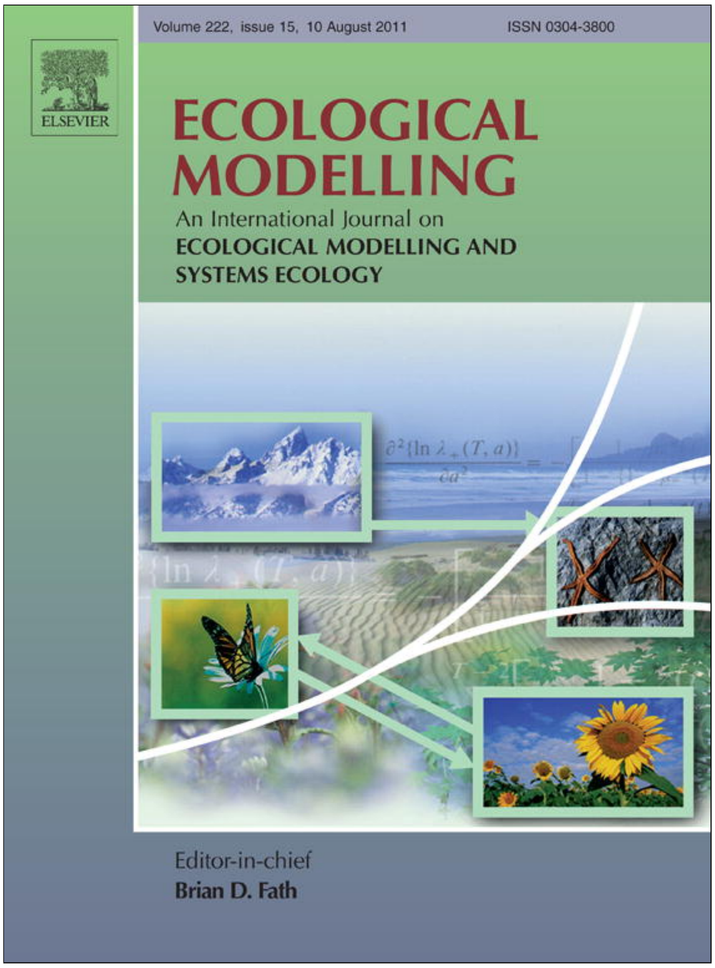
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Modelling the responses of wildlife to human disturbance: An evaluation of alternative management scenarios for black-crowned night-herons

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ABSTRACT

The impact of anthropogenic disturbance on wildlife is increasing becoming a source of concern as the popularity of outdoor recreation rises. There is now more pressure on site managers to simultaneously ensure the continued persistence of wildlife and provide recreational opportunities. Using 'Simulation of Disturbance Activities', a model designed to investigate the impact of recreational disturbance on wildlife, we demonstrate how a simulation modelling approach can effectively inform such management decisions. As an example, we explored the implications of various design and management options for a proposed recreational area containing a historic breeding bird colony. By manipulating the proximity, orientation and intensity of recreation, we were able to evaluate the impact of recreational activities on the behaviour of black-crowned night-heron nestlings (*Nycticorax nycticorax*). Using a classification and regression tree (CART) procedure to analyse simulation output, we explored the dynamics of multiple strategies in concert. Our analysis revealed that there are inherent advantages in implementing multiple strategies as opposed to any single strategy. Nestlings were not disturbed by recreation when bird-watching facility placement (proximity and orientation) and type were considered in combination. In comparison, proximity alone only led to a <10% reduction in disturbance. Thus we demonstrate how simulation models based on customised empirical data can bridge the gap between field studies and active management, enabling users to test novel management scenarios that are otherwise logistically difficult. Furthermore, such models potentially have broad application in understanding human-wildlife interactions (e.g. exploring the implications of roads on wildlife, probability of bird strikes around airports, etc.). They therefore represent a valuable decision-making tool in the ecological design of urban infrastructures.

1. Introduction

Minimising the disruption caused by eco-tourism and outdoor recreation to wildlife is becoming increasingly important in the 'in situ' preservation of many species globally (Boyle and Samson, 1985; Giannecchini and Ecotourism:, 1993; Reed and Merenlender, 2008). Hence, there is a pressing need for conservation biologists, wildlife ecologists, land use planners and site managers to make active management decisions that address the trade-offs between recreation and species of concern (Beale and Monoghan, 2004). Ensuring the continued persistence of a species or wildlife community without limiting an area's recreational opportunities often requires targeted site-specific management and design (Knight and Temple, 1995; Fernández-Juricic et al., 2001). How effective management strategies are depends on the sensitivity of a species, or even an individual, to anthropogenic disturbance (Gutzwiller et al., 1998; Frid and Dill, 2002; Webb and Blumstein, 2005). Currently, management decisions are mostly based on the results of empirical studies (Ellenberg et al., 2006; Beale, 2007), the evaluations of current management practices (Holmes et al., 2005; Fernández-Juricic et al., 2005), and the expertise of professionals (Peterson et al., 2003; Blanc et al., 2006; Gill, 2007). One dilemma of conservation biology is that managers often are required to make management decisions intended to benefit a species (crisis management) even when the quality and quantity of available empirical data is limited (Soulé, 1986). Empirical studies, for example, can be hindered by a number of constraints, such as time, budget and logistics. Moreover, when dealing with a species of concern investi-

Abbreviations: SODA, simulation of disturbance activities; ROC, receiver operating characteristic.

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gators may not have the option to undertake studies that may have detrimental implications, so empirical data may not available. Thus, rigorous a priori evaluation of management strategies using available data and the application of simulation models is proving to be very useful approach to investigating and predicting the effects of disturbance on wildlife (Haag and Kaupenjohann, 2001; Beissinger et al., 2006; Beale, 2007). While a number of simulation models have been used to guide practical management, none appear to have application beyond the study system they were developed for (see review in Bennett et al., 2009). Simulation of Disturbance Activities (referred to as SODA here after; Bennett et al., 2009), a spatially explicit individual-based model, is one of the first models with the flexibility to be applied to a broad range of species (or groups of species) across a variety of ecological circumstances and management challenges (Ellenberg et al., 2006). This flexibility has further advantages as it can be used to explore novel strategies (Gill et al., 2001), and infer the implications of applying long-term (Knight and Temple, 1995; Guillemain et al., 2007; Sutherland, 2007) and/or multiple management strategies at a site (Taylor and Knight, 2003; Blanc et al., 2006; Reed and Merenlender, 2008).

In this manuscript, we applied SODA to an example case study for which empirical investigations were specifically designed and conducted to parameterise the model (Fernández-Juricic et al., 2007). We demonstrate that combining a modelling simulation with targeted field surveys can be a logistically feasible and effective method of exploring the impacts of various management strategies on wildlife.

2. Model system

2.1. Species of concern

Our model system was a nesting colony of black-crowned night-herons (*Nycticorax nycticorax*). Despite its widespread distribution in the USA, many regional populations of black-crowned night-herons are declining due to habitat loss and disturbance leading to the abandonment of historic breeding colonies (Dahl and Wetlands, 1990; Sauer et al., 2005; PGC, 2006). Hence, it has been declared a species of conservation concern in a number of states, including Illinois and Pennsylvania. The preservation of nesting colonies where they occur has subsequently become a management priority (PGC, 2006; INRIN, 2007).

During the day, adult night-herons do not tend to the nestlings but instead roost in trees and shrubs surrounding the nesting colony. Exposed and unable to move from the nest, the nestlings are therefore vulnerable to recreational disturbance. Fernández-Juricic et al. (2007) confirmed that nestlings exhibited a series of disturbance-related behaviours in the presence of recreationists. The degree to which nestlings responded was related to the type and behaviour of recreationists. For example, nestlings spent more time freezing when pedestrians were inquisitive rather than walking by without stopping. Frequent displays of disturbance-related behaviour can potentially lead to exhaustion, raised stress levels and increased parasite loads (Bonier et al., 2007; Cyr & Romero, 2007; French et al., 2010; Thiel et al., 2011). Each of these outcomes risks chick mortality, nest failure and ultimately reduced breeding success (Bouton et al., 2005; Bonier et al., 2009).

2.2. Study site

For our case study, a wetland remnant historically used by a colony of black-crowned night herons in Illinois has been selected as part of a wetland rehabilitation program to be developed into a nature reserve (CoC, 1998; CDOE, 2002; Levengood et al., 2005). The site is to be (1) preserved and enhanced primarily for the black-crowned night-heron, and (2) developed to encourage wildlife-oriented, non-consumptive recreation (CDOE, 2002; CDOPD, 2002). Preliminary plans focused on providing appropriate pathways and facilities that promoted bird-watching, such as viewing platforms. However, the location of these pathways and facilities within the site could have implications for black-crowned night-heron nestlings (Tremblay and Ellison, 1979; Parsons and Burger, 1982). Comprising an area of 0.59 km^2, Indian Ridge Marsh is one of five remnant wetland sites (currently brown field sites with no official public access) that form a nearly contiguous area (a total of 4.5 km^2) selected for ecological rehabilitation (CDOE, 2002; Angold et al., 2006).

Indian Ridge Marsh is a long, narrow rectangle of land and water bordered on all sides by roads, a railway line and industrial development (Fig. 1). The black-crowned night-herons have been nesting annually at the site since 1993 (Levengood et al., 2005). Originally this area comprised mixed wetland and sand prairie lying just beyond the eastern shoreline of Lake Calumet. Currently, habitat types include open water wetland pools (connected to the Calumet River), marsh and scrubland that host a number of bird species of local ecological value (such as little blue heron (*Egretta caerulea*) and least bittern (*Ixobrychus exilis*); CDOE, 2002). The open water habitat consists of several wetland pools connected to the Calumet River. Since the influx of surface and groundwaters containing large amounts of road salt, organic nutrients and other industrial materials, altered hydrology (due to damming and reversed flow of the Calumet River) and the invasion of non-native plant species, water quality on the site has become degraded (Roadcap et al., 1999). As part of its restoration, the hydrology and water quality of the area is to be improved and thereafter maintained in order to increase overall habitat quality for wildlife.

3. Materials and methods

3.1. Model overview

SODA is a non-species specific spatially explicit individual-based model for exploring the effects of spatial and temporal patterns of anthropogenic disturbance on wildlife (Bennett et al., 2009). It is designed explicitly to investigate the fate of individual animals under a user-defined disturbance regime (Bennett et al., 2009). By modifying the environmental, recreational and wildlife characteristics that comprise a regime, such as the frequency of visitors to a site, we can (a) evaluate novel management scenarios, (b) forecast the outcome of multiple management options in concert (c) prioritise management for minimising disturbance, (d) identify further data and research needs, and (e) improve scientific understanding. The state variables and parameters used to build a simulation define a specific disturbance regime (existing or hypothetical) within which wildlife individuals may exist. More explicitly, a user can shape any aspect of the environment (landscape topology, etc.), the anthropogenic activities that occur (including the type, density, and frequency of activities, both spatially and temporally) and the ecological, biological and behavioural characteristics that describe individual animals. Using SODA allows us to evaluate the outcome of a diverse array of possible scenarios, including novel management strategies and proposed site designs. Fig. 2 provides a conceptual delineation of the variables and parameters used to define model structure. A full model description is provided in Bennett et al. (2009). In the following sections, we do not discuss the mechanics of the model. Instead, we focus on the scenario development.

3.2. Scenarios

To explore the effectiveness of alternative, novel and multiple management strategies available to managers at the Indian Ridge

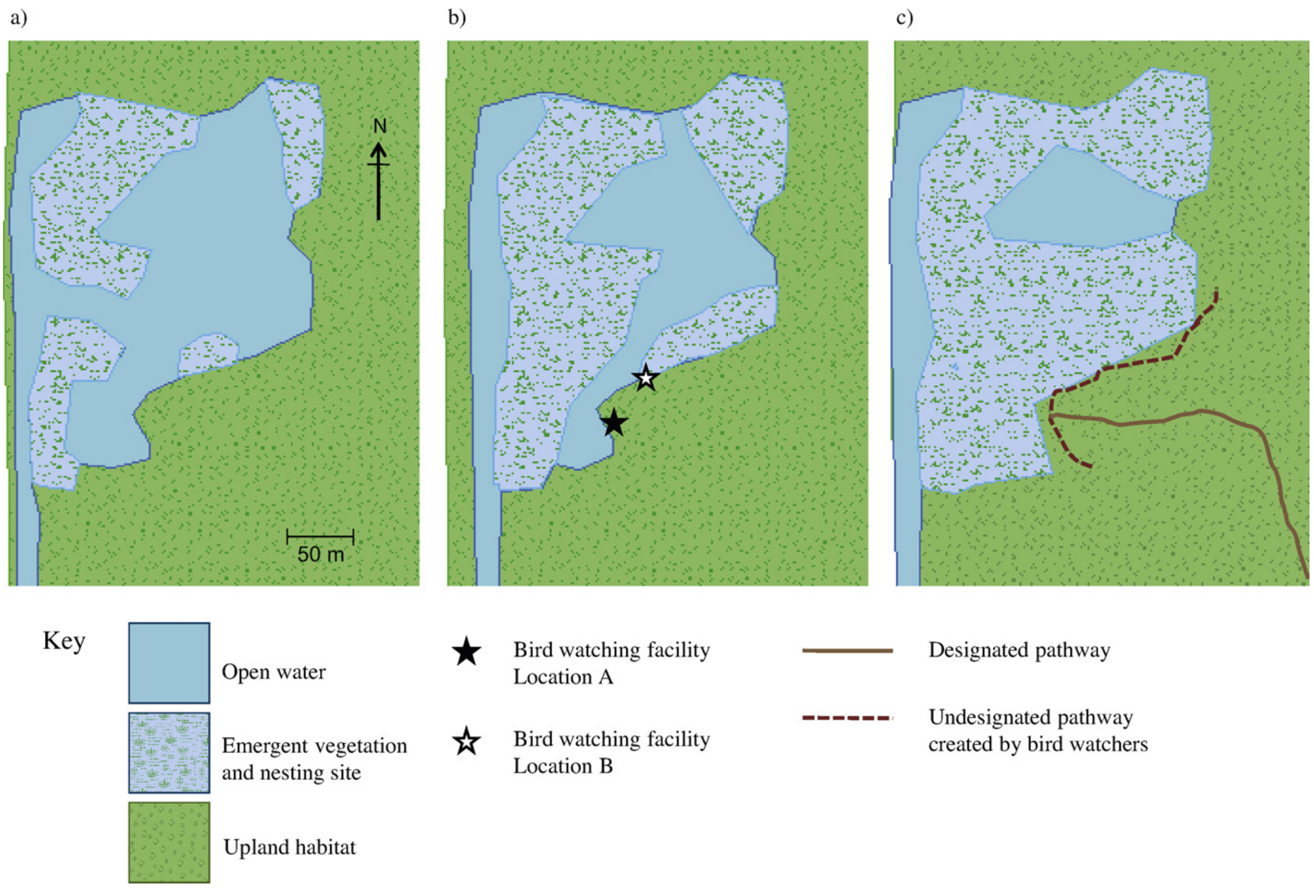

Fig. 1. Map of Indian Ridge March in the Calumet Region of Illinois, USA, delineating its habitat types when water levels are (a) high, (b) intermediate and (c) low. Also shown are the locations of a designated pathway to the nesting site, an undesignated pathway used by bird-watchers and the two proposed positions for the bird-watching facilities. This maps represent the GIS shape files used to parameterise 'Simulation of Disturbance Activities' model to explore anthropogenic disturbance on black-crown night-heron nestlings at Indian Ridge Marsh.

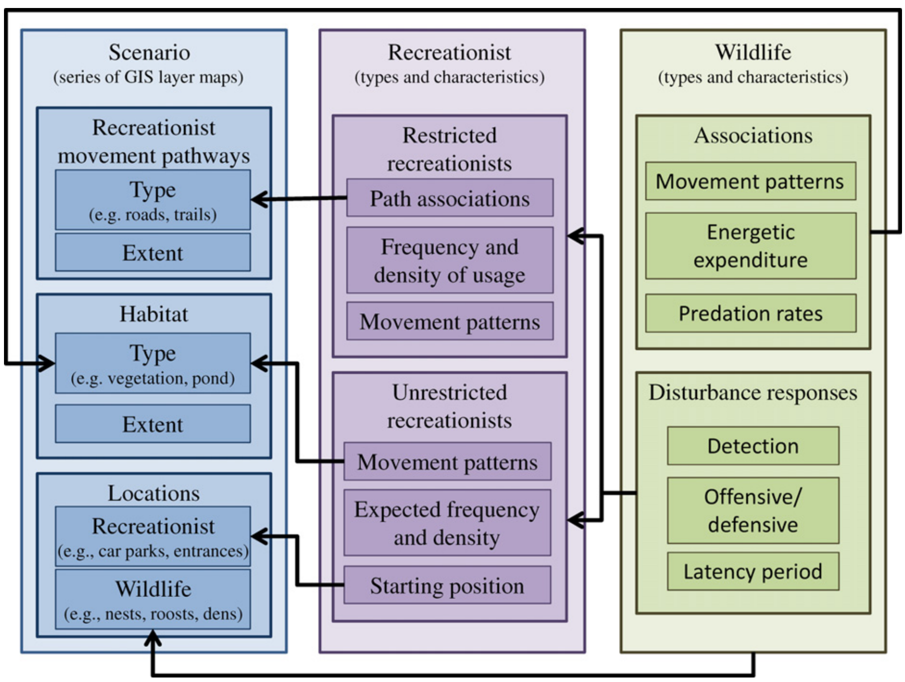

Fig. 2. Conceptual delineation of the variables and parameters used to define the 'Simulation of Disturbance Activities' model. The three main categories depicted (Scenario, Anthropogenic and Wildlife) define site lay-out, virtual recreationist activity patterns and virtual wildlife individuals respectively. Arrows indicate where parameters are influenced or associated with variables from other categories.

Table 1
Spatial and temporal environmental data used to parameterise 'Simulation of Disturbance Activities' model to explore anthropogenic disturbance on black-crown night-heron nestlings at Indian Ridge Marsh in Illinois, USA.

Temporal scales			
Length of simulation e.g., year, season or activity period	30 days		
User specified timestep length	5 min		
Spatial scale			
User specified unit	m		
Environmental characteristics			
Habitat patches			
Type	Open water	Emergent vegetation	Upland habitat
Location and size	Site equivalent	Hydrological option (a) High (b) Intermediate (c) Low	Site equivalent
Paths	Consistent throughout: 1 designated path in the direction of the nesting colony.	Scenario dependent: 1 undesignated path created by bird watchers along shoreline.	

Marsh site, we constructed 60 different management-orientated scenarios (listed in Appendix A). The set of parameters and state variables used to build each of these scenarios are provided in Tables 1–3 and discussed below.

We also conducted a sensitivity analysis (Saltelli et al., 2004, 2006). This analysis allowed us to assess how the outcome of our simulations were influenced by the parameters we used to describe the virtual nestlings responses to recreationists (discussed in detail below). We identified three response levels and ran all 60 management scenarios at each level. A total of 180 scenarios were therefore built. Finally, each scenario was replicated five times using an alternative random number seed to account for stochastic variance. We therefore conducted a total of 900 simulation runs.

3.2.1. Environment

Three general habitat types were included in the simulations: (1) open water, (2) patches of emergent vegetation, primarily giant (common) reed (*Phragmites australis*) where the birds commonly nest (Levengood et al., 2005), and (3) upland habitat types, which are not utilised by the heron nestlings. As a brown-field site, Indian Ridge Marsh has been subject to annual fluctuations in its water levels (Roadcap et al., 1999). Monitoring surveys of the black-crown night-heron colony undertaken since 1993 have revealed that where there is suitable emergent vegetation the birds will nest (Levengood per comm.). As water levels can vary depending on the hydrological option selected for the site (Roadcap et al., 1999), the amount of emergent vegetation (which thrives in shallow water) can be manipulated. By regulating the water levels and thus vegetation, a buffer zone can be generated that maintains the proximity of nestlings from upland habitat (Levengood per comm.) and therefore recreationists. The effects of three hydrological scenarios observed in the existing system (Roadcap et al., 1999) were simulated to evaluate which option minimised wildlife-human interactions (Fig. 1). These included; (1) water levels at their upper limits (HIGH), (2) water levels at their lowest limits (LOW), and (3) an intermediate of these water level extremes (INT). Thus we created three maps (more specifically a series of map layers) depicting these three water levels and the resulting positions of nest sites in ArcGIS (version 9.3; ESRI, Redlands CA; Fig. 1 and Table 2). To create these maps we used aerial photographs and maps of Indian Ridge Marsh provided by Illinois State Water Survey. Note that GIS map layers are used to build the parameter space in SODA (Bennett et al., 2009).

In preliminary plans for Indian Ridge Marsh, a bird-watching facility was proposed to provide viewing opportunities. Two potentially suitable locations for this facility were identified. We used SODA to compare the reactions of nestlings to recreationists at these locations. As a control we included two scenarios in which no facilities were provided (Burger et al., 2004); (1) where bird watchers walked along the shoreline adjacent to the nesting colony (Boyle and Samson, 1985; Sekercioglu, 2002), and (2) where all recreationists were restricted to a main pathway that did not approach the shore. Based on these alternative options, four GIS layers were created with (1) the main pathway leading to a facility directly in front of the core nesting colony (Location 'A'; Fig. 1a), (2) the main pathway leading to a facility positioned to the north of the core nesting colony (Location 'B'; Fig, 1b), (3) a main pathway alone (RES) and (4) a pathway that runs up to and along the shoreline (UNRES; Fig. 1c).

For the black-crowned night-heron case study simulation length was established to be the nestling life-history stage. This stage was determined to be approximately 30 days (Table 1). To ensure that this runtime would yield relatively realistic levels of variation we conducted a series of pilot simulation runs in which we varied runtime. We established that the stochastic variation generated over 30 days reached an asymptote. This asymptote confirmed that we could run all simulations conducted in this case study across a timeframe equivalent to the nestling period.

Table 2
Recreationist data used to parameterise 'Simulation of Disturbance Activities' model to explore anthropogenic disturbance on black-crown night-heron nestlings at Indian Ridge Marsh in Illinois, USA.

Type	Stroller	Jogger	Bird-watcher	School group
Timestep distance	300 m/TS	600 m/TS	225 m/TS	400 m/TS
Persistence	6 TS	2 TS	12 TS	6 TS
Density	1/TS	½/TS	2/TS	1/day
Frequency				
Daily activity patterns	10am–6pm	7am–10am 4pm–6pm	6am–9am 5pm–8pm	2pm–3pm
Associations	All recreationists are associated with main designated path Bird-watchers are associated with undesignated pathway All recreationists except walkers are associated with birding facilities			

Table 3
Wildlife data used to parameterise 'Simulation of Disturbance Activities' model to explore anthropogenic disturbance on black-crown night-heron nestlings at Indian Ridge Marsh in Illinois, USA. Values in bold indicate baseline values derived from empirical data. SEN represents SENSITIVE disturbance parameters, AVE represents AVERAGE and TOL represents TOLERANT.

	Hydrological option											
Number of nestlings	(a) Low water levels 101				(b) Intermediate water levels 137				(c) High water levels 159			
Natural behavioural modes *Sleeping and grooming*	Time spent per day 14 h								Daily activity pattern 6:00am to 8:00pm			
Behavioural responses to disturbance	Bird-watching facility option: Observation tower			Emergent platform without cover			Emergent platform with cover			Bird hide		
	SEN	AVE	TOL	SEN	AVE	TOL	SEN	AVE	TOL	SEN	AVE	TOL
Alert												
Detection distance												
Stroller	50 m	60 m	70 m	45 m	**55 m**	65 m	40 m	50 m	60 m	30 m	40 m	50 m
Jogger	73 m	83 m	93 m	68 m	**78 m**	88 m	63 m	73 m	83 m	53 m	63 m	73 m
Bird-watcher	71 m	81 m	91 m	66 m	**76 m**	86 m	61 m	71 m	81 m	54 m	64 m	74 m
School group	72 m	82 m	92 m	67 m	**77 m**	87 m	62 m	72 m	82 m	52 m	62 m	72 m
Fleeing												
Flight initiation distance												
Bird-watcher	27 m	37 m	47 m	22 m	**32 m**	42 m	17 m	27 m	37 m	7 m	17 m	27 m
School group	28 m	38 m	48 m	23 m	**33 m**	43 m	18 m	28 m	38 m	8 m	18 m	28 m
Latent												
Time spent latent	2 TS											
Habitat multipliers												
Crossing probability	0%			Nestlings only use the emergent vegetation habitat.								

3.2.2. Recreation

Plans for Indian Ridge Marsh outline that the area be designed to encourage passive recreation, such as bird-watching, hiking and environmental education (CODE, 2002). We identified four types of recreationist expected to visit the site. These included joggers (recreationists frequenting the main pathway only for exercise), strollers (relatively slow-paced recreationists using both the main pathway and bird-watching facilities where applicable), bird watchers (inquisitive recreationists who remain in the facilities or move along the shoreline pathway for extended periods) and school groups (inquisitive recreationists that use both the main pathway and birding facilities where applicable). With the exception of school groups, we considered that these recreationists would visit the site regularly (Table 2); thus the parameters describing their daily frequencies and densities were not varied among our scenarios. In contrast, we generated scenarios with (PRES) and without (ABS) school groups. These scenarios address concerns that the presence of local school groups, however infrequent, would have a detrimental impact on the nestlings (see Knight and Temple, 1995; Martín et al., 2004; Geist et al., 2005).

During the design process, managers also needed to make a decision on the type of the bird-watching facility to include at the site (Sekercioglu, 2002; Guillemain et al., 2007). Four potential designs were identified, including (1) a 6 m high tower with platform (OBS), (2) a 1 m high elevated platform without vegetation cover (PEV), (3) a 1 m high elevated platform with surrounding vegetation cover (PIV) and (4) a bird hide (a closed cabin at ground level; HID). Experts acknowledge that more concealed bird-watching structures reduce recreational disturbance (Dunning personal communication). While no studies to date have confirmed this specifically, a few studies have shown that visually and/or audibly screening recreationists from wildlife is an effective form of disturbance management (Knight and Temple, 1995; Phillips et al., 2001). We thus used SODA to hypothetically evaluate the implications of facility design at Indian Ridge Marsh. We assigned a set of disturbance parameters for each facility based on (1) the range of nestling responses recorded by Fernández-Juricic et al. (2007), (2) the patterns of disturbance reported among similar management strategies in practice (Phillips et al., 2001; Ikuta and Blumstein, 2003; Martín et al., 2004), and (3) expert opinion (Table 3).

3.2.3. Wildlife

Previous studies have shown that nestlings diverge from their natural behaviour (such as sleeping and grooming) in the presence of recreationists and exhibit various disturbance-related behaviour, including freezing (when the nestlings become aware of a recreationist), displaying agitation (when a recreationist is perceived as being too close) and scanning (after a recreationist has moved away; Parsons and Burger, 1982; Fernández-Juricic et al., 2007). These disturbance responses occur in succession and can be simulated in SODA using the ALERT, FLEEING and LATENT behavioural modes (Bennett et al., 2009).We also determined from the empirical data that (1) the responses of nestlings to different types of recreation varied, (2) the occurrence of responses depended on the distance of the recreationist from the nestlings, (3) the severity of the responses to the recreationists did not vary with distance, (4) recreationist group size had no influence and (5) the responses of nestlings to the types of management proposed would not vary when multiple options were implemented (Fernández-Juricic et al., 2007). Thus from the empirical data we established disturbance parameters for each nestling response brought about by each type of recreationist. We regressed nestling response distances against time spent exhibiting each response behaviour for each recreationist type (Appendix B). We also calculated the mean responses of nestlings in the absence of recreationists. Using the point of interception between the regression and means, we defined a set of disturbance parameters (hereafter referred to as AVERAGE) that were applied to our 60 original scenarios (Table 3).

For the sensitivity analysis, we created two additional sets of disturbance parameters. These were based on the response distances and times of nestlings at the upper 95% confidence limit of our regressions (i.e. representing the most sensitive individuals; hereafter referred to as SENSITIVE), and the lower 95% confidence limit (i.e. the responses of tolerant nestlings; hereafter referred to as TOLERANT; Table 3).

3.3. Analyses

For the sensitivity analysis, we used multivariate analysis of variance (MANOVA) to establish whether the three alternative sets of disturbance parameters significantly influenced the outcome of our simulations. This statistical analysis was computed using PROC GLM in SAS (1988). The dependant variable was identified as the total number of timesteps nestlings exhibited each disturbance-related behaviour (ALERT, FLEEING and LATENT), in each scenario output. We used a %MULTINORM in SAS to confirm that the variables demonstrated multivariate normality as required by the MANOVA and all *P* values used were conservative (0.05). The independent variables comprised the three disturbance parameter categories; TOLERANT, AVERAGE and SENSITVE, and 9 zones. The latter represented 10 m wide intervals from the western edge of the nesting habitat to the eastern shoreline of Indian Ridge Marsh where the proposed bird-watching facilities would be located. By differentiating nestling disturbance into a succession of zones, we were able to discern a spatial pattern of disturbance. The result of this test then dictated how we would proceed with our analysis. For example, if the results of the MANOVA proved non-significant, we would continue our analysis using the AVERAGE scenarios. Alternatively, if the results were found to be significantly different, we proceeded using the SENSITIVE scenarios. By adopting a minimax approach (a decision rule for minimizing the possible loss while maximizing the potential gain) we can offset the uncertainties associated with the nestling responses and focus on evaluating the management strategies and design options that will minimise the disturbance to the entire nestling colony (Prato, 2009).

To explore the extent to which black-crowned night-heron nestlings were affected by anthropogenic disturbance in each scenario, we used Classification and Regression Trees (CART) procedure. This recursive partitioning method allowed us to stratify the responses of nestlings under each set of management options imposed on them. We selected this statistical technique because (1) it can manage complex, context dependent multivariate data, (2) it is free of distributional assumptions, and (3) it is more accurate in generating predictions than equivalent polynomial logistic regression models (Vayssiéres et al., 2000; McGrath et al., 2003; Swihart et al., 2007). As nestling response time was a continuous dependent variable we build a regression tree. Our categorical independent predictors included the hydrological options (LEV), bird-watching facility location (LOC), bird-watching facility type (TYPE) and the presence or absence of school groups (SCH). A receiver operating characteristic (ROC) curve and relative error values were used to optimally prune the tree as part of a V-form cross validation (Vayssiéres et al., 2000). The ROC, a graphical plot of the sensitivity (1 − specificity), represents an index of the model's ability to discriminate between the effects of the different predictor variables (Swihart et al., 2007). In models that cannot be discriminated beyond chance an index <0.5 is shown, for models with poor accuracy the index lies between 0.5 and 0.7, for acceptable accuracy values between 0.7 and 0.9 are given and for excellent accuracy the index will be >0.9 (Fielding and Bell, 1997). The relative error provides another measure of accuracy based on the 'goodness of split', and thus the number of nodes (i.e. tree size). It also ranges from 0 to 1.0, where 0 indicates a perfect fit and 1 emphasizes that the predictor variables cannot be discriminated beyond chance.

4. Results

The sensitivity analysis revealed significant variation in the total time nestlings spent exhibiting disturbance-related behaviour between the three sets of alternative disturbance parameters ($F_{2,117}$=16.12, P < 0.0001). Fig. 3 shows that they varied in (1) the extent to which the nestlings exhibited each type of response behaviour (e.g. there was up to a ±20% difference in amount of agitated (FLEEING) behaviour recorded) and (2) the spatial pattern of disturbance that occurred across the nesting site (i.e. across the zones). Thus we only used the scenarios with SENSITIVE disturbance parameters in the subsequent CART analysis.

The regression tree built from simulation outputs demonstrated an acceptable accuracy with a very good fit (area under ROC curve = 0.72 with a relative error value of 0.307). The level of disturbance experienced by nestlings was influenced primarily by bird-watching facility type. Facility type represented an important variable in 100% of the scenarios. Water levels represented the second most important variable (63%), then bird-watching facility location (43%), and finally school groups (10%).

The first split in the regression tree indicates that while a bird hide and concealed platform reduced disturbance to nestlings (left branch), an observation tower and an exposed platform caused more disturbance (right branch; Fig. 4). Following the right branch, the position of the bird-watching facility did not significantly contribute or alleviate disturbance, nor did variations in the water levels. However, the presence of school groups in combination with these two types of bird-watching facility did increase the levels of disturbance experienced by nestlings significantly.

On the left-hand branch, the second split was associated with water level. High water levels (left branch) in combination with a bird hide or concealed platform led to significantly less nestling disturbance than if intermediate or low water levels were implemented (right branch). This pattern of disturbance corresponds to our findings in Fig. 3 that nestlings 0–50 m from the shore (when water levels ranged from low to intermediate) experienced greater levels of disturbance, than those 50–70 m away (where nesting opportunities would be restricted if water levels from intermediate to high), and nestlings 70–90 m away consecutively displayed less disturbance-related behaviour than the preceding zones.

Proceeding right down the second split, the regression tree also demonstrated that when water levels were low, (1) a bird hide reduced disturbance to nestlings more than a concealed platform and (2) the presence of school groups exacerbated disturbance at the concealed platform, but not the bird hide. However, when water levels were intermediate, a concealed platform at the northern location 'B' generated disturbance levels equivalent to that of a bird hide at the southern location 'A' (Fig. 2).

In all instances the presence of school groups did not cause any additional disturbance to the nestlings. Furthermore, in scenarios with no bird-watching facilities provided, recreation restricted to a main path resulted in disturbance levels equivalent to a concealed platform at location 'B'. In contrast, allowing unrestricted movement of bird-watchers incurred disturbance comparable to a concealed platform at location 'A'. Finally, only one scenario caused no recreational disturbance to the nestlings. The management options associated with this outcome included high water levels and a bird hide at location 'B'.

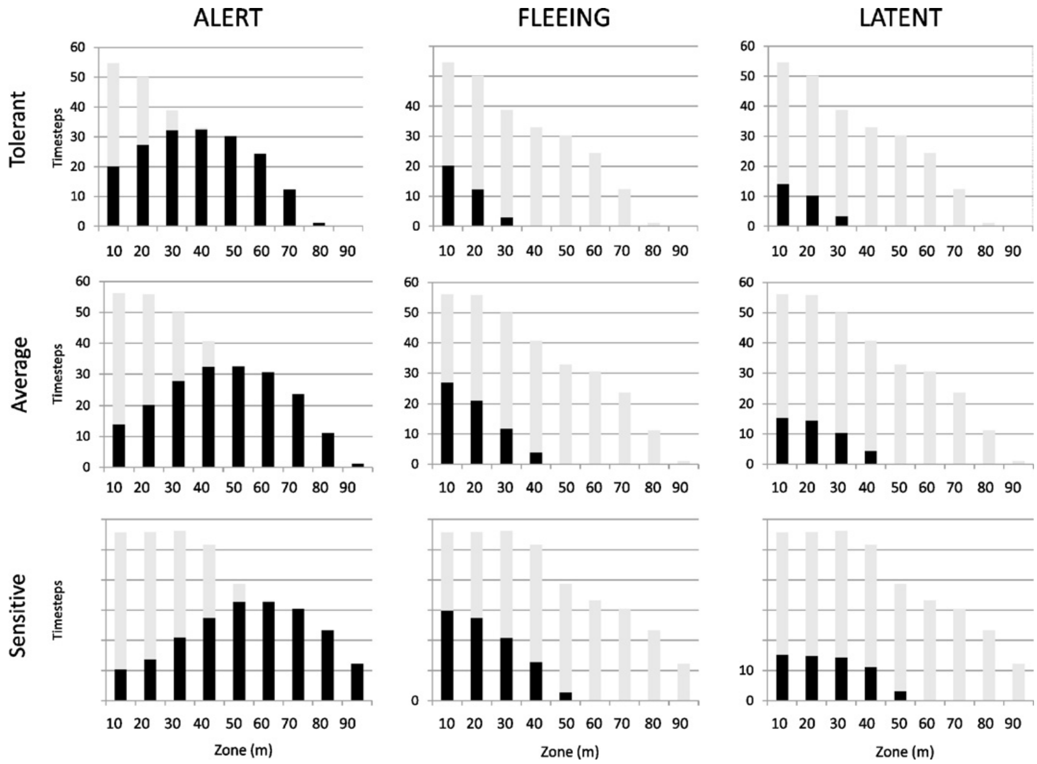

Fig. 3. Mean number of timesteps black-crowned night-heron nestlings exhibited ALERT, FLEEING and LATENT disturbance-related behavioural modes at 10 m wide zones from Indian Ridge Marsh's eastern shoreline in Illinois, USA, and across the three sets of wildlife response parameters; SENSITIVE (upper 95% confidence limit), AVERAGE and TOLERANT (lower 95% confidence limit). The cumulative responses of nestlings at each zone are also included (shown in grey).

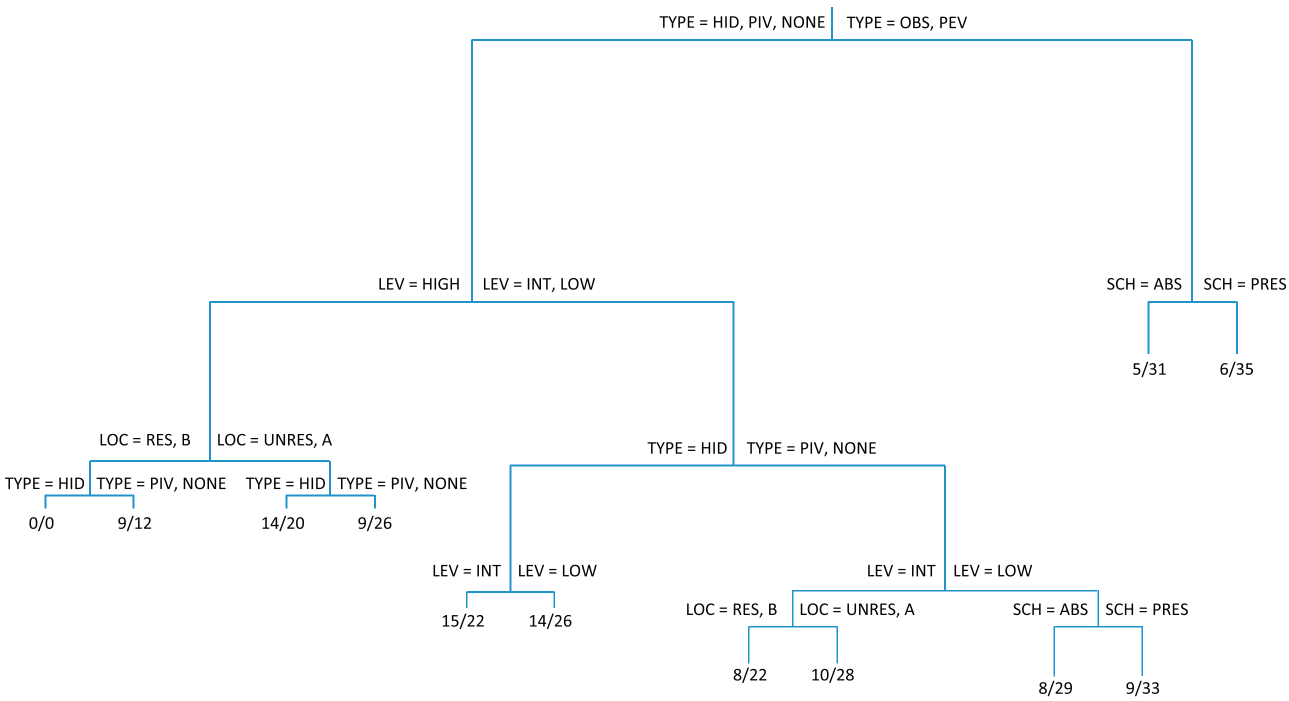

Fig. 4. Regression tree comparing the amount of recreational disturbance experienced by black-crowned night-heron nestling at Indian Ridge Marsh in Illinois, USA, under different management scenarios. Predictor variables defining a split are labelled at each branch split. Branch lengths are proportional to the number of scenarios represented. Below each terminal node the values represent (a) the standard deviation and (b) the average time spent exhibiting disturbance responses by nestlings over the simulated nestling period. The management strategies represented are (1) bird watching facility type (TYPE), including the options of a hide (HID), platform with vegetation (PIV), platform without vegetation (PEV) and an observation tower (OBS); (2) the bird watching facility location (LOC), including a facility directly in front of the colony (A), a facility to the north of the colony (B), and no bird watching facility (i) with (RES) and (ii) without (UNRES) restricted access to the shoreline; (3) water level (LEV), including high (HIGH), intermediate (INT) and low (LOW); and the presence (PRES) and absence (ABS) of school groups (SCH).

5. Discussion

Our case study provided an excellent opportunity to explore scenarios that can help developers and managers to more effectively manage protected species *in situ* in the presence of recreational activities. One conservative approach is to prevent all recreational activities. However, our simulation modelling approach has demonstrated that a set of management and design strategies exists that should allow recreation at the site as intended without a substantial increase in disturbance to the nestlings. We found that a combination of high water levels and bird hide at the northern location 'B' caused no recreational disturbance to nestlings even in the presence of school groups. By maintaining high water levels at Indian Ridge Marsh ensures that the black-crowned night-herons nest in emergent vegetation to the west of the site, thus creating a buffer between the nesting colony and the shoreline (Rodgers and Smith, 1997). In addition, by erecting a bird hide at location 'B', it not only conceals recreationists from nestlings, but also decreases the line of sight from the nestling colony. Both these strategies further lessen nestling disturbance.

In this case study, without available data on disturbance thresholds (i.e. when disturbance has detrimental implications for the survival of the nestlings), we are constrained from making broader management recommendations. Thus we could not speculate on whether management scenarios that cause little disturbance could also be a viable management option. However, in situations where disturbance thresholds are available and/or managers can make trade-offs between recreationists and the wildlife species, a simulation modelling approach would substantially aid decision-making (Sekercioglu, 2002; Taylor and Knight, 2003).

Furthermore, as a form of scenario planning, our approach provides valuable insights into whether there are inherent advantages to implementing multiple management strategies as opposed to any single strategy (Peterson et al., 2003). In other words, we were able to identify subtle relationships between the combinations of management and design strategies available to managers. In our case study, the presence of school groups had a negative impact on nestlings not only when exposed bird-watching facilities were provided, but also when a concealed platform was combined with low water levels. In all other scenarios, the presence of school groups had no significant influence. Similarly, we found that the spatial orientation of the bird-watching facility only had positive implications when water levels were not low. The primary inference is that specific combinations of management and design options can augment or diminish the impacts of recreational disturbance on wildlife. Simply prescribing a bird hide may be insufficient when it only reduces average disturbance levels by 7%, compared to 100% when combined with high water levels and placement at the northern location 'B'. This level of variation between a single strategy and multiple strategies in concert supports the consideration of multiple management and design criteria in the decision-making process. It also demonstrates that a simulation modelling approach can aid site and wildlife managers in this process. Moreover, the application of management practices that take into account recreational facility design, and both the orientation and proximity of recreationists to nesting, roosting or critical foraging sites, is widely applicable. For example, such insights have broad implications for other bird communities in similar aquatic systems that attract non-consumptive recreation (Carney and Sydeman, 1999; Blanc et al., 2006; González et al., 2006).

Finally, we must stress that these inferences are the results of a modelling exercise rather than an empirical study, and thus need to be taken with caution. It is strongly recommended that targeted field surveys are conducted to investigate the responses of black-crowned night-heron nestlings or a similar colonial nesting species to recreationists using different bird-watching facility designs (for which targeted empirical data was not available). This independent data should then be used to verify our model parameter space and simulation outcome before management options are implemented. In addition, we recommend that any management implemented should be subject to an annual monitoring regime and an adaptive management approach taken by managers post-site development. This approach can also take the form of an adaptive resource management (ARM) framework (Holling, 1978; Walters, 1986). ARM is appropriate when model hypotheses for management strategies fall within a range of options. For example, the distance of a bird watching facility can be between 50 and 70 m. In this instance, managers can experiment with the hydrology of the site within the given range to establish a more defined threshold distance.

We acknowledge that the application of models that explore the population level impacts of anthropogenic disturbance is generally regarded to be a more appropriate approach when devising management strategies for the conservation of an endangered and/or threatened species across a large geographic area (Mallord et al., 2007; Sutherland, 2007). However, the quantitative information generated by the current version of SODA is of great value to the management of wildlife in many real world circumstances. Under the U.S. Endangered Species Act, for example, listed species are protected at the level of the individual (it is illegal to "harass" an individual). By law active management should be implemented that prevents the harassment (i.e. disturbance) of such individuals at the sites they use. European legislation, such as the EC Habitats Directive (1992), has equivalent caveats. The current version of SODA therefore fills a vital niche in identifying where wildlife are exposed to potentially detrimental levels of recreational disturbance and informs management decisions to aid the local persistence of wildlife individuals *in situ*.

6. Conclusion

As a decision-making tool, we have demonstrated that incorporating a simulation modelling approach into the management planning process is of great value. For example, as part of an ARM framework, simulation modelling can be used to refine the management options available. Individual-based models, such as SODA, also provide novel insights into the disturbance regimes within which wildlife individuals exist. Effectively manipulating the dimensions that comprise a regime (landscape aesthetics, climate conditions, etc.), allows us to evaluate complex and uncertain circumstances that would be difficult to replicate and test empirically (Bohensky et al., 2006; Baron et al., 2009; Frachetti et al., 2009). The management of threatened or endangered species, for example, is often constrained by uncertainties (Regan et al., 2005). By exploring a diverse array of management scenarios in a virtual environment (thus with no risk to the target species), we can forecast, identify and prioritise more resilient long-term strategies.

Moreover, we believe that a simulation modelling approach has great potential beyond that demonstrated in this manuscript. As a flexible tool, such models can be tailored to address a wide variety of human-wildlife interactions, such as exploring the barrier effects of roads on wildlife, the probability of bird strikes around airports, and so forth (Peterson et al., 2010). In other words, landscape architects and planners can strategically use simulation models to inform to the ecological design of urban infrastructure (Hostetler and Drake, 2009).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.04.025.

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