	$v_{\lambda_{13}}$	$v_{\lambda_{14}}$	$v_{\lambda_{15}}$
Hawksbill:	<i>no light</i>	0.3028	0.9432	0.1360	0.0084	0.0037
	<i>light</i>	0.2635	0.9521	0.1546	0.0110	0.0064
Green:	<i>no light</i>	0.1604	0.9855	0.055	0.0002	0.0054
	<i>light</i>	0.1500	0.9870	0.0581	0.0003	0.0077
Leatherback:	<i>no light</i>	0.4223	0.9	0.1064	0.0169	0.0047
	<i>light</i>	0.3783	0.9168	0.1257	0.0230	0.0076

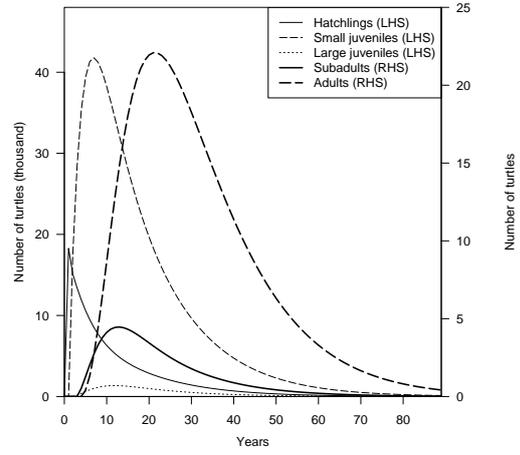
Table A.9: Long-run stage distribution (%)

Stage	Description		Hawksbill	Green	Leatherback
1	Eggs/hatchlings	<i>no light</i>	21.72	13.29	29.12
		<i>light</i>	18.99	12.47	26.06
2	Small juveniles	<i>no light</i>	67.65	81.69	62.06
		<i>light</i>	68.62	82.05	63.17
3	Large juveniles	<i>no light</i>	9.76	4.56	7.34
		<i>light</i>	11.14	4.83	8.66
4	Subadults	<i>no light</i>	0.61	0.019	1.17
		<i>light</i>	0.79	0.021	1.58
5	Adults	<i>no light</i>	0.26	0.44	0.32
		<i>light</i>	0.43	0.46	0.64

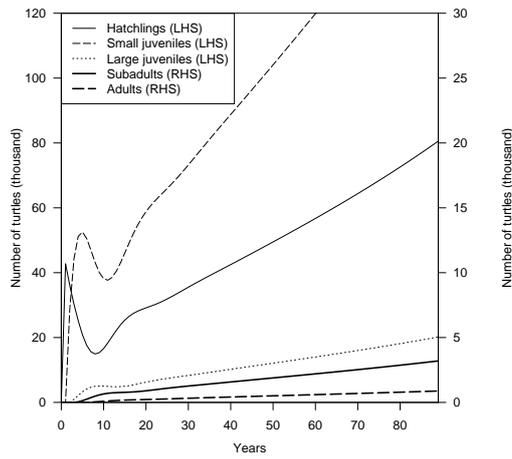
Figure A.1: Population difference per stage



(a) hawksbill

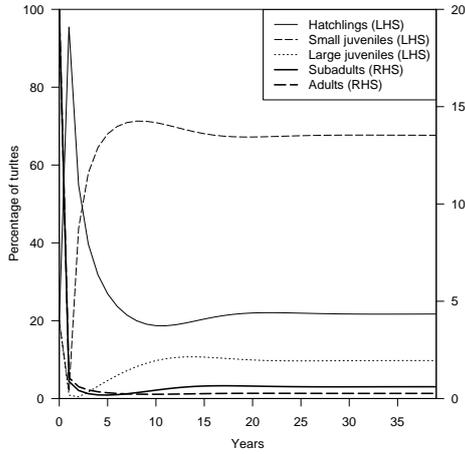


(b) green

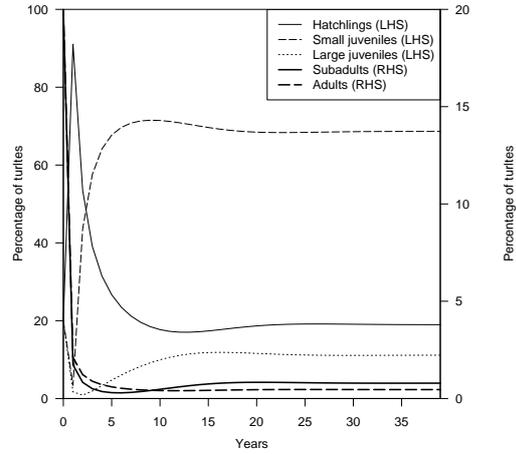


(c) leatherback

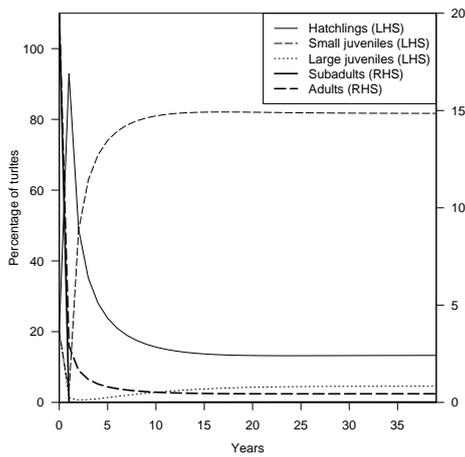
Figure A.2: Stage distribution



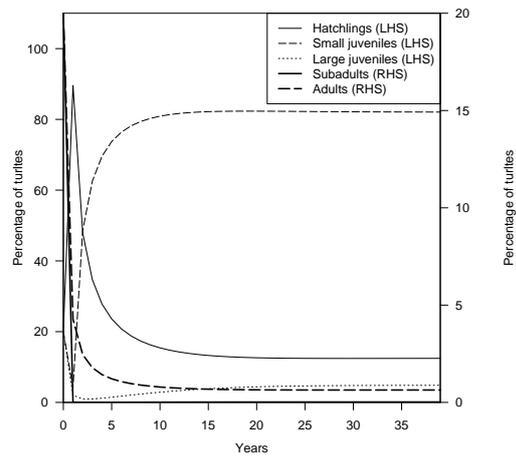
(a) hawksbill – no nightlights



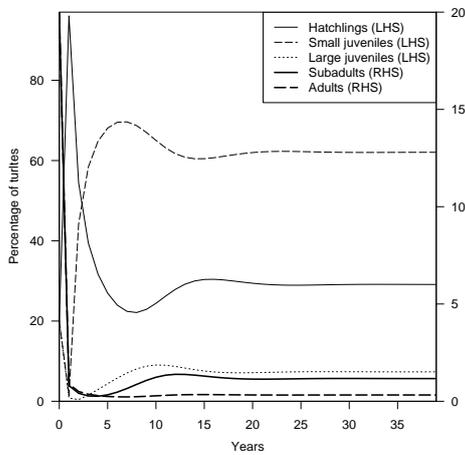
(b) hawksbill – nightlights



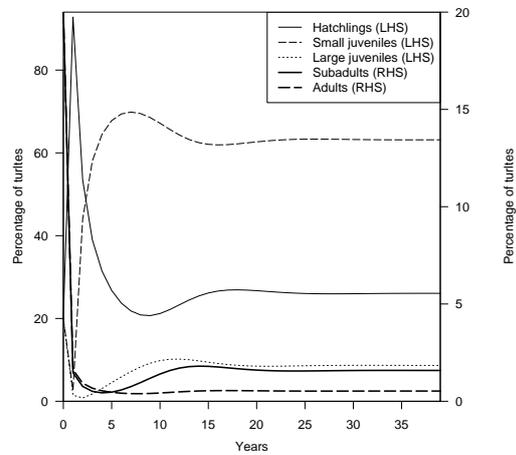
(c) green – no nightlights



(d) green – nightlights



(e) leatherback – no nightlights



(f) leatherback – nightlights