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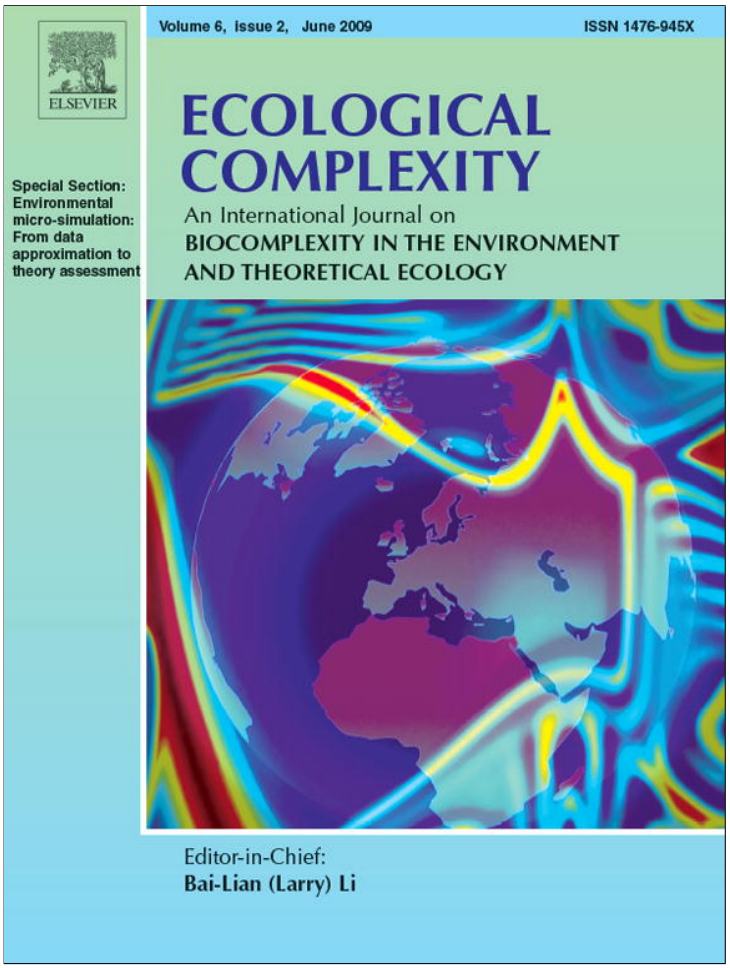

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Understanding wildlife responses to human disturbance through simulation modelling: A management tool

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ABSTRACT

With conservation awareness and the demand for wildlife preservation increasing, ecotourism and outdoor recreational activities are becoming more popular. If such activities go unmanaged, the disruption to many species may have implications on their breeding success, survival and abundance and these, in turn, may have cascading ecosystem effects. By developing management strategies, through the application of simulation models, to simultaneously maintain recreational opportunities and sustain wildlife populations, these detrimental impacts can be minimised. Simulation of Disturbance Activities (SODA) is a spatially explicit individual-based model designed as a flexible and transferable practical tool to explore the effects of spatial and temporal patterns of anthropogenic disturbance on wildlife.

Two case studies were used to illustrate the capabilities of SODA, one explored the effect of potential park designs on a nesting population of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) in Calumet, IL and the other investigated the influence of visitor frequency on the breeding success of barbastelle bats (*Barbastella barbastellus*) in the south west of England. For the yellow-headed blackbird, SODA revealed that pathways in close proximity to their main nesting and foraging habitat increased the level of disturbance experienced by the birds, although not to an extent that was detrimental to their breeding success. However, establishing paths beyond the zone of influence may ensure that the yellow-headed blackbird and other avian species continue to use the area in its entirety. In the second case study, SODA demonstrated that female barbastelle bats are significantly disturbed by the unrestricted movement of recreationists at their breeding colony site. However, SODA also revealed a lack of confidence in the critical energetic threshold value applied in the simulation. Subsequently, the overall effect of anthropogenic disturbance on the breeding success of this species could not be fully ascertained.

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1. Introduction

The popularity of ecotourism and outdoor recreation is expected to double by 2020 (Christ et al., 2003; Flather and Cordell, 1995; see also Boyle and Samson, 1985). While this benefits conservation through increased revenue, awareness and, ultimately, support for wildlife preservation (Gray et al., 2003; Goss-Custard et al., 2006b; Larson, 1995), it is also likely to disrupt wildlife (Bathe, 2007; Langston et al., 2007a,b; Drewitt, 2007). The aim of this paper is to present a spatially explicit, behavioural, individual-based model (IBM) capable of forecasting the impact of anthropogenic disturbance on wildlife when the appropriate inputs are applied (i.e. maps, knowledge of behavioural responses and life cycle parameters).

Understanding the potential effect of ecotourism and recreational activities on wildlife is key in the conservation of many species of conservation interest (Knight and Cole, 1995a; Vaske et al., 1995; Langston et al., 2007a). This is particularly relevant to those species more prone to disturbance, where their behavioural responses to recreational activities can have direct consequences on individual breeding success, abundance and survival (Strauss and Dane, 1989; Frid and Dill, 2002; Beale and Monaghan, 2004b). For instance, studies have shown that dog walkers on heathlands cause ground-nesting European nightjars (*Caprimulgus europaeus*) to expose their eggs for prolonged periods, increasing the risk of chilling and predation (Langston et al., 2007b); the abundance of the endemic Iberian frog (*Rana iberica*) in stream banks significantly decreases with proximity to recreational areas (Rodrıguez-Prieto and Fernández-Juricic, 2005); and auditory anthropogenic disturbance of hibernating insectivorous European bats leads to the reduction of vital fat reserves (Speakman et al., 1991).

There is a need to develop management strategies designed to simultaneously maintain recreational opportunities and sustain wildlife populations (Nisbet, 2000; Langston et al., 2007a,b). In practice, there are a variety of spatial, temporal, behavioural and visual management approaches that can be applied to an area to mitigate the effects of human disturbance (Fernández-Juricic et al., 2004; Beale, 2007; Knight and Temple, 1995). For example, the spatial aspects of land management can involve reducing the intensity and/or frequency of disturbance (Williams et al., 2002). This can be achieved by managing the distance between wildlife and visitors (Galicia and Baldassarre, 1997; Müllner et al., 2004; Hodgson and Marsh, 2007), limiting visitor numbers (Harris and Wanless, 1995; Beale and Monaghan, 2005; Rodrıguez-Prieto and Fernández-Juricic, 2005), and/or managing visitor distribution by either concentrating visitor activities or ensuring that they are evenly dispersed (Higham, 1998; Fernández-Juricic et al., 2004; Pearce-Higgins et al., 2007). Temporally, management can be focused towards restricting visitor activities and/or numbers during periods when wildlife populations are considered vulnerable, i.e. during breeding season or during hibernation when additional energy expenditure can be draining on limited reserves (Vaske et al., 1995; Knight and Temple, 1995). Other viable management approaches would be to alter human behaviour, such as noise levels, speed and type of recreational activity undertaken, or to use visual buffers and other components to provide visual screening (Knight and Temple, 1995).

However, to devise and implement effective management strategies targeted towards species of conservation concern requires a thorough understanding of: (1) the ecology of those species; (2) the type and intensity of recreational activities disturbing that population; and (3) the spatially explicit behavioural responses of individuals to that disturbance (such as detection distance and flight initiation distance) and the fitness consequences of recurring responses (Gill et al., 2001; Beale and Monaghan, 2004a, 2005; Knight and Temple, 1995). The use of simulation models enable us to explore the repercussions of the rules that govern the behavioural responses of wildlife to human stressors and extrapolate the implications of such behaviour in a species-specific context (West and Caldow, 2006; Beissinger et al., 2006; Preisler et al., 2006). In addition, generalised behavioural patterns may be drawn across a suite of study systems and species of ecological interest. As a simulation tool, such models can be used to guide our choice of practical management (Williams et al., 2002; Dale, 2003; Lurz et al., 2003).

To date, a variety of simulation models have been developed and employed to demonstrate the effects of disturbance on wildlife (Beale, 2007; Beissinger et al., 2006; Drewitt, 2007). These range from analytical to individual-based models, physiological to behaviour-based models, and spatially implicit to spatially explicit models (O'Connell et al., 2007; West and Caldow, 2006; Beissinger et al., 2006; see also McCoy, 2003). All have been created for specific case studies (Langston et al., 2007a; Gustafson et al., 2006). They have been used to quantify species-specific responses to a particular type of anthropogenic disturbance and the majority apply to a specific site under constant and/or uniform environmental conditions (McCoy, 2003; Taylor and Knight, 2003). For example, Taylor et al.'s (2007) Stone-Curlew Access Response Evaluator (SCARE); Goss-Custard et al.'s (2006a,b) behavioural-based IBM to establish critical thresholds of disturbance on oystercatchers (*Haematopus ostralegus*) before they die of starvation; Liley and Sutherland's (2007) spatially explicit behaviour-based IBM for ringed plovers (*Charadrius hiticula*) nesting at the Snettisham RSPB reserve in Norfolk, England; and Preisler et al's (2006) model to estimate the impact of all-terrain vehicles (ATVs) on Rocky Mountain elk (*Cervus elaphus*). As a consequence, these models are limited in their general application.

In this paper we present Simulation of Disturbance Activities (SODA), a spatially explicit individual-based model designed as a flexible and transferable practical tool for exploring species-specific responses to the spatial and temporal patterns of anthropogenic disturbance. To demonstrate SODA's capabilities and range of application, we explore two case studies. In the first case study, we explore whether various potential park designs have disturbance-related repercussions on the breeding success of a nesting population of yellow-headed black birds (*Xanthocephalus xanthocephalus*) in a proposed nature reserve in Calumet, Illinois (USA). In the second case study, we investigate whether levels of visitor activity in Chedworth Wood nature reserve in the south west of England are contributing to the abandonment of young by female barbastelle bats (*Barbastella barbastellus*).

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2. The model

2.1. Model purpose

SODA is a tool designed specifically to explore the repercussions (for example, variations in foraging rate, sleep deprivation, increased energy expenditure and decreased time spent feeding or in contact with young) of ecotourism and other outdoor recreational activities (such as dog-walking, bird-watching, mountain-biking, snowmobiling and kayaking) on wildlife. As such, SODA makes predictions regarding the implications of wildlife behavioural rules in novel circumstances (e.g. alternative pathway locations within a park). The model can therefore be used to provide insight into the relative impacts of alternative strategies for human recreation (spatial configurations and/or intensity of human activities) upon habitat use by wildlife (e.g. breeding, foraging and sleeping) in diverse settings (such as pedestrians in urban parks and off-road vehicles in national forests).

Note the application of SODA, as a simulation tool, can provide insights into the management options available which minimise the negative impacts of recreational activities on wildlife at a specific site. The detailed quantitative information generated by examining the cumulative behavioural responses of wildlife to human disturbance is of great value to many real world situations (as demonstrated in the following case studies), and even though SODA does not investigate population level implications of anthropogenic disturbance, its practical application to explore the persistence of species locally is useful.

2.2. Model overview

As a behavioural-explicit IBM (written in C++), SODA tracks the fates of individuals relative to the behavioural decisions and the corresponding changes in physiological status made by each animal (Blumstein et al., 2005; Grimm and Railsback, 2005). As a result the simulated interaction between wildlife individuals and human recreationalists is likely to generate responses similar to those of individuals in the wild. In addition, the cumulative response of the virtual individuals can be used to predict the probability of an animal surviving or successfully breeding according to a defined level of human disturbance and/or type(s) of recreation.

Using an individual-based approach also allows virtual animals to respond to environmental change as actual animals would (Goss-Custard et al., 2006a; Grimm and Railsback, 2005). As SODA is spatially explicit, it allows the user to create a virtual environment to the specifications of a particular study site. Input maps can represent the type, size and location of habitat patches, wildlife shelters (dens, nests, burrows, etc.) and public routes. Alternatively, the user can customise an environment; a feature which can be utilised to investigate site designs, the effectiveness of various management strategies that involve habitat modification and/or the more complex spatial and temporal patterns of human recreation.

2.2.1. Output

Four main processes emerge from SODA based on the interactions between wildlife individuals, human recreationists and habitat (conceptually delineated in Fig. 1). These include the behaviour and movement patterns of each wildlife individual for the length of the simulation, their energetic status, mortality and/or breeding success. The output data from these processes can then be converted into a series of maps and tabular data enabling us to delineate movement patterns, investigate the probability, intensity and consequences of human activity on local wildlife and compare the responses of wildlife to a range of potential disturbance scenarios.

2.3. Model parameters

SODA comprises four main entities: (1) habitat, (2) spatially constrained recreationists, (3) unconstrained recreationists and (4) individual animals. The user-specified parameters and state variables associated with these entities can be divided into three basic input categories: Scenario, Recreationist and Wildlife. Refer to Tables 1 and 2 for definitions and a full list of the parameters and state variables required by SODA, respectively.

Table 1 – Definitions.

	Definition
Timestep (TS)	Discrete interval for which the status of each individual is recorded in the output. These intervals can be from 5 min to 6 h in length.
Timestep distance (TSD)	Distance travelled over the period of one timestep interval.
Random walk correlation	A range (0–1) which dictates how an individual moves while foraging. At one extreme individuals will move in a straight line (1) and at the other in a highly erratic meander (0).
Minimum homing distance	Distance from which an individual has a 1% probability of moving back towards its home/shelter.
Maximum homing distance	Distance beyond which an individual will not forage.
Detection distance (DD)	Distance between virtual recreationist and virtual wildlife at which the wildlife becomes aware of the presence of the recreationist and exhibits alert behaviour.
Flight initiation distance	Distance between virtual recreationist and virtual wildlife at which the wildlife flees/take flight.
Latent period	Post fleeing an individual will remain static for a period before resuming pre-disturbance activity.
Predation risk	The probability (0–1) of an individual being predated over the course of the simulation period.
Virtual recreationist density	This is the number of virtual recreationists that are present at any one timestep
Virtual recreationist frequency	This multiplicative modifier which can be used to vary the number of virtual recreationists present over the period of a day.
Energy threshold	When the available energy reserves of an individual fall below this value, the individual is considered to have starved.

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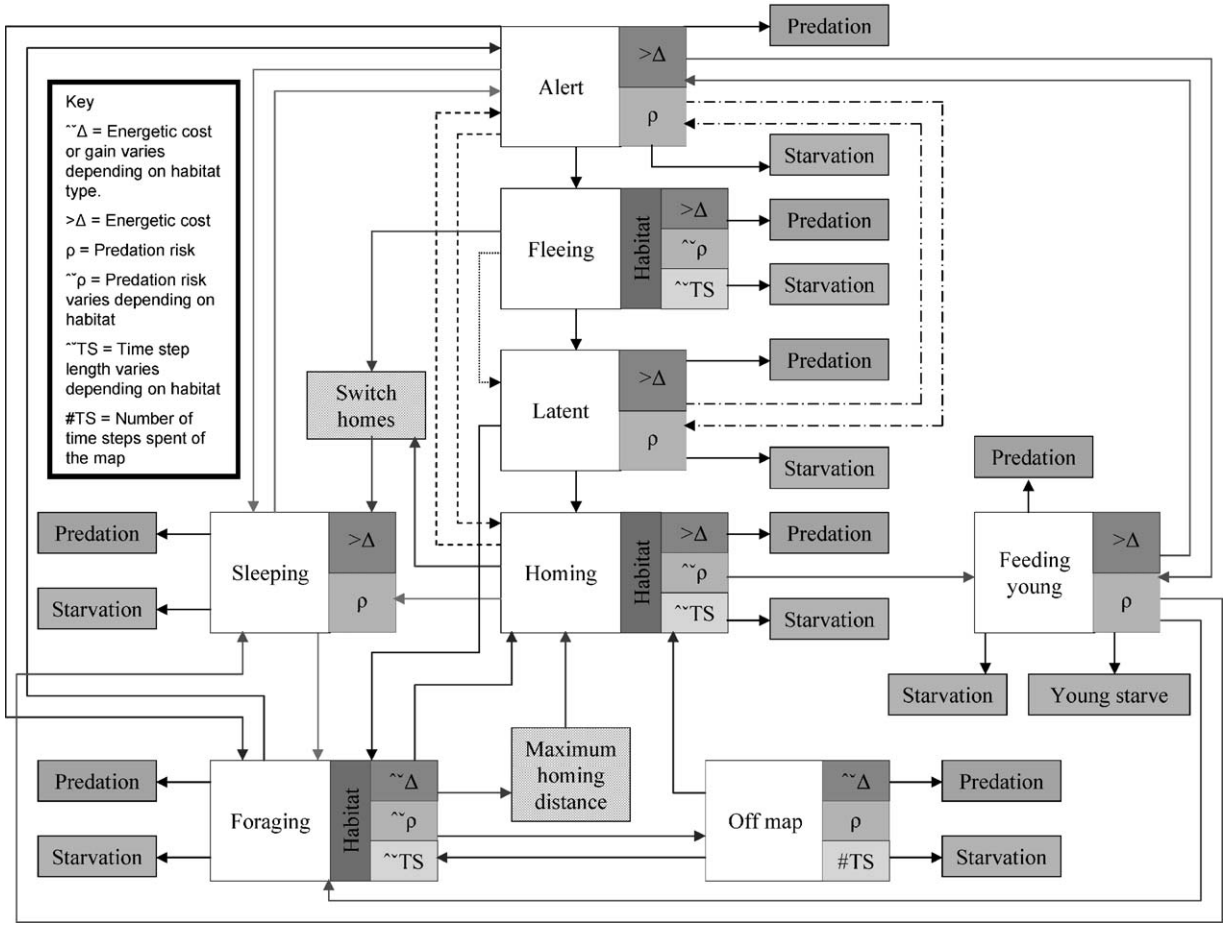

Fig. 1 – Conceptual delineation of the main wildlife processes employed by SODA to simulate the interactions between wildlife individuals, human recreationalists and habitats. It includes the eight different behaviour modes exhibited by wildlife mobile objects, movement patterns with and without disturbance, energetic status and predation potential.

Table 2 – Scales, variables and parameters used to define model structure, i.e. the state of individuals, parameters describing individual behaviour, and variables and parameters describing the individuals' environment. As an example the variables and parameters for the two case studies have been included.

			Case study 1	Case study 2
(a) Scenario				
Temporal scales	Length of simulation, e.g. year, season or activity period		12 days	62 days
	User specified timestep length		5 min	5 min
Spatial scale	User specified unit		Metres	Metres
Environmental characteristics	Habitat patches	Type	(a) Hemi-marsh	(a) Deciduous woodland
			(b) Wet savannah	(b) Conifer woodland
			(c) Forested wetland	(c) Mixed woodland
			(d) Black willow marsh	(d) Grassland
			(e) Wet prairie	(e) Hedgerow
		Location	See Fig. 2	See Fig. 4
		Size	See Fig. 2	See Fig. 4

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Table 2 (*Continued*)

				Case study 1	Case study 2
	Paths	Number of paths		Ranges from 2 to 5 depending on scenario	11
		Type		All the same	Bridleways, foot paths and tracks
		Length of path		See Fig. 2	See Fig. 4
	Other features and characteristics	Multiple shelters/ homes identified (e.g. dens, roosts or nests)		N/A	15 potential roost ites
				Case study 1	Case study 2
(b) Recreationist					
Virtual recreationists	Virtual recreationists restricted to paths	Starting position		N/A	N/A
		Direction		N/A	N/A
		Type		(1) Walker (2) Jogger (3) Bird watcher, (4) Dog walker (5) Cyclist	(1) Walker (2) Dog walker (3) Horse rider (4) Mountain biker
		Timestep distance		(1) 200 (2) 275 (3) 125 (4) 220 (5) 500	(1) 175 (2) 210 (3) 750 (4) 500
		Persistence		(1) 12 TS (2) 6 TS (3) 12 TS (4) 6 TS (5) 6 TS	(1) 12 TS (2) 6 TS (3) 6 TS (4) 12 TS
		Density		(1) 3/TS (2) 2/TS (3) 5/TS (4) 5/TS (5) 2/TS	Scenario specific
		Frequency	Daily activity patterns	6:00 a.m. to 8:00 p.m.	Scenario specific
		Associations between type of path and type of virtual recreationist		(1) Main pathways only (2) Main pathways only (3) All pathways (4) Main pathways only (5) Main pathways only	(1) Foot paths, bridleways (2) Foot paths, bridleways (3) Bridleways, tracks (4) Tracks
	Virtual recreationist with unrestricted movement	Starting position		N/A	Six car parks entrances (see Fig. 4)
		Direction		N/A	N/A
		Type		N/A	Dog walkers
		Timestep distance		N/A	190 m/TS
		Persistence		N/A	6 TS
		Density		N/A	100
		Frequency	Daily activity patterns	N/A	5:30 a.m. to 8 a.m. (1), 8:05–4:55 (0.5), 5:00–8:30 (1)
		Random walk correlation		N/A	0.5
		Habitat-related characteristics	Probability of crossing certain habitat types	N/A	(a) 1 (b) 1 (c) 1 (d) 0.1 (e) 1.2

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Table 2 (*Continued*)

				Case study 1	Case study 2
			Timestep distance	N/A	(a) 1 (b) 1 (c) 1 (d) 0.1 (e) 1.1
				Case study 1	Case study 2
(c) Wildlife					
Virtual animals	Number and name of individuals			10	20 individuals
	Behavioural modes	Foraging	Direction	N/A	N/A
			Time spent foraging over period of a day	16 h (5:00 a.m. to 9:00 p.m.)	8 h (9:00 p.m. to 5:00 a.m.)
			Timestep distance	30 m	800 m
			Random walk correlation	0.5	0.1
			Energetic gain	0.1 per timestep	0.0001 g
			Predation risk	1.00E−14	3.00E−08
		Sleeping	Time spent sleeping over the period of a day	8 h (9:00 p.m. to 5:00 a.m.)	16 h (5:00 a.m. to 9:00 p.m.)
			Energetic cost	N/A	−0.00005 g
			Predation risk	1.00E−14	1.00E−8
		Homing	Timestep distance	35 m	1000 m
			Energetic cost	0	−0.000205 g
			Predation risk	1.00E−14	3.00E−08
			Minimum homing distance	10 m	500 m
			Maximum homing distance	150 m	8000 m
		Return to feed young	Timestep distance	30 m	1000 m
			Energetic cost	0	−0.000205 g
			Predation risk	1.00E−14	3.00E−08
		Feeding young	Yes/no	Yes	No
			Individual returns to feed young when energy reaches	3	N/A
			Amount of energy given to young per feeding event	3	N/A
			Check energy levels every	1	N/A
			Predation risk	1.00E−14	N/A
	Behavioural responses to disturbance	Alert	Detection distance	5 m	75 m
			Energetic cost	N/A	−0.0001 g
			Predation risk	1.00E−14	1.00E−08
		Fleeing	Direction	N/A	N/A
			Flight initiation distance	2 m	50 m
			Fleeing distance	6 m	Dependent on location of new roost
			Energetic cost	N/A	−0.000233 g
			Predation risk	1.00E−14	3.00E−08
		Latent	Time spent latent	1 TS	0 TS
			Energetic cost	N/A	N/A
			Predation risk	1.00E−14	N/A

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Table 2 (*Continued*)

			Case study 1	Case study 2
	Probability of switching shelters/homes		N/A	25%
	Off map movement	Maximum number of timestep spent off the map	0	10 TS
		Energy gain/cost	N/A	0.0001
		Predation risk	N/A	3.00E−08
Energetic status	Individuals initial energy level		1 (food item)	9 g (maximum weight)
	Energy threshold (death occurs if equal to or below)		4 (food items)	6 g (minimum weight)
Habitat multipliers	Virtual animal-related characteristics while foraging	Probability of crossing certain habitat types	(a) 100% (b) 100% (c) 25% (d) 25% (e) 100%	(a) 100% (b) 100% (c) 100% (d) 25% (e) 100%
		Timestep distance	No variation between habitat types	(a) 1 (b) 1.1 (c) 1 (d) 1 (e) 1.2
		Energetic gain/cost	100% 100% 25% 0.001% 100%	(a) 1 (b) 0.8 (c) 0.9 (d) 1.2 (e) 1
		Predation risk	No variation between habitat types	(a) 1 (b) 1 (c) 1 (d) 0.8 (e) 1.2

NB: Those variables in small caps are calculated or randomly chosen by the simulation program and therefore not user specified. All distances are based on the user-specified spatial scale, as are energy units user specified. #TS means number of timesteps and can therefore such variables can only be positive integers. For case study 1 references included Ward (unpublished data) and Twedt and Crawford (1995). For case study 2 references included Wells (personal communication), Palmer (personal communication), Billington (2004), Altringham (2003), Anon. (2005), Greenaway and Hill (2004), Sierro and Arlettaz (1997), Willis et al. (2005a,b), Turbill and Geiser (2006), Geiser and Brigham (2000) and Greenaway (2004).

2.3.1. *Scenario*

Scenario parameters include duration of each timestep, overall simulation length (such as a season or period of activity) and the specification of a series of maps that describe the study site. The timestep is a discrete time interval ranging from 5 min to 6 h. Throughout the course of the simulation, SODA records the location, behavioural mode (e.g. foraging or responses to encounters with human recreationists) and status of each virtual animal during each timestep. The input maps, which are created in ArcGIS (ESRI, Redlands, CA) as shape files, define habitat types used to determine scale movement patterns, linear features (such as trail, paths and roads) used to determine human movements, and wildlife and human point features (such as roost trees, nest sites, dens, burrows, car parks, entrances and gates) from which the movements of virtual animal and virtual recreationists are based.

2.3.2. *Recreationists*

Under the Recreationist category, SODA provides the opportunity to define the two virtual recreationist entities, those that are restricted to linear features (Type 1) and those that are not (Type 2). For Type 1 virtual recreationists, any number of different recreationists (such as dog-walkers, mountain-bikers and snowmobiles) can be defined, each associated with a specific set of user-defined movement rules (including rate of movement, persistence, associations with linear features, temporal activity patterns and visitor frequency). Type 2 virtual recreationists have additional movement rules, such as random walk correlation and habitat-related movement (such as speed and crossing probability). By altering the density of the virtual recreationists (number of recreationists per timestep), either moving along specified paths, such as trails, or randomly moving throughout the extent of the study site, the responses of virtual animals to

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varying levels of anthropogenic disturbance can be investigated.

2.3.3. *Wildlife*

SODA ascribes empirically estimated parameters to each individual virtual animal, including demographic, behavioural, physiological and habitat-specific characteristics. Consequently, their responses (i.e. the number of prey items captured, time spent at the breeding site, or the amount of time spent latent) are empirically derived estimates of the rules animals employ, therefore they represent realistic behaviour (see Section 2.4). Contrasting different characteristics of virtual animals (such as detection distance, flight initiation distance, time spent fleeing, time spent latent temporal patterns of activity, movement rules, energetic expenditure and predation risk) between scenarios can provide an insight into the sensitivity of wildlife to various management strategies, (see case studies below for examples).

2.3.4. *Multipliers*

SODA incorporates several parameters which in specific circumstances are multiplied by the baseline values to modify them prior to implementation. For example, a virtual animal may be at greater risk from predation when fleeing through grassland habitats or at less risk when fleeing along hedgerows. Multiplying the user-defined predation value for fleeing by appropriate modification values, such as 1.2 or 0.5, respectively, will adjust the predation risk for these different habitat types accordingly. Other modification values that can be incorporated into the simulation include the virtual animal values given for the energetic costs and gains, and movement rules in each behavioural mode (such as foraging); the movement rules governing Type 2 virtual recreationists; and the density of virtual recreationists. As with predation, the energetic parameters allow the user to specify variations between each habitat type. By modifying baseline parameter values with habitat-specific multiplier values, SODA generates a more realistic level of environmental variation. Additionally, the frequency of different types of virtual recreationist within the simulated site can be varied by applying multiplier values to their density parameters over time. In this way, the various peaks and troughs in activity (i.e. visitor numbers) that occur over a 24 h period can be incorporated in the simulation.

2.4. *Model set-up*

In SODA, all spatial units are described in terms of steps, which we defined as the distance (conceptually in metres) that a mobile object moves in one time interval (Zollner and Lima, 1999). For each timestep, the movement of a mobile object through the landscape (i.e. from one habitat patch (polygon) to another or along a pathway (line)) is determined by a set of user-defined parameters (see preceding section). The distance a mobile object moves in one timestep can be varied with behavioural mode and habitat type (via the multipliers).

During a timestep unit, SODA addresses the parameters sequentially for each mobile object in combination with its current position and status. First, SODA compares the location of each virtual animal with the position of each virtual recreationist. If the distance between the two is less than or equal to the detection distance prescribed to that virtual animal, then it remains at its current location and its behavioural status becomes ALERT. However, if the distance between the virtual animal and nearest virtual recreationist is less than or equal to the flight initiation distance of that virtual animal, then the virtual animal behavioural status becomes FLEEING. The virtual animal moves a set distance from its current position away from the virtual recreationist and will then continue to flee for the set number of timesteps in the same direction. That is unless another virtual recreationist in a proceeding timestep is within the flight initiation distance of that virtual animal or an impenetrable habitat type is reached. For the first scenario, the fleeing procedure resets, so the virtual animal changes direction in order to flee away from the new virtual recreationist. Alternatively, if habitat crossing probabilities are set at '0' for a particular habitat type, then a fleeing virtual animal will simply refract at a randomly selected angle from the boundary of this habitat. If two or more virtual recreationists are within the flight initiation distance the virtual animal flees away in a direction that is furthest from the combined direction of these virtual recreationists. Once the virtual animal ceases fleeing, it becomes LATENT for the designated number of timesteps. This latent behavioural mode can be overridden by an alert or fleeing event, after which the virtual animal will complete its scheduled latent phase or initiate an entire latent period, respectively.

At the conclusion of any disturbance event (encounter with virtual recreationist), the virtual animal will return to a normal activity (i.e. sleeping, foraging, returning home to sleep, returning to young or feeding young). During each timestep, SODA assesses the activity parameters to ascertain whether a virtual animal should be sleeping or foraging. If a virtual animal is due to forage in that timestep, the behavioural mode assigned is FORAGING and the virtual animal moves the prescribed distance (for that activity) away from its current location. SODA fundamentally investigates interactions between human recreationists and wildlife, and thus the movement of mobile objects was required to emulate realistic movement patterns (Zollner and Lima, 1999). Consequently, a correlated random walk movement strategy was applied to all foraging virtual animals and Type 2 virtual recreationists, when turning angles in successive steps are drawn from a wrapped Cauchy distribution (Blumstein et al., 2005; Lima and Zollner, 1996):

$$\beta = 2\arctan\left[\left(\frac{(1-\rho)}{(1+\rho)}\right)\tan(\psi)\right] \quad (1)$$

where β is the random angle at which the mobile object moves between successive steps, ρ the degree of correlation between successive moves taken by the mobile object, and ψ the uniform distribution of angles between -90° and 90° from which β was randomly drawn. Note that after each step there was a change in direction by a random angle β.

Conversely, the initial direction of any mobile object moving from its point of origin (i.e. a virtual animal home or a Type 2 virtual recreationist entrance) is randomly generated in the simulation, as is the initial location and direction (two ways) of Type 1 virtual recreationists along pathways. Comparable to the virtual animals, all the virtual recreationists move the prescribed distance at each timestep

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and remain in the simulation for the set number of timesteps. In addition, an off-map feature, not only reflects a virtual animal back onto the defined map once its movement causes it to cross the edge of the map, but also allows the user to specify how many timesteps the virtual animal can spend off the map.

To investigate the energetic consequences of disturbance, a user defines the energetic costs and gains of each behavioural mode and associated habitat type. During each timestep their energetic values are deduced from or added each virtual animal's energetic reserves accordingly. If the user stipulates that the virtual animal is to feed young, after a prescribed amount of energy is accumulated, for example, while foraging (which is checked every set number of timesteps) the behavioural status will change to RETURNING TO FEED YOUNG. The virtual animal will move in the direction of its home/young and once this destination is reached the behavioural status will become FEEDING YOUNG. In that timestep, a prescribed amount of energy is deducted from the energetic/food reserves of the virtual animal. During the following timestep, the behavioural status returns to appropriate activity, such as foraging and the virtual animal moves accordingly from its home/young.

When a foraging virtual animal is due to sleep, the behavioural status will be assigned as HOMING and the virtual animal will move from its current location in the direction of its current home (multiple home scenarios are discussed below). As previously mentioned a virtual animal only changes direction in this mode when confronted by an impenetrable habitat type. If habitat crossing probabilities are set at '0' for a particular habitat type, then a homing virtual animal will refract from the boundary of this habitat at an angle that is directed towards home. The number of timesteps spent homing is, therefore, dependent on how far the virtual animal is from its home, as well as the composition of the intervening landscape. Once a virtual animal has reached its home, the behavioural status immediately changes to SLEEPING and remains in this state until the user-defined sleep period ends where upon the virtual animal begins to forage or a disturbance event occurs.

For every timestep, the probability of predation associated with the virtual animal's relevant behavioural mode is applied by generating a random number between 0 and 1. If this value is less than or equal to the defined risk of predation then the behavioural status of the virtual animal is overridden to PREDATED. If the virtual animal is not predated, the energetic cost of the current behavioural mode is deducted from the virtual animal's energy/food reserves. If these reserves are then less than the threshold energy level the behavioural status of the virtual animal is overridden by STARVATION.

Finally, for every timestep the probability of a virtual animal switching homes after foraging or a fleeing event (two independent user specified probabilities) is applied. Again, a random number is generated between 0 and 1; if this falls within the range of the defined probability value then the virtual animal's current home location will be replaced by a new home location randomly selected from the list of available homes (generated by the user and incorporated to the simulation via the point shape file). A virtual animal then moves directly to that home if they are not disturbed.

3. Case study 1: the yellow-headed blackbird

3.1. *Introduction*

As part of an extensive rehabilitation effort, plans are underway to preserve and enhance areas of ecological significance in the Calumet region of Chicago, Illinois (CDOE, 2002). This includes a number of remnant wetland sites considered to be some of the richest in Illinois. It is proposed that these areas, known collectively as the Calumet Open Space Reserve, will be preserved, enhanced and managed to allow the general public to interact with nature.

We used SODA to review potential designs for the reserve, specifically access points, pathways and any park regulations that might be required (e.g. signage implementing restrictions, such as 'keep dogs on lead'). For this paper, one site in the Calumet Open Space Reserve plan was chosen as the focal point for the case study. Hegewisch Marsh holds a breeding population of yellow-headed blackbirds, a State protected species and listed under the US Migratory Bird Act. As a migrant, the yellow-headed blackbird moves north to west-central Canada and the United States during the summer to breed (Twedt and Crawford, 1995). Its core breeding range is primarily permanent deep-water palustrine wetlands characterised by an interspersion of open water and emergent vegetation (such as cattail (*Typha* spp.), bulrush (*Schoenoplectus* spp.) and reed (*Phragmites* spp.)) (Weller and Spatcher, 1965). In this habitat, known as a hemi-marsh, males claim breeding territories that can contain up to eight mates depending on territory quality during the breeding season (Twedt and Crawford, 1995).

Currently, populations in Illinois appear to be secure provided the suitable remnant wetlands, such as Hegweisch Marsh, remain with low levels of human disturbance (Twedt and Crawford, 1995). Subsequently, a major priority for the proposed designs is that human impact on this species is kept at a minimum. By applying SODA we can investigate various reserve designs for this target species.

3.2. *Methods*

3.2.1. *The study site*

Hegewisch Marsh is one of eight fragments of palustrine wetland remaining in the heavily industrialized Calumet Region of Chicago, Illinois. It is bordered to the north by a railroad track, roads to the east and south and the Little Calumet River to the west. However, despite the site's isolated nature and relatively small size (an area of 0.34 km^2) it currently provides substantial foraging and nesting opportunities for the yellow-headed blackbird breeding population. In the 0.12 km^2 area of hemi-marsh towards the north of the site, males are able to set up territories containing ample nest sites and an adequate source of prey on which foraging adults feed their young. Surrounding the hemi-marsh are four other wetland habitat types, each of value to varying extents to the yellow-headed blackbird. These include (1) wet savannah (0.12 km^2) comprising primarily of cottonwood (*Populus deltoides*) and a native ground cover dominated by switchgrass (*Panicum virgatum*) and goldenrods (*Solidago* sp.); (2) forested wetland (0.05 km^2) which is similar to the savannah areas with

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a greater tree density; (3) black willow marsh (0.02 km^2), a low-lying, wooded area dominated by black willow (*Salix nigra*) and cottonwood; and 4) wet prairie (0.03 km^2) with a fairly high quality assemblage of native prairie species (CDOE, 2006). As it stands, there are currently no park-like features or infrastructure (e.g. pathways) on the site.

3.2.2. *Model parameters*

All parameters used to populate the simulations for this case study are listed in Table 2. Each was selected based on available information, primarily, a Phase 1 survey of Hegewisch Marsh undertaken in 2006 in accordance with the ecological rehabilitation plan proposed by Chicago Department of Environment (CDOE) and research undertaken by Mike Ward (personal communication) on the yellow-headed blackbird in the marsh from 1998 to 2004. A summary of and rationale behind the information used is provided in this section.

3.2.2.1. Scenario. Using the phase 1 data provided by CDOE and aerial photographs, GIS maps were created to delineate these habitat types within Hegewisch Marsh (see Fig. 2). For this case study, seven path location scenarios were run to ascertain which would have the least impact to the yellow-headed blackbird. These scenarios were based on a circular path system, the position of which was adjusted so that it bisected suitable foraging habitat (i.e. wet prairie and wet savannah) in Scenario 1; bordered suitable and unsuitable habitat (forested woodland and black willow swamp) in Scenario 2; bisected unsuitable habitat in Scenario 3; and crossed all habitat types in Scenario 4. In addition, a further three scenarios were run to investigate whether proximity of the main path from the edge of the hemi-marsh caused significant disturbance to the nesting colony. Therefore for the last three scenarios, a path was placed along the edge of the hemi-marsh in Scenario 5, 5 m away in Scenario 6 and 10 m from the border in Scenario 7. In all scenarios, no paths were placed in the hemi-marsh, as the majority of this habitat is unsuitable for public access. It has also been proposed that park design include two bird blinds and an observation tower along the edge of the hemi-marsh habitat allowing the public to view the yellow-headed blackbird breeding colony (see Fig. 2). Due to the limited size and location of the hemi-marsh habitat within the site, the position of these structures was fairly constrained. As a result they were maintained at the fixed location in each of the above scenarios and direct tracks from the blinds and tower to the nearest main path were included in each pathway system.

From research undertaken by Ward (unpublished data) the location of the nests and average annual density of females within the hemi-marsh habitat were used to create a GIS layer to delineate the location and number of virtual animals. After the yellow-headed blackbird migrates to Hegewisch Marsh to breed, anthropogenic disturbance at the site could have a negative impact on breeding success (Ward, personal communication). It is during the nestling period when the nestlings are dependent on adults for food (see wildlife section below) that human disturbance could lead to a reduction in chick survival (Ward, personal communication). The simulation runtime was, therefore, set for the duration of this nestling period, a total of 12 days.

3.2.2.2. Recreationists. As the site currently has no public access, there is no empirical data on the frequency and density of visitors to the area. Subsequently, a series of runs were undertaken to establish whether visitor numbers and activity levels over a period of a day had a significant influence on the breeding success of the yellow-headed blackbird.

By its very nature, size and location, Hegewisch Marsh is limited to a sub-set of recreational activities, mainly foot traffic and possibly cycling, restricted to designated pathways. It is anticipated based on the size, nature of the site and activities to be encouraged that the most likely types of recreationist (i.e. Type 1 virtual recreationists) to visit the nature reserve will be walkers with and without dogs, joggers, cyclists and bird watchers. Of these, the latter was considered particularly relevant to the case study, as this activity will be directed at the yellow-headed blackbirds. Furthermore, as one of the most popular forms of nonconsumptive wildlife associated recreation (Kerlinger and Brett, 1995), bird watching will undoubtedly be common in Hegewisch Marsh, particularly as initial proposals for the site are focused towards encouraging this activity.

3.2.2.3. Wildlife. Ward (unpublished data) observed that in the first of a potential two broods females laid up to five eggs; however as brood reduction is common in this species, three nestlings were generally recorded in nests. For the duration of the nestling period, females were observed feeding young on insects, primarily aquatic prey, such as odonata, gathered on regular foraging trips within the confines of the site. For the purposes of the model, males were not included in the simulations as they infrequently, if at all, fed nestlings.

The most plausible mechanism whereby anthropogenic disturbance could have deleterious consequences for the yellow-headed blackbird at Hegewisch Marsh (Ward, personal communication), is that human presence could disrupt the foraging rate of females. By becoming alert or fleeing at the presence of humans female yellow-headed blackbirds deviate from foraging, subsequently collecting and delivering fewer prey items to their young over the period of a day.

3.2.2.4. Analysis. From the output of each simulation run, we analysed sets of response variables in a multivariate analysis of variance (MANOVA) to test the hypothesis that the average value of each response variable was not influenced across replicates or between scenarios. Response variables were also decomposed into separate ANOVAs to examine each response variable's sensitivity to the alternative scenarios. The MANOVA was computed using PROC GLM in SAS (1988). In addition, Ryan–Einot–Gabriel–Welsch multiple range tests were used to examine the relative ranks of the alternative scenario for each response variable.

For the yellow-headed blackbird analysis, three sets of related-response variables were identified and tested to assess whether there was significant variation between the seven proposed path designs. These groups included the behavioural responses (i.e. the number of timesteps spent foraging, alert,

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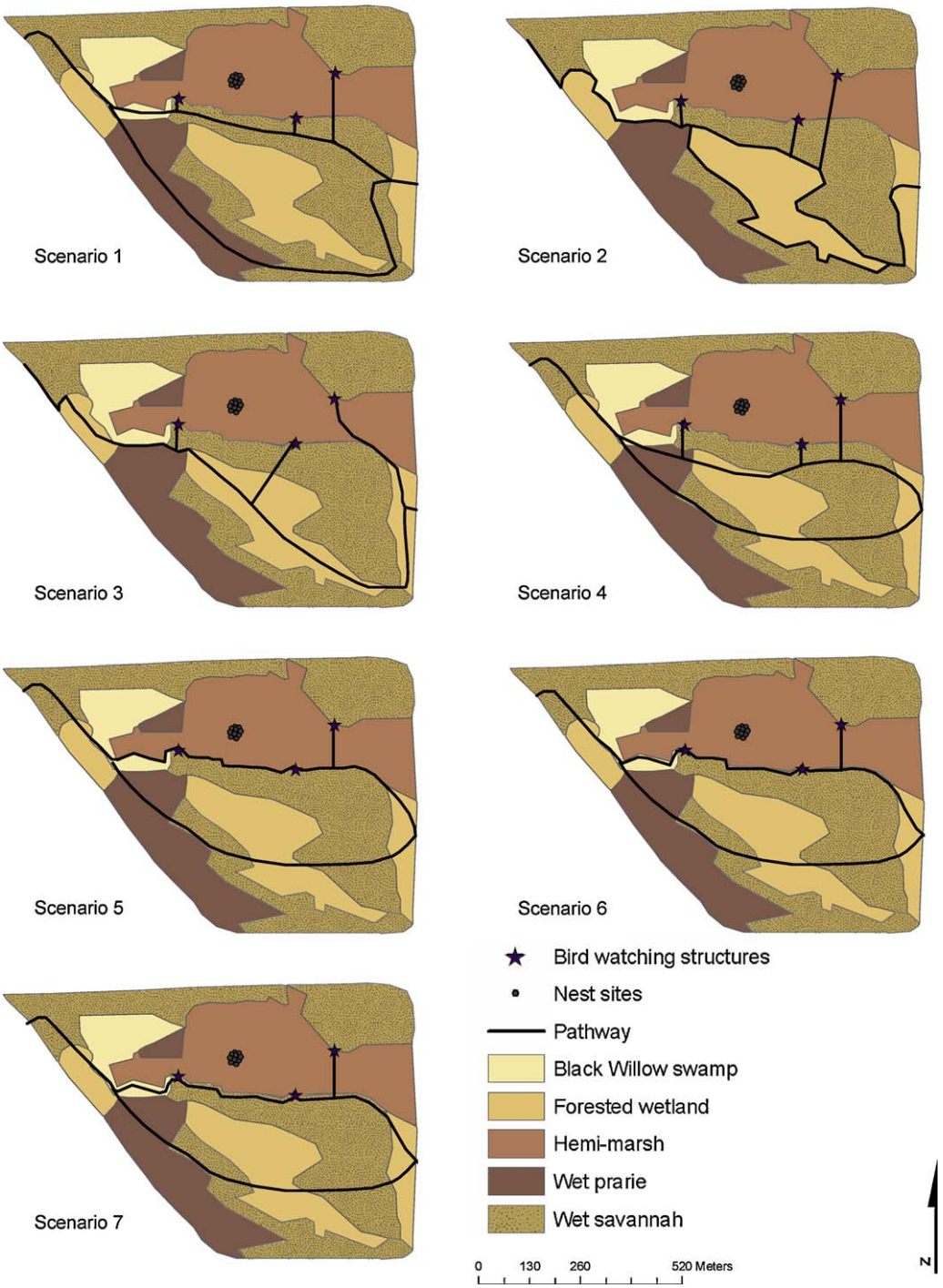

Fig. 2 – Series of seven maps representing Hegewisch Marsh in Calumet, IL, USA. Each map represents a different proposed circular path system with additional paths providing access to two proposed bird blinds and an observation tower, where required. Scenario 1 has a path system that bisects suitable foraging habitat (i.e. wet prairie and wet savannah); Scenario 2 borders suitable and unsuitable habitat (forested woodland and black willow swamp); Scenario 3 bisects unsuitable habitat; Scenario 4 crosses all habitat types; Scenario 5 runs along the edge of the hemi-marsh; Scenario 6 has a path system 5 m away from the edge of the hemi-marsh; and Scenario 7 has a path 10 m from the edge.

fleeing, latent, feeding young, returning to feed young and homing), habitat responses (i.e. the time spent foraging in each habitat type) and pathway responses (the number of timesteps in which virtual animals were within detection distance of the each proposed pathway).

3.3. *Results*

The main objective was to establish whether the yellow-headed blackbird breeding population would be negatively influenced by potential anthropogenic disturbance generated

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by each path design. The results of this analysis revealed that there was little variation in the number of timesteps females spent foraging, feeding young, returning to feed young and homing between any of the proposed park designs (see Fig. 3 and Table 3a). In contrast, the number of disturbance responses (i.e. alert, fleeing and latent) varied significantly ($P < 0.001$) among the different scenarios, with a substantial increase in disturbance events observed among the scenarios in close proximity to the hemi-marsh (i.e. Scenarios 5, 6 and 7). The analysis also revealed that there was no significant variation in the foraging activities of females within the different habitat types on site (see Table 3b). Each scenario exhibited similar usage of the surrounding habitat. Finally, the placement of certain pathways in Hegewisch Marsh was the significant source of variation between the proposed park designs (see Table 3c). The largest disparity in the number of disturbance events between scenarios was generated with proximity of the main pathway to the hemi-marsh. Thus the closer the path the greater the encounter rate between recreationists and foraging female yellow-headed blackbirds.

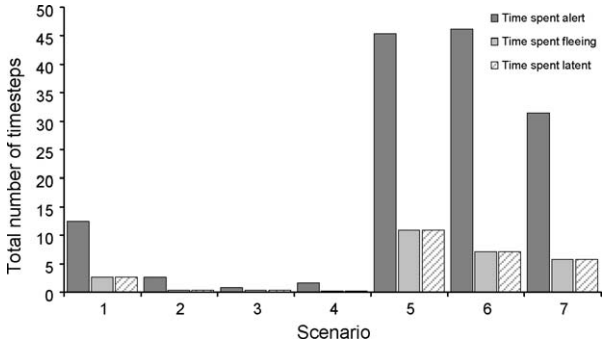

Fig. 3 – Total number of timesteps yellow-headed blackbird spent alert, fleeing and latent following a disturbance event while foraging.

3.4. *Discussion*

From the results of the simulation runs, it is clear that anthropogenic disturbance does not negatively influence yellow-headed blackbird breeding success. In each scenario, females were collecting and delivering an adequate number of food items to their young. This suggests that the majority of their foraging range, within and adjacent to the hemi-marsh, was predominantly disturbance free. However, where the main path cuts across the southern edge of the female yellow-headed blackbirds' foraging range disturbance events did occur. In particular, where the main path intersected a greater proportion of this range it resulted in higher levels of disturbance-related behaviour (as observed in Scenarios 5, 6 and 7).

Table 3 – Yellow-headed blackbird results of statistical analysis for (a) behavioural responses, (b) use habitats types and (c) interception of pathways.

		d.f.	Sum of squares	Mean square	*F* value	Pr > *F*	Multiple comparison of scenarios based on REGW tests
(a)							
Behavioural responses (based on number of timesteps spent in each behavioural mode)	Foraging	6	20607.48571	3434.58095	2.12	0.0819	
	Alert	6	12646.28571	2107.71429	30.18	<0.0001	Scenarios 5, 6 and 7 significantly differs from 1, 2, 3 and 4
	Fleeing	6	523.8857143	87.3142857	23.51	<0.0001	Scenario 5 significantly differs from 6 and 7, from 1, 2, 3 and 4
	Latent	6	523.8857143	87.3142857	23.51	<0.0001	Scenario 5 significantly differs from 6 and 7, from 1, 2, 3 and 4
	Feeding young	6	330.571429	55.095238	1.93	0.1110	
	Returning to feed young	6	5029.8	848.8	0.36	0.8996	
	Homing	6	75369.3714	12561.5619	2.55	0.0429	
	Wilks' Lambda				4.42	<0.0001	
	Pillai's Trace				1.88	0.0041	
	Hotelling-Lawley Trace				14.73	<0.0001	
	Roy's Greatest Root				108.61	<0.0001	

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Table 3 (*Continued*)

		d.f.	Sum of squares	Mean square	*F* value	Pr > *F*	Multiple comparison of scenarios based on REGW tests
(b)							
Use of habitat types (based on number of timesteps spent in each habitat)	Hemi-marsh	6	26659.54286	4443.25714	2.21	0.0724	
	Wet savannah	6	5923.08571	987.18095	1.08	0.3969	
	Forested wetland	6	175.3714286	29.2285714	1.05	0.4162	
	Wet prairie	6	222.	37	1.09	0.3950	
	Black willow marsh	6	8.1714	1.3619	0.81	0.5676	
	Wilks' Lambda				1.24	0.2145	
	Pillai's Trace				1.25	0.1968	
	Hotelling-Lawley Trace				1.23	0.2473	
	Roy's Greatest Root				4.08	0.0046	
(c)							
Pathways (based on number of timesteps spent within detection distance of each pathway)	All pathways	6	1861838.171	310306.362	791.40	<0.0001	Scenario 5 significantly differs from 6, from 7, from 1, from 2 and from 3 and 4
	Main pathway 1	6	1897222.171	316203.695	844.14	<0.0001	Scenario 5 significantly differs from 6, from 7, from 1, from 2 and from 3 and 4
	Main pathway 2	6	0.74285714	0.12380952	1.73	0.1501	
	Bird blind pathway 1	6	154.5714286	25.7619048	7.48	<0.0001	Scenarios 1, 4, 2, 3, and 7 significantly differ from 5 and 6
	Bird blind pathway 2	6	12.17142857	2.02857134	9.47	<0.0001	Scenarios 2 and 3 significantly differ from Scenarios 1, 4, 5, 6 and 7
	Observation tower pathway	6	0	0	–	–	
	Wilks' Lambda				16.02	<0.0001	
	Pillai's Trace				3.48	<0.0001	
	Hotelling-Lawley Trace				153.92	<0.0001	
	Roy's Greatest Root				927.04	<0.0001	

Although the responses of the yellow-headed blackbird to recreationists in the park will not have a significant impact on their breeding success, SODA has demonstrated that the level of disturbance experienced by foraging females dramatically increases amongst those scenarios where the main pathways are within 15 m of the hemi-marsh. This will potentially manifest as an avoidance of the area in proximity to and beyond the pathways by the birds (Pearce-Higgins et al., 2007; Knight and Cole, 1995a). As a result, this could lead to a reduction in the number of yellow-headed blackbirds observed at bird blinds positioned along the edge of the hemi-marsh (George and Crooks, 2006; Guillemain et al., 2007). At a broader level, this restricted use may cause Hegewisch Marsh yellow-headed blackbirds to nest in alterative marshes. Such scenarios may therefore not be conducive to the objectives set out for the proposed park, as they may deprive the public visiting the park the opportunity to see this state protected species.

Furthermore, the site is currently being used by other species of rare wetland birds and waterfowl, including common moorhen (*Gallinula chloropus*) and Wilson's phalarope (*Phalarope tricolour*) (CDOE, 2006). The presence of these other species of interest enhances the overall ecological quality and diversity of the area. By demonstrating the disturbance-related effects of various path designs on the yellow-headed blackbird (a species considered to be fairly tolerant of disturbance; Ward, personal communication), SODA has also given us an insight into the general impact these path proposals are likely to have on other avian species using the

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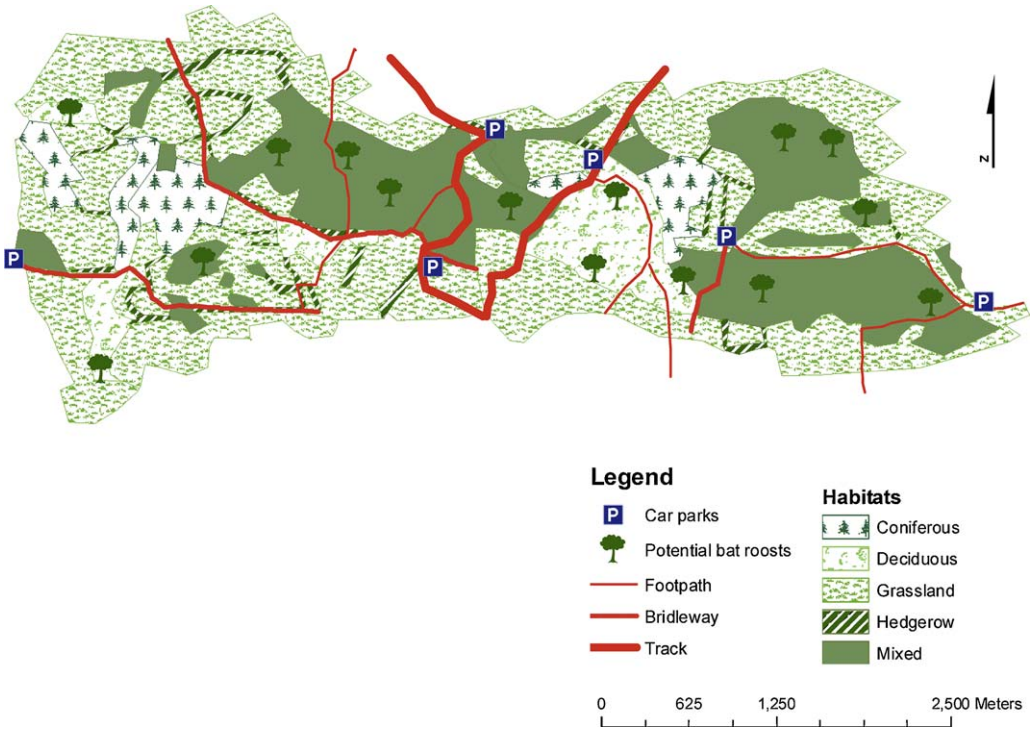

Fig. 4 – Map of Chedworth Wood, Gloustershire, delineating its habitat types, the placement of pathways throughout the site, and the location of potential barbastelle bat maternity roosts and car path entrances.

hemi-marsh. Consequently, if Hegewisch Marsh is to reach its full potential as a nature reserve, a main path more than 10 m from the edge of the hemi-marsh is recommended.

4. Case study 2: the barbastelle bat

4.1. *Introduction*

According to UK population monitoring data, despite being widely distributed in England and Wales (with population centres in the south-west and mid-west of England, and Norfolk) the barbastelle bat appears to be rare and declining in numbers (Nowak, 1994; Altringham, 2003). As a consequence, it has been identified as a conservation priority. Thus, recovery programmes have been initiated to establish baseline data about this species and identify its habitat requirements (Greenaway, 2004; Anon., 1992; Hutson et al., 2001). From such studies it has been ascertained that a potential threat and cause of the bat's population decline is disturbance. This presents an ideal opportunity for the application of SODA to investigate whether the sensitivity of this species to human-disturbance has fitness consequences.

For this case study, we focused our investigations on the breeding season, known to be a vulnerable period in the barbastelle bat's life history when anthropogenic disturbance could have severe repercussions on breeding success, i.e. when disturbance could potentially lead to the abandonment of young. From early June to late August, females setup maternity roosts beneath loose bark, behind thick stemmed ivy, within the cracks and slits of trunks and branches and in the hollows of veteran trees in ancient woodlands (Altringham, 2003; Greenaway and Hill, 2004). As an anti-predator defence regularly switching roost sites reduces a barbastelle bat's chances of predation in the roost (Anon., 2005; Altringham, 2003; see also Lewis, 1995). This energetically expensive behaviour, involving the transportation of young to a new maternity roost, is also exhibited when the bats are disturbed by a predator or what they perceive to be a predator (Billington, unpublished data; Russo et al., 2004). Conceptually, above a certain frequency the energetic demand of roost switching is expected to exceed available energetic budgets, at which point a female will abandon her young the next time a disturbance event occurs. Using SODA to investigate this threshold may have important implications for the management of suitable habitat containing or adjacent to potential maternity roosts.

4.2. *Methods*

4.2.1. *The study site*

For this case study a site was selected in which barbastelle bats were known to be present. Chedworth Wood, an area of ancient beechwood woodland in Gloucestershire, constituted suitable habitat with ample foraging opportunities and a high density of potential roost sites. Although, the presence of barbastelle bats in the wood has been confirmed (Palmer, personal communication), no maternity colonies have been identified to date. This presents an additional opportunity to investigate whether anthropogenic disturbance levels in Chedworth Wood could be preventing the bats from successfully reproducing in the area.

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4.2.2. Model parameters

4.2.2.1. *Scenario*. The parameters for the case study are listed in Table 2. Five habitat types were identified using aerial photographs of Chedworth Wood (Fig. 4). Once groundtruthed these were mapped in ArcGIS, along with the location, length and type of the roads and paths interspersed within the wood and the position of potential bat roosts and public entrance points to the wood. A potential roost site was identified as a mature tree with one or more features suitable for a maternity roost, such as peeling bark, cracks in branches, thick stemmed ivy and hollows (Russo et al., 2004; also see Menzel et al., 2002 as a similar example). In Chedworth Wood there may be as many as 30 trees that meet these criteria. Of these 15 trees were identified as being of optimum quality constituting appropriate refugia for a maternity roost (Fig. 4). However, as trees mature and become weathered over time the suitability of a particular roost site is likely to change and it is a natural process in any established woodland that there will be a constant succession of available roosts (Swystun et al., 2007; Kalcounis-Ruppell et al., 2005). A sensitivity analysis was therefore undertaken to investigate whether the location of the 15 maternity roost trees identified in this case study significantly influenced the propensity of barbastelle bats. Five additional scenarios were run in which all parameters were kept the same, except for the location of the roosts (see Table 4). In each of these five alternative scenarios, the position of the roost trees were randomly generated within suitable habitat types using Hawth's Analysis Tools for ArcGIS (Beyer, 2004) and the degree of variation between the outcomes of each scenario was compared.

The simulation runtime denotes the length of time the maternity roosts are formed, approximately 61 days.

4.2.2.2. *Recreationist*. Based on the general patterns of visitor activity to Chedworth Wood, the frequency and density of virtual recreationists were varied over a series of simulations to investigate the effects of different levels of disturbance on female barbastelle bats in their maternity roosts. The nature and isolated location of the Chedworth Wood in the Gloucestershire countryside attracts four types of recreationist; horse riders, walkers with and without dogs and mountain bikers. Each type of recreationist is also associated with certain types of pathways. The UK Countryside code dictates that horse riders are only permitted to use designated bridleways and tracks, and these same routes are generally used by mountain bikers. In contrast, walkers are less likely to use tracks, but will commonly use foot paths and dog walkers will often move unrestricted throughout the wood. The latter therefore constituted both the Types 1 and 2 virtual recreationists.

Five scenarios were run to investigate the relationship between the frequency and density of visitor activity and the level of response by bats to this disturbance (see Table 4). As a baseline for this investigation, the first scenario included virtual recreationist activity parameters equivalent to the current patterns of activity (as an average) in the study site (see Table 2). In the second scenario activity parameters representing peak activity levels (i.e. weekend usage) in the Chedworth Wood were applied for the duration of the simulation. While in the third scenario activity levels equivalent to the least active period in the wood (i.e. weekdays) were applied. Finally, the last two scenarios were intermediates of the first and second scenario, and the first and third scenario, respectively.

An additional five scenarios were run to assess the extent by which each type of recreationist contributed to the overall

Table 4 – The various scenarios applied to SODA for the barbastelle bat case study.

Scenario	Activity levels	Roost tree location	Recreationists present
1	Weekly average	Positions correspond to potential roost trees identified in Chedworth Wood	Walkers; type 1 dog walkers; type 2 dog walkers; mountain bikers; horse riders
2	Peak (equivalent of weekends)	See Scenario 1	See Scenario 1
3	Intermediate between peak and average activity	See Scenario 1	See Scenario 1
4	Low (equivalent of weekdays)	See Scenario 1	See Scenario 1
5	Intermediate between low and average activity	See Scenario 1	See Scenario 1
6	See Scenario 1	Roost trees positions randomly (alternative 1)	See Scenario 1
7	See Scenario 1	Roost trees positions randomly (alternative 2)	See Scenario 1
8	See Scenario 1	Roost trees positions randomly (alternative 3)	See Scenario 1
9	See Scenario 1	Roost trees positions randomly (alternative 4)	See Scenario 1
10	See Scenario 1	Roost trees positions randomly (alternative 5)	See Scenario 1
11	See Scenario 1	See Scenario 1	Type 1 dog walkers; type 2 dog walkers; mountain bikers; horse riders
12	See Scenario 1	See Scenario 1	Walkers; type 2 dog walkers; mountain bikers; horse riders
13	See Scenario 1	See Scenario 1	Walkers; type 1 dog walkers; mountain bikers; horse riders
14	See Scenario 1	See Scenario 1	Walkers; type 1 dog walkers; type 2 dog walkers; horse riders
15	See Scenario 1	See Scenario 1	Walkers; type 1 dog walkers; type 2 dog walkers; mountain bikers

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disturbance of female barbastelle bats in the wood (see Table 4). All the parameters applied in these scenarios were equivalent to those used in Scenario 1. However, a different type of recreationist was left out of each, i.e. walkers, type 1 dog walkers; type 2 dog walkers, mountain bikers and horse riding.

4.2.2.3. *Wildlife*. In the UK maternity roosts typically contain up to 20 females (Altringham, 2003). From the size of Chedworth woodland and number of roosting opportunities, it was reasoned that the wood could support a nursery colony of 20 individuals. Subsequently, 20 virtual animals were incorporated in each simulation. Based on known activity patterns, foraging was set to occur between 9:30 p.m. and 5:30 a.m. unhindered by human activities and for the other 16 h of the day females remained in their roosts (Wells, personal communication; Rydell et al., 1996). For the physiological parameters, the minimum recorded weight (6 g; Altringham, 2003) of the barbastelle bat was used as an indicator (the energetic threshold value) that available fat reserves had been exhausted. Thus, when a female's body weight falls below this threshold value, it was deemed that the energetic cost of transporting young to a new roost could not be met and that the female had abandoned her young. The energetic costs and gains of each behavioural mode were extrapolated from the relationship between known Microchiropteran body weights and their metabolic rates (Turbill and Geiser, 2006; Willis et al., 2005a,b; Geiser and Brigham, 2000). In addition, as an alternative feature in SODA, females disturbed from their roosts were set to flee from the roost with their young and randomly relocate to one of the other 14 potential roost sites.

4.2.2.4. *Analysis*. A statistical analysis was undertaken to establish whether barbastelle bats abandon their young in their maternity roosts due to disturbance and at what level of anthropogenic disturbance this occurs. From the output of each simulation run, we analysed response variables in a multivariate analysis of variance (MANOVA) to test the hypothesis that the average value of each response variable was not influenced across replicates or between scenarios. Response variables were also decomposed into separate ANOVAs to examine each response variable's sensitivity to the alternative scenarios. The MANOVA was computed using PROC GLM in SAS (1988). In addition, Ryan–Einot–Gabriel–Welsch multiple range tests were used to examine the relative ranks of the alternative scenario for each response variable.

For the barbastelle bat case study, scenarios were analysed as three separate groups (as conceived above in the Scenario and Recreationist sections), in which related-response variables (i.e. number of times bats switch roost sites as a result of disturbance, timesteps spent alert, timesteps spent fleeing and the energy status of female bats at the end of breeding season) were tested to assess whether there was significant variation within each group (see Table 4 for a full list of the scenarios). For the purposes of the analysis, group 1 included Scenarios 1–5 investigating the relationship between the frequency and density of visitor activity and the level of response by bats to this disturbance. Scenario 1 represented visitor activity parameters equivalent to the current patterns of activity in Chedworth Wood; Scenario 2 incorporated activity parameters representing peak activity levels; Scenario 3 represented an intermediate of Scenarios 1 and 2; Scenario 4 represented activities levels equivalent to the least active period; and Scenario 5 represented an intermediate of Scenarios 1 and 4. Group 2 included Scenario 1 and Scenarios 6–10 investigating whether the location of maternity roost trees significantly influenced the propensity of barbastelle bats to abandon their young. Scenarios 6–10 each represent a different set of randomly generated roost trees locations (as discussed in the *Scenario* section of this Methodology). Finally, group 3 included Scenario 1 and Scenarios 11–15 investigating the extent by which each type of recreationist contributed to the overall disturbance. In Scenario 11 walkers were not included in the simulation; in Scenario 12 type 1 dog walkers; in Scenario 13 type 2 dog walkers; in Scenario 14 mountain bikers; and in Scenario 15 horse riding were left out of the simulation.

4.3. *Results*

We found that among the various scenarios, the maximum number of female barbastelle bats to abandon their young did not exceed 2 individuals (<5% of females) in any of the replicates for all scenarios (1–15).

Varying visitor density and frequency was found to cause significant variation in the number of disturbance events experienced by the bats (see Table 5a). Predictably, bats were disturbed more when visitor numbers were equivalent to weekend attendance (Scenario 2) and disturbed less when numbers were equivalent to a weekday turnout (Scenario 4). Between these two extremes, disturbance levels were appropriately incremented amongst the three remaining intermediate scenarios (Scenarios 1, 3 and 5), delineating a linear relationship between disturbance responses and visitor numbers.

Randomly distributing the roost trees throughout the appropriate habitat types within the study site had a significant effect on the number of disturbance events experienced by the barbastelle bat breeding population (see Table 5b). The source of this variation was generated by Scenarios 7 and 9. By chance, Scenario 7 had the more roost sites located in close proximity to car park entrances. By contrast, the least roost sites were positioned near car park entrances in Scenario 9. As a result of this finding, a regression analysis pooling all observations from Scenarios 6 to 10 was undertaken to distinguish if there was a relationship between bat disturbance and the location of car park entrances relative to the position of potential roost trees. For this the number of timesteps bats spent alert at a particular roost site and number of bats to have fled from that same site were regressed against the minimum distance of each roost from a car park, the average distance of each roost from a car park and the standard deviation from these average distances. A variable selection procedure was used to compare all possible models based on Mallow's C (SAS, 1988). Two best models were selected as indistinguishable for each other (for alert $P \leq 0.0005$; for fleeing $P \leq 0.0001$ in both models). The first

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Table 5 – Barbastelle results of statistical analysis for (a) varied visitor frequency, (b) random distribution of maternity roosts, and (c) varied types of recreationists.

		d.f.	Sum of squares	Mean square	F value	Pr > F	Multiple comparison of scenarios based on REGW tests
(a)							
Varied visitor frequency	Number of times females switch roosts	4	663.045970	165.761493	21.77	<0.0001	Scenario 2 is significantly different from 1 and 3, 1 is significantly different from 5, from 4
	Number of timesteps spent alert	4	3103.49240	775.87310	23.53	<0.0001	Scenarios 1 and 2 are significantly different from 5 and 3, from 4
	Number of timesteps spend fleeing	4	1768.804903	442.201226	33.78	<0.0001	Scenario 2 is significantly different from 1, from 3 and 5, from 4
	Total energy reserves at end of simulation run.	4	5.70571770	1.42642943	19.57	<0.0001	Scenario 4 is significantly different from 5 and 3, 5 is significantly different from 2 and 1
	Wilks' Lambda				11.62	<0.0001	
	Pillai's Trace				10.01	<0.0001	
	Hotelling-Lawley Trace				12.85	<0.0001	
	Roy's Greatest Root				40.70	<0.0001	
(b)							
Random distribution of maternity roosts	Number of times females switch roosts	7	88.625364	12.660766	2.02	0.0533	
	Number of timesteps spent alert	7	292.354111	41.764873	1.46	0.1836	
	Number of timesteps spend fleeing	7	299.299754	42.757108	3.61	0.0010	Scenarios 7 and 9 significantly differ from 1, 6, 8 and 10
	Total energy reserves at end of simulation run.	7	9.8	1.40435808	12.11	<0.0001	Scenarios 1 significantly differ from 6, 7, 8, 9 and 10
	Wilks' Lambda				8.96	<0.0001	
	Pillai's Trace				7.94	<0.0001	
	Hotelling-Lawley Trace				9.83	<0.0001	
	Roy's Greatest Root				29.82	<0.0001	
(c)							
Varied presence of recreationist	Number of times females switch roosts	5	1931.583309	386.316662	75.68	<0.0001	Scenario 13 is significantly different from 1, 11, 12, 14 and 15
	Number of timesteps spent alert	5	8015.82336	1603.16467	39.53	<0.0001	Scenario 13 is significantly different from 12, with 15 significantly different from 11 and 14
	Number of timesteps spend fleeing	5	2658.557037	531.711407	45.49	<0.0001	Scenario 13 is significantly different from 12, 14, 15, with 1 significantly different from 11
	Total energy reserves at end of simulation run.	5	5.04455359	1.00891072	11.43	<0.0001	Scenario 13 is significantly different from 1, 11, 12. 14 and 15
	Wilks' Lambda				18.38	<0.0001	
	Pillai's Trace				12.91	<0.0001	
	Hotelling-Lawley Trace				25.08	<0.0001	
	Roy's Greatest Root				90.59	<0.0001	

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model used a combination of standard deviation and minimum distance values from roosts to car parks, while the second model used the minimum distance values alone. In both cases, under 10% of the variation in disturbance events at roost sites was attributed to proximity with car parks (for alert $R^2 = 0.0552$ and 0.0465; for fleeing $R^2 = 0.0961$ and 0.0866, respectively), therefore the majority of variation was due to other factors.

From the analysis of the third set of scenarios, which investigated whether the levels of disturbance experienced by bats in roosts were attributed to a particular type of recreationist or combination of recreationists, a significant level of variation was revealed (see Table 5c; $P \leq 0.0001$ for all variables across all MANOVA tests). The source of this variation was associated with Scenario 13, where a very dramatic drop in disturbance events was observed when walkers with dogs (Type 2 virtual recreationists), were not included in the simulation (seen as a decrease from >200 disturbance events consistent with all the other scenarios to <30 disturbance events). A minor, but significant, reduction in the number of alert and fleeing responses in Scenario 11 (walkers were not included) also lead to some observable disparity between the scenarios. However this did not reflect on energetic status of the bats or the number of times they switched roost sites. Similarly, Scenario 1 (which included all recreationists) had a significantly higher number of fleeing responses and Scenario 14 (excluding mountain bikers) had a significant reduction in alert responses.

4.4. *Discussion*

From the results of the simulation runs, anthropogenic disturbance does not appear to be negatively influencing barbastelle bat breeding success. There are, however, two assumptions, which could potentially affect the outcome of the simulation output. The first assumption is that following a disturbance event fleeing females randomly select a new roost site. In reality, it is possible that roosts are selected based on distance and direction from the disturbance event. Consequently, the total energetic cost to female barbastelle bats for this type of fleeing behaviour may have been an over- or underestimated in the simulation runs. The second assumption is that females abandon their young when their energy reserves have reached a critical threshold of 6 g (their minimum weight). It is plausible that females could abandon their young prior to this threshold, therefore before the females are themselves at risk and because they can have young the following year (Wells, personal communication). If this is the case, an increase as small as 0.2 g to the threshold would lead to 77% of females abandoning their young when visitor activity levels are highest (Scenario 2), 21% at the lowest levels (Scenario 4) and 47% at intermediate visitor density and frequency (Scenario 1). This implies that if visitor activity in Chedworth Wood was equivalent to Scenario 1, barbastelle bats would have a 53% probability of success. Subsequently, local population numbers of the barbastelle bat in the area would be stable if there were no other influencing factors. However, the major difference between Chedworth Wood and the simulated version (Scenario 1) is that Chedworth Wood is primarily maintained by its landowners for pheasant hunting in the winter (Bradford, personal communication). As a consequence, access to the majority of the area is prohibited and visitors are restricted to the Public Rights of Way (designated footpaths and bridleways). Thus Type 2 virtual recreationists (recreationists with unrestricted movement) are not normally present in Chedworth Wood. This type of recreationist was shown to be the major source of disturbance to female barbastelle bats in the simulation, therefore Chedworth Wood will not experience equivalent levels of disturbance. In conclusion, SODA simulation suggests that anthropogenic disturbance of the barbastelle bat is not preventing the females from establishing maternity roosts in Chedworth Wood. Given the suitability of Chedworth Wood, it is likely that a breeding population of barbastelle bats is present in the wood, but the maternity roosts have yet to be discovered (potentially because individuals switch between available roosts frequently (Wells, personal communication). Alternatively, factors other than human disturbance may be influencing the use of the potentially suitable roost trees within the wood.

SODA demonstrated that the greatest cause of anthropogenic disturbance to barbastelle bats would be the presence of recreationists with unrestricted movement. It also revealed that the probability of this type of recreationist coming within detection distance of a potential roost site is increased with increasing proximity to car park entrances (i.e. where such recreationists enter a woodland site). Finally, SODA demonstrates the implications of the energy threshold parameter applied to the simulations, suggesting that if this value were higher, the densities and frequencies of unrestricted recreationists could have a detrimental affect on barbastelle bat breeding populations. Further investigation of this critical threshold value (i.e. the weight of females when they choose to abandon their young) is required to understand the impacts of human disturbance on these bats.

These insights represent a general pattern in the behavioural responses of barbastelle bats to anthropogenic disturbance and are not specific to Chedworth Wood. SODA has therefore increased our understanding of this species of conservation concern, provided valuable information of use to recovery programmes and uncovered insights which could be considered when designing management plans for sites with barbastelle bats.

5. Discussion

Vaske et al. (1995) suggest that identifying the impacts of recreation on wildlife is difficult to do, particularly because there is no single, predictable behavioural response to recreational use. We propose that SODA, an IBM model specifically designed to enable a user to understand how wildlife is affected by recreational use, can be utilised to overcome this issue (see recommendations in Flather and Cordell, 1995). From the two case studies given in this paper, we have been able to demonstrate a number of SODA's capabilities and applications. These are summarised below.

In a basic application, SODA can provide an insight into the consequences of the behavioural responses of wildlife to anthropogenic disturbance under a set of site-specific and activity-specific conditions equivalent to any given site (Weller and Spatcher, 1965). To understand how wildlife is

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affected by recreational use, it is necessary to consider a range of possible causes of disturbance (Vaske et al., 1995). SODA allows the user to create a variety of virtual recreationists, each with specific characteristics relating to their behaviour and the type of activity undertaken.

As the relationship between recreational use and disturbance response can not be considered as simple or uniform (Vaske et al., 1995), SODA allows the user to investigate the degree of influence of different types of activity and/or recreationists (as behavioural variations can be applied) on the overall disturbance of wildlife (Knight and Cole, 1995b); as demonstrated in the barbastelle bat case study. Subsequently, not only are the cumulative effects of simultaneous activities revealed, but also the synergisms or interactions between recreational activities and the level of contribution of each activity (Bell and Austin, 1985).

In some instances wildlife individuals may have differing tolerances for interactions with recreationists (Vaske et al., 1995). SODA has the flexible option of enabling the user to specify behavioural and physiological characteristics for virtual wildlife individuals.

As the outcome of recreational use may depend on the time and place of the human activity (Vaske et al., 1995), SODA allows the user to vary the density and frequency of recreationists over a period of 24 h. It also permits the user to specify the presence or absence, density and frequency of visitors along individual pathways and trails, or moving freely throughout a site (also demonstrated in the barbastelle bat case study). With ecotourism and outdoor recreational activities expected to increase, SODA can provide foresight into the cumulative effects an increasing number of recreationists will have on wildlife. By manipulating recreationist characteristics, such as frequency of use and density of visitors, to represent anticipated visitor activity patterns, a user can investigate these effects and appropriate management strategies devised in order to counteract any disturbance-related negative impacts (HaySmith and Hunt, 1995). SODA can also be used to investigate the effectiveness of a range of management strategies (Stillman et al., 2001), aiding the user to adapt and evolve management plans that do not simply minimise wildlife disturbance but provide a balance between wildlife and recreation (Larson, 1995; Knight and Cole, 1995b; Manfredo et al., 1995).

As demonstrated in the yellow-headed blackbird case study, SODA can also be used to investigate the effects of proposed ecotourism and recreational activities on wildlife or proposed land-use changes, such conversion of disused land to a nature reserve or park facility (Stillman et al., 2000).

Finally, in all applications of SODA sensitivity analysis can be used to ascertain whether the parameters input have a significant influence on the resulting output thereby establishing priorities for future research. Management strategies can then be chosen based on confidence or prompt further field studies to address areas of uncertainty. This feature was used twice in the barbastelle bat case study, first when the position of roost sites was investigated and second more informally when the critical threshold value used to determine whether females abandoned their young provoked uncertainty.

Currently SODA does not incorporate a number of features that may be of value to our understanding of the wildlife–recreationist relationships. Modifications to the model could comprise the inclusion of interactions that occur between individuals virtual animals of the same species and between individuals of different species. Such interactions may affect habitat-use, foraging abilities and even disturbance-related responses. Similarly, the inclusion of habituation and sensitisation may be a useful feature in the model, as certain species may perceive a frequent disturbance as 'expected' and non-threatening (Knight and Cole, 1995a,b; MacArthur et al., 1982; Conomy et al., 1998) or alternatively as more dangerous as encounters accumulate (Papouchis et al., 2001). As a result, wildlife responses may vary over time. Including a feature which allows the user to specify whether the frequency and magnitude of disturbance will influence wildlife responses over a particular timescale, may reduce potential over- or under-estimates of impact that could occur with wildlife species that exhibit such characteristics. Similarly, seasonal changes in disturbance-related responses of wildlife cannot be investigated with a single model run currently using SODA. The ability for a user to vary responses, food available and recreationist characteristics is a feature that would allow for more accurate estimates of the impact of recreationists on wildlife. Finally, although SODA was not constructed as a population model, it could currently be used for such purposes by iteratively feeding the output from one simulation into another. Through a succession of simulations a relatively basic demographic analysis could be conducted to gain insights into population responses. Using SODA in this context would be cumbersome and thus we hope in the future to build a population function into the SODA framework to produce an individual-based behavioural model aptly named SODA Pop.

It is our intention that SODA continues to evolve incorporating these additional features, but as demonstrated in the case studies, we consider the current version of SODA, with its flexible combination of behavioural modelling and GIS analysis, to be a very useful spatially explicit conservation tool in the management of wildlife–recreationist interactions.

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