

Research Paper

Simulating the responses of forest bird species to multi-use recreational trails



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HIGHLIGHTS

- We model the potential recreational disturbance of a bird community.
- We evaluate three proposed trail designs and invasive vegetation removal.
- Trail design selection is highly species dependent even between species of concern.
- Invasive vegetation removal did not have a cumulative impact on bird disturbance.

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ABSTRACT

Although non-consumptive recreation can promote wildlife preservation and add socio-economic value to parks and nature reserves, such activities can have negative implications for wildlife. For sensitive species, recreation can lead to displacement, influence breeding success and reduce survival. Thus managing recreational activities by regulating visitor access, densities and frequency can effectively reduce human–wildlife interactions. In many instances, simulation modeling has been used as a management tool, as it allows the user to explore the impact of alternative park designs and management strategies on wildlife in a risk-free environment. Such exercises tend to focus on single species, generally a species of conservation concern, on which management decisions are based. As an alternative approach, we used a modeling simulation to compare the disturbance caused by different trail designs, trail use rates and the management of invasive vegetation (i.e., removal) on a forest community of breeding birds at a state park in Indiana, USA. Our multi-species approach revealed that an appropriate trail design for one species was not necessarily appropriate for another, even among species of concern. We therefore caution that management based on a single high profile species could have far-reaching implications on the local community. We also found that invasive vegetation removal did not have a cumulative influence on the recreational disturbance experienced by birds. This study demonstrates that by identifying and comparing the differences between individual species within a community, we gain valuable insights that can be used to devise more resilient long-term management strategies that aim to preserve biodiversity.

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1. Introduction

Natural resource-based outdoor recreation can contribute to the conservation of biodiversity by promoting public support for

wildlife preservation and adding socio-economic value to natural areas (Christ, Hillel, Matus, & Sweeting, 2003; Stronza & Durham, 2008). However, recreational activities can also have negative impacts on wildlife populations (Knight & Gutzwiller, 1995; Rochelle, Pickering, & Castley, 2011), thereby decreasing an area's ecological value (Reed & Merenlender, 2008). For example, the development of recreation infrastructure can directly degrade habitat (Christ et al., 2003; Laiolo, 2004). In addition, recreation can have indirect effects when wildlife allocate time and energy reacting to humans as though they were potential predators (Bennett, Quinn, & Zollner, 2013; Frid & Dill, 2002). Continued disruptions to

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natural behavior (e.g. foraging) can in turn impact energetic budgets (Houston, Prosser, & Sans, 2012) and parental care (Verhulst, Oosterbeek, & Ens, 2001), potentially affecting population viability in areas with high levels of disturbance (Kerbirou et al., 2009). Thus for some species, recreational activities can have substantial fitness consequences (Beale & Monaghan, 2004) and population-level effects (Creel & Christianson, 2008). For these vulnerable species, managing visitor density and/or frequency may be an effective strategy to alleviate the negative implications of human–wildlife interactions (Cole, 1993; Rodríguez-Prieto & Fernández-Juricic, 2005).

In natural areas, a network of trails can be used to direct recreationist movements, potentially influencing both visitor experience and level of disturbance to wildlife. The design of this network may, therefore, indirectly affect wildlife by changing the spatial and temporal patterns of human–wildlife encounters (Cole, 1993; Ferrarini, Rossi, Parolo, & Ferloni, 2008). Trail design is usually informed by standard practices, such as (1) reducing trail density in pristine areas, (2) avoiding placing long stretches of trail along stream/river banks, and (3) using vegetation or topography to screen sensitive wildlife from recreationists (Flink, Olka, & Searns, 2001; Hellmund, 1998). However, such practices are often too general to obtain a design that effectively balances recreation and conservation in a given location. More detailed recommendations can be generated from empirical research (e.g., Fernández-Juricic, Jiménez, & Lucas, 2001; Fernández-Juricic, Zollner, LeBlanc, & Westphal, 2007). However, studies investigating optimal trail networks may require considerable logistical resources to manipulate the levels of human disturbance and assess wildlife responses, which could actually be detrimental for species of conservation concern.

The application of simulation models can help address the conflicts associated with managing recreational activities in natural areas (Beissinger et al., 2006; Stillman & Goss-Custard, 2010). Simulation models, particularly individual- or agent-based models (McLane, Semeniuk, McDermid, & Marceau, 2011), can provide detailed and cost-effective answers to local management questions, and they are especially suited to predict disturbance outcomes for a wide variety of management scenarios before they are implemented in situ (Bennett et al., 2009; Taylor, Green, & Perrins, 2007).

Most studies that model wildlife responses to recreation focus on single species (e.g., Liley & Sutherland, 2007; Taylor et al., 2007). However, recommendations based on the responses of one species can produce management decisions that are unsuitable for other species, because species vary in their sensitivity to disturbance and/or spatial/temporal distribution. Thus the implementation of species-specific management may contradict the fundamental multi-species conservation goals that many agencies are striving to achieve (Smith & Zollner, 2005). Furthermore, many of the simulation models currently applied to human–wildlife interactions are only associated with discrete landscape features, like shorelines or nest colonies (e.g., Beale, 2007; Bennett et al., 2011). However, conservation practitioners may face situations where the species of concern are widespread across a fairly homogeneous forested area. In these cases, the application of standard practices, like placing the trail as far from a nesting colony as possible or avoiding placing trails through a rare critical habitat (Hellmund, 1998), may not be an option for some species. SODA (Simulation of Disturbance Activities; Bennett et al., 2009, 2011) is a flexible and spatially explicit individual-based model that can be applied to multiple species and habitats. In this study, we used SODA to develop some principles for the implementation of a multi-use recreational trail on a breeding bird community in a natural area.

Our goal was to assess the degree to which different trail designs in a forested area previously subject to low levels of recreation, would potentially affect the frequency of disturbance experienced by the local forest bird community. We hypothesize that trails that

expose species to increased frequencies of disturbance by recreationists across multiple patches of suitable habitat could lead to a reduction in the spatial and temporal availability of resources (Rodríguez-Prieto & Fernández-Juricic, 2005), and eventually lower chances of population persistence at local scales (Fernández-Juricic, 2002). These fitness costs associated with human disturbance are typically a consequence of animals responding to human activity as they do to threats from predators (Frid & Dill, 2002).

We modeled the responses of 9 virtual bird species (differing in sensitivity to recreationists, microhabitat preferences, and breeding densities) to virtual recreationists (pedestrians and cyclists) along three alternative trail designs during the breeding season. Additionally, managers planned to remove invasive honeysuckle (*Lonicera* spp.) considered to be a threat to native ecosystems in North America (Hutchinson & Vankat, 1997). However, honeysuckle provides dense refuge for many bird species (McCusker, Ward, & Brawn, 2010), which could change bird tolerance to recreationists (Fernández-Juricic et al., 2001; Fernández-Juricic, Jiménez, & Lucas, 2002). Under these conditions, we hypothesized that honeysuckle removal would increase the frequency at which birds encountered recreationists. Therefore, a second goal was to evaluate whether the impact of each of the alternative trail designs differed in habitats with or without honeysuckle. Furthermore, since the process of removing honeysuckle takes multiple years to complete, we also investigated how different removal strategies (i.e., a staggered removal starting with honeysuckle near to or far from the trail) would affect the frequency at which birds encountered recreationists. We used the insights gained from the simulation to derive some recommendations on trail placement and honeysuckle management.

2. Methods

2.1. Study area

Fort Harrison State Park is a forested preserve located near the city of Indianapolis in central Indiana, USA (39°52'10.21" N; 86°1'18.06" W; Fig. 1). It is a 680 ha area, covered by predominantly young deciduous forests, lakes, riparian habitats, picnic and lawn areas, and a golf course. Due to its proximity to Indianapolis, the park is popular with recreationists who use its extensive network of trails. The Lawrence Creek Forest Unit is one of the park's better conserved tracts of forest, covering an 84 ha area including several areas of mature forest receiving low to moderate recreational use. Almost half of its area has been invaded by honeysuckle which now constitutes the major component of the forest understory. At the inception of this study the Lawrence Creek Forest Unit had an existing pedestrian trail 2.7 km in length with no bicycle access (Fig. 2a).

2.2. Model overview

SODA is an individual-based model that simulates the movement patterns of wildlife individuals when subject to human disturbance in a spatially explicit virtual environment. Note that a full model description is available in Bennett et al. (2009) and previous applications of the model include simulating the responses of chicks in a Black-crowned Night-Heron colony to alternative path designs (Bennett et al., 2011) and simulating the responses of ovipositing karner blue butterflies (*Lycaeidea melissa samuelis*) to pedestrians (Bennett et al., 2013a), as well as Indiana bats (*Myotis sodalis*) to vehicular traffic (Bennett, Sparks, & Zollner, 2013). Users develop GIS maps to build a virtual environment within the model (environmental inputs), and define a set of variables that characterize both anthropogenic activities (anthropogenic inputs) and the

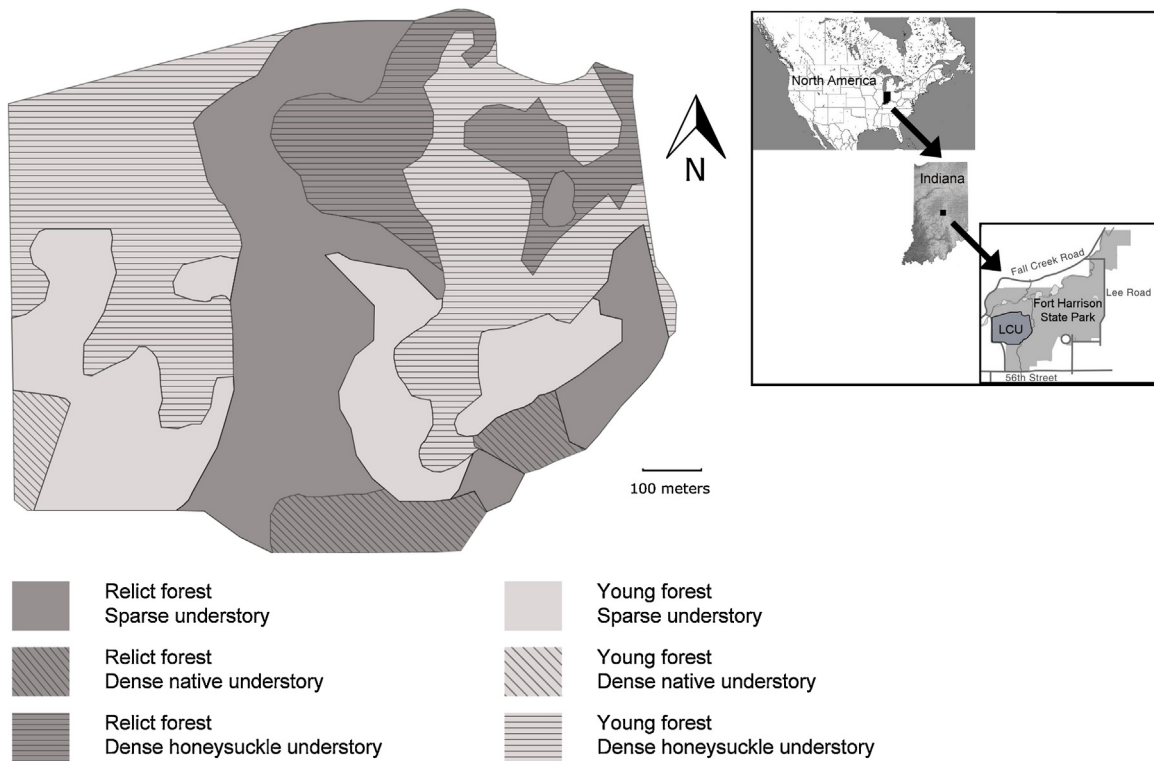


Fig. 1. Habitat map and location of Lawrence Creek Forest Unit (LCU) in Fort Harrison State Park near Indianapolis in central Indiana, USA.

responses of wildlife to these activities (wildlife inputs) in alternative scenarios (Bennett et al., 2009).

2.3. Environmental inputs

The study was focused on nine breeding bird species (see Section 2.5). We set the duration of the simulation at 17 virtual days as this represented the mean brooding period of the species included (range 10–21 days; Poole, 2005). Virtual birds in our model moved from their nests through virtual habitats searching for food and returned to nests to feed nestlings. Human visitors moved only along trails. The behavior (detailed in Section 2.5) and position of each bird and recreationist was updated every 5 min (also used in Bennett et al., 2009, 2011). We considered that this fine-scale time resolution would effectively capture the interactions of birds and recreationists moving in and through the Lawrence Creek Forest Unit. We included three GIS maps in the model, depicting (1) the distribution and types of habitat, (2) placement of the trail, and (3) bird nest locations (see below).

2.3.1. Habitat

Three characteristics were considered when constructing the GIS map delineating habitat types for the simulation model: (1) density of understory, as it influenced both the responses of birds to humans (Fernández-Juricic et al., 2001, 2002), and the distribution of nests across the Lawrence Creek Forest Unit (Poole, 2005); (2) composition of the understory (native versus honeysuckle), thus enabling us to assess the implications of honeysuckle removal, and; (3) age of forest stands, allowing us to vary the distribution of nests across the study area based on species-specific micro-habitat selection (Poole, 2005). We identified two understory densities; dense and sparse, with ‘dense understory’ representing patches with >90% bush cover, while ‘sparse understory’ represented patches with 0–10% of bush cover. We found no patches with intermediate bush cover. The combination of the above resulted in six habitat type classes defined as: (1) relict forest with sparse understory (22.0 ha), (2) young forest with sparse understory (17.5 ha), (3) relict forest with dense native understory (3.9 ha), (4) young forest with dense native understory (1.3 ha), (5) relict forest with dense honeysuckle

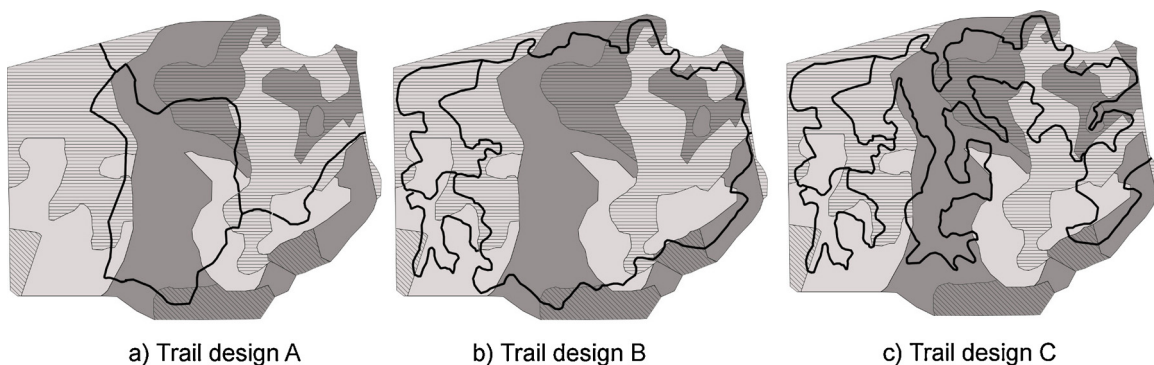


Fig. 2. The three alternative cycle-friendly trail designs proposed for the Lawrence Creek Unit in Fort Harrison State Park near Indianapolis in central Indiana, USA.

understory (10.4), and (6) young forest with dense honeysuckle understory (28.9 ha).

We constructed the habitat GIS map depicting the distribution of the six habitat types across the Lawrence Creek Forest Unit using ArcGIS 9.31 (ESRI, Redlands, California) and data from three different sources (Fig. 1). During the fall of 2009 the Indiana Department of Natural Resources implemented 48 fixed radius 0.4 ha plots that were placed uniformly (130 m between plots) across the Lawrence Creek Forest Unit. We used this information to characterize the density and distribution of understory vegetation across the study area. We used remote sensing images obtained from the USGS National Satellite Land Remote Sensing (NSLRS) database and ground truth data to delineate the extent of the understory vegetation that was composed of invasive honeysuckle. It was feasible to delineate the extent of honeysuckle across the study area in the Normalized Difference Vegetation Index (NDVI) we produced from this imagery because we used a combination of scenes from November 2005, October 2006, and January 2007 (i.e., trees and native shrubs were leafless in the fall but honeysuckle bushes retained their leaves). Finally, the age of forest stands was obtained from a GIS map developed by the Indiana Department of Natural Resources based on historical aerial photographs and ground surveys. In this coverage relict forest was distinguished from young regrowth forest based upon canopy closure, diversity of tree age classes present and ages of trees.

2.3.2. Trail designs

We simulated three alternative trail designs, as proposed by stakeholders (designs A, B and C; Fig. 2a). Design A represented a modification of the existing 2.7 km pedestrian trail to accommodate cyclists (Fig. 2a). Design B depicted a longer trail (6.0 km) running through young forest in the western part of the Lawrence Creek Forest Unit and around the periphery of the central and eastern part of the unit predominantly comprising relict forest (Fig. 2b). This design was developed by the Indiana Department of Natural Resources as an alternative to design C, and was intended to limit human disturbance in the core forest. In contrast, design C, proposed by the local Mountain Bike Association, represented the longest trail design (9.7 km), running through a large proportion of the Lawrence Creek Forest Unit (Fig. 2c). This design was intended to enhance visitor experience by placing the trail through the highest diversity of habitat types. Additionally, we simulated a control trail scenario representing existing conditions (i.e., design A with pedestrians only, see Section 2.4). Thus, a total of four GIS maps depicting alternative trail designs were constructed.

2.3.3. Honeysuckle removal strategies

We simulated four strategies for honeysuckle removal: (1) no removal, in which current conditions remained the same (Fig. 1); (2) total removal of honeysuckle, for which we build a new habitat map substituting the patches of dense honeysuckle with sparse understory. This strategy took into account that managers had no plans to plant native shrubs post-removal and we also assumed that no short-term regrowth of native shrubs would occur in the areas where honeysuckle was removed due to the allelopathic nature of the scrub (Bauer, Shannon, Stoops, & Reynolds, 2012; McEwan, Arthur-Paratley, Rieske, & Arthur, 2010); (3) initial removal far from the trails, in which 25% of honeysuckle furthest from the trails was substituted by sparse understory, and; (4) initial removal near trails, in which 25% of honeysuckle adjacent to the trails was substituted by sparse understory. In addition, as standard practice, honeysuckle removal operations are conducted in the non-breeding bird season and honeysuckle was either pulled by hand or cut at ground level using a gas-powered clearing saw (Anderson, 1990). A herbicide was then applied to the stumps of the honeysuckle to prevent re-growth (Anderson, 1990). Thus, we

assumed that these activities would not have any additional impact on the bird community.

2.3.4. Nest locations

As bird nest locations often change from year to year, we used a stratified random method to randomly generate hypothetical nest locations to produce a series of nest maps. Based on known local nesting habitat preferences and nesting density for each species (Table 1), we assigned a set number of nests for each species in each habitat type present at Lawrence Creek Forest Unit. The number of nests varied between scenarios with different patterns of honeysuckle removal because the nesting density of some of the bird species we simulated was influenced by understory cover. The number of nests simulated for each species can be found in Appendix A of the supplementary material. Then, individual nests for all nine species were randomly placed within their corresponding habitat type using Hawth's Analysis Tools for ArcGIS (www.spatial ecology.com). We produced four different nest map replicates for each of the 16 combinations of honeysuckle removal strategy ($n = 4$) and trail designs ($n = 4$). This resulted in the creation of 64 nest location maps.

2.4. Anthropogenic inputs

The anthropogenic parameters used to characterize trail usage by recreationists (existing and expected) were estimated from current rates of pedestrian traffic at Lawrence Creek Forest Unit and the number of cyclists predicted to use the new trail once it opened. Current rates of pedestrian traffic were provided by Fort Harrison State Park staff (Jeff Cummings pers. comm.), and we estimated the intensity of park use by cyclists based upon the expectations of the property manager from the Indiana Department of Natural Resources (Caryn Atkinson pers. comm.), as well as estimates of current cyclist visitor rates along a similar trail at Brown County State Park in Indiana (Paul Arlinghaus pers. comm.). Based on these sources, we estimated rates of 6 visitors (5 cyclists + 1 pedestrian) on trails within the Lawrence Creek Forest Unit during any given 5 min time-step between 6:00 am and 12:00 pm on weekdays. Likewise, we estimated 40 visitors (34 cyclists + 6 pedestrians) at any given time-step during the evenings (6:00–10:00 pm) and all day (6:00–10:00 pm) on weekends. As the visitor rates we used were estimates and actual visitor rates remain uncertain until the new trail opens, we conducted a sensitivity test, in which we simulated three different visitor rates: moderate (representing our estimated visitor rates described above), low (50% lower rates than in the moderate rate), and high (50% higher visitors than the moderate rate). For the control trail design, we created visitor rate scenarios there were 50% greater and lesser than current pedestrian activity for the Lawrence Creek Forest Unit, but did not simulate any bicyclists.

2.5. Wildlife inputs

From long-term monitoring, we selected nine forest bird species known to be breeding in the Lawrence Creek Forest Unit (Table 1). Based upon our knowledge of similar species we expected the nine species we modeled to encompass a wide range of sensitivities to human activity. Among these species, two were listed as threatened at national level in Audubon yellow list: the Kentucky Warbler (*Oporornis formosus*) and Wood Thrush (*Hylocichla mustelina*). Another three species were known to be affected by forest fragmentation in the Midwestern United States (Herbert et al., 1993): the Ovenbird (*Seiurus aurocapilla*), Hooded Warbler (*Wilsonia citrina*), and Brown Creeper (*Certhia americana*). The Ovenbird, for example, despite an overall population increase in the Midwest, seems to be declining in the central and northern parts of Indiana

Table 1
Density, habitat preferences, and behavioral responses (m) to park visitors estimated for 9 different forest bird species present in the Lawrence Creek Forest Unit of Fort Harrison State Park, Indiana, USA.

Species	Estimated density	Habitat preferences	Responses parameters in <i>sparse</i> understory			Response parameters in <i>dense</i> understory		
			Alert distance	Flight initiation distance	Distance fled	Alert distance	Flight initiation distance	Distance fled
Downy Woodpecker <i>Picoides pubescens</i>	2 pairs/10 ha	Slight preference for less mature stands	13	8	15	11	7	12
Eastern Wood-Pewee <i>Contopus virens</i>	2 pairs/10 ha	Slight abundance of dense understory. Slight preference for less mature stands	20	12	15	17	10	12
Acadian Flycatcher <i>Empidonax vireescens</i>	3 pairs/10 ha	Avoids dense understory. More abundant in mature forest	18	11	12	15	9	10
Carolina Chickadee <i>Poecile carolinensis</i>	2 pairs/10 ha	No clear preference for understory density or stand age	9	5	12	8	4	10
Brown Creeper <i>Certhia americana</i>	1 pair/10 ha	Avoid dense understory	12	7	12	10	6	10
Wood Thrush <i>Hylocichla mustelina</i>	2 pairs/10 ha	Slight preference for dense understory	22	15	20	16	11	16
Kentucky Warbler <i>Oporornis formosus</i>	1 pair/10 ha	More abundant in dense understory	20	12	15	15	9	12
Hooded Warbler <i>Wilsonia citrina</i>	1 pair/10 ha	More abundant in areas with dense understory	17	9	10	12	6	8
Ovenbird <i>Seiurus aurocapilla</i>	1 pair/10 ha	Avoid dense understory. More abundant in mature forest	30	18	25	23	14	20

where forest fragmentation is most severe (Potts et al., 2004). Furthermore, Ovenbird numbers appear to be declining from areas of Fort Harrison State Park where recreational visitation is highest (Don Gorney pers. comm.). The Brown Creeper is also considered an uncommon nesting bird in Indiana (Gorney, 2000).

We obtained information on habitat preferences and breeding density for the species from published studies (Poole, 2005 and references therein) and from local ornithologists (John B. Dunning, Purdue University, Don Gorney, Amos W. Butler Audubon Society).

Using parameters that simulate the typical behavior of our nine forest bird species, we programmed virtual birds to move through habitats to forage during the day and return to their nest location periodically to feed their young. The position and behavior exhibited by each bird was recorded every 5 min. Virtual birds were also programmed to exhibit three disturbance-related responses to approaching virtual humans: (1) alert distance, defined as the human-to-bird distance at which a bird ceases typical behavior (such as foraging) and focuses its attention on the approaching human through alert behaviors (Fernández-Juricic et al., 2001); (2) flight initiation distance (hereafter FID), defined as the distance between an approaching human and a bird, which causes the bird to flee from the patch (Ydenberg & Dill, 1986); and (3) distance fled, defined as the distance that a bird traveled after fleeing from a human (Fernández-Juricic, Zahn, Parker, & Stankowich, 2009). Note that these behaviors are anti-predator responses that birds exhibit because they perceive recreationists to be potential predators (Beale & Monaghan, 2004; Frid & Dill, 2002). While the birds are not at risk of predation by recreationists, these behaviors still incur energetic costs, as well as reducing the time the birds spend conducting activities that will increase their fitness and breeding success, such as foraging, mating, incubating eggs, and feeding young. Frequent and regular disturbance by recreationists can therefore have consequences for the survival, breeding success, abundance and distribution of birds in the area.

For our 9 study species, we did not find any published information that quantified the three disturbance-related responses of these species to humans. Therefore, we estimated the responses

using data from ecologically similar and phylogenetically related species (see Appendix B in the supplementary materials for more details). Estimates for the disturbance-related responses were refined based on expert advice, body mass, microhabitat preferences, and the foraging behavior of both target and surrogate species (Blumstein, Fernández-Juricic, Zollner, & Garity, 2005; Fernández-Juricic et al., 2001, 2002; Stankowich & Blumstein, 2005). For resident species (Brown Creeper, Carolina Chickadee (*Poecile carolinensis*), and Downy Woodpecker (*Picoides pubescens*)), we also collected some direct information in the field (see Appendix C in the supplementary materials for more details). We parameterized the model so that the disturbance-related responses of birds to human presence were reduced in areas with dense shrub cover (following Fernández-Juricic et al., 2001, 2002). Finally, a number of studies have compared the alert distances, FIDs, and distance fled for similar forest bird species in response to pedestrians and cyclists (Gander & Ingold, 1997; Taylor & Knight, 2003). As these studies found no significant differences between the two types of recreation, we assumed in our model that alert distance, FID, and distance fled were similar for both virtual pedestrian and cyclist encounters.

2.6. Statistical analysis

Once the model parameter space was constructed, we ran 192 different model simulations, each simulation represented a unique combination of one honeysuckle removal strategy, one trail design, one level of trail usage by recreationists, and one replicate nest map (see Appendix D in the supplementary materials for full list of the variables). The outputs from each simulation included the number of times each virtual bird became alert and the number of instances in which they fled. Thus for each model simulation, our dependent variable was the mean number of times each virtual bird species was disturbed by recreationists (i.e. the sum of alert and fleeing events) over the simulation period (17 days). For example, the dependent variable for each simulation was the average number of times Carolina Chickadees (32 Carolina Chickadees/simulation;

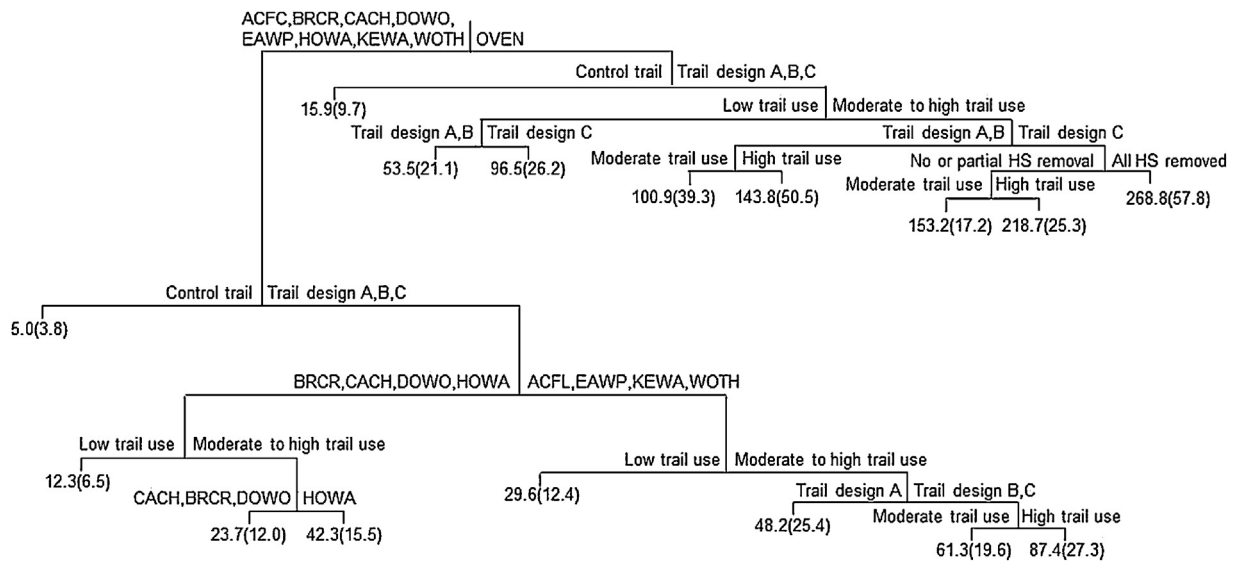


Fig. 3. Regression tree evaluating the levels of disturbance experienced by nine breeding bird species (standard AOC codes are used to identify each species) among three alternate trail designs, three different levels of trail usage by recreationists and four honeysuckle (HS) removal strategies including no honeysuckle removal, in a virtual environment equivalent to the Lawrence Creek Forest Unit in Fort Harrison State Park near Indianapolis in central Indiana, USA. Predictor variables defining a split are labeled at each branch split. Branch lengths are proportional to the number of scenarios represented. Below each terminal node the values represent the average and (standard deviation) of the number of times each bird species was disturbed per replicate simulation run.

Appendix A supplementary materials) were disturbed by recreationists.

We used Classification and Regression Trees (CART) procedure to compare the model output from our 192 simulations. We considered this recursive partitioning method ideal, as it could handle complex, context dependent multivariate data without distributional assumptions (Bennett et al., 2013a, 2013b; Vayssières, Plant, & Allen-Diaz, 2000). As the mean number of disturbances of each bird species per simulation was a continuous dependent variable, we built a regression tree. In contrast, all our predictor variables, including species, trail design (A, B, C and control), trail use by visitors (low, moderate and high) and honey suckle removal strategy (none, all, 25% removed far from trail and 25% removed near to trail) were categorical. Thus, for each combination of predictor variables, we had four replicates (labeled as nest maps in Appendix D in the supplementary materials). A V-form cross validation procedure was used to determine the maximum tree size. To do this, we used 10 different 10% subsets of our dataset to identify the 'minimum Cross Validation cost' (i.e., the error rate associated with a particular tree size). The maximum tree size was then restricted so that the relative cost of tree did not exceed the minimum Cross Validation cost. A relative error index and R^2 value were then used to optimally prune the tree (Vayssières et al., 2000). The relative error provides a measure of the accuracy of each split, and thus the number of nodes (i.e. tree size). It ranges from 0 to 1.0, where 0 indicates a perfect fit and 1 emphasizes that the predictor variables cannot be discriminated beyond chance. R^2 represents the proportion of the variation explained by the tree, where 0 shows no relationship and 1 explains all the variation.

3. Results

The average number of times each bird species was disturbed per replicated simulation run ranged from 0 to 407 over the 17 days of the simulation. The regression tree built in CART demonstrated a very good fit to our data and explained 83% of the variation ($R^2 = 0.83$ with a relative error index of 0.19; Fig. 3). By stratifying response variables in CART, we found that disturbance rates were primarily influenced by species, which represented an important

overall variable in 100% of the scenarios. Trail design represented the second most important variable in 92% of scenarios, then trail use by visitors (50%), and finally honeysuckle removal strategy (4%).

The regression tree revealed significant difference in the frequency at which Ovenbirds ($\bar{x} = 96$ disturbances/simulation) were disturbed compared to the other eight species ($\bar{x} = 30$ disturbances/simulation; first split; Fig. 3). Not surprisingly, across all species, the three proposed trail designs resulted in approximately 9 times more disturbance than the control trail ($\bar{x} = 16$ disturbances/simulation for Ovenbirds and $\bar{x} = 5$ disturbances/simulation for other eight species; second split, both left and right branch).

Among the other eight species, along trail designs A, B and C, CART revealed that Acadian Flycatcher (*Empidonax virescens*), Eastern Wood-Pewees (*Contopus virens*), Kentucky Warblers and Wood Thrushes ($\bar{x} = 54$ disturbances/simulation) were significantly more disturbed by recreationists than Brown Creepers, Downy Woodpeckers, Carolina Chickadees, and Hooded Warblers ($\bar{x} = 23$ disturbances/simulation; third split). Of the latter, disturbance further decreased at low trail use ($\bar{x} = 12$ disturbances/simulation) compared to moderate and high trail use ($\bar{x} = 28$ disturbances/simulation; fourth split). Furthermore, at moderate and high trail use, Hooded warbler experienced 8 times more disturbance compared to the control ($\bar{x} = 42$ disturbances/simulation), which was significantly higher than the other three species ($\bar{x} = 24$ disturbances/simulation; fifth split). Similarly, Acadian Flycatcher, Eastern Wood-Pewees, Kentucky Warblers and Wood Thrushes experienced less disturbances at low trail usage ($\bar{x} = 30$ disturbances/simulation), compared to moderate and high trail use ($\bar{x} = 66$ disturbances/simulation; fourth split). Trail design then influenced these four bird species, with trail design A resulting in lower levels of disturbance ($\bar{x} = 48$ disturbances/simulation), than trail designs B and C ($\bar{x} = 74$ disturbances/simulation; fifth split). Finally, among the latter two trail designs, high trail use led to 17 times more disturbance than the control ($\bar{x} = 87$ disturbances/simulation), whereas moderate trail use resulted in 12 times more disturbance than the control ($\bar{x} = 48$ disturbances/simulation; sixth split).

Among the Ovenbirds, trail use then influenced frequency of disturbance with significantly less disturbance occurring when trail use was low (4 times more disturbance than the control) compared to moderate to high use (9 times more disturbance than the control; third split). At low trail use, both designs A and B incurred similar levels of Ovenbird disturbance (3 times more disturbance than the control), yet design C resulted in 6 times more disturbance than the control ($\bar{x} = 53$ and $\bar{x} = 96$ disturbances/simulation respectively; fourth split, left branch). Similarly, at moderate to high trail use, Ovenbird disturbance was 8 times higher at trail designs A and B than the control, and 13 times higher at trail design C ($\bar{x} = 122$ and $\bar{x} = 207$ disturbances/simulation respectively; fourth split, right branch). Furthermore, when honeysuckle was completely removed along trail design C with either moderate to high trail use, Ovenbird disturbance was at its highest ($\bar{x} = 269$ disturbances/simulation), resulting in 17 times more disturbance than the control (fifth split). In comparison, when no honeysuckle was removed or a partial honeysuckle removal strategy was implemented, Ovenbird disturbance was significantly lower (10 times more than the control) when trail design C received moderate trail use and 14 times at high trail use ($\bar{x} = 153$ and $\bar{x} = 219$ disturbances/simulation respectively; sixth split).

4. Discussion

Our study revealed that the amount of recreational disturbance experienced by a forest bird community can be strongly influenced by trail design and use. Among the three proposed trail designs for the Lawrence Creek Forest Unit, all nine breeding bird species experienced from 3 to 17 times more disturbance than current conditions. Not surprisingly, the longer the trail and the more habitat types the trail intersects, the more frequently the bird community is disturbed by recreationists (McKinney, 2005). Trail design C, therefore, caused the most disturbances across all species regardless of trail usage. In contrast, trail design A, in which the existing pedestrian trail was simply modified for cyclists, showed the lowest increased rates of disturbance. Nevertheless, this significant increase in breeding bird disturbance at trail design A demonstrates that visitor frequency and trail use are important factors that contribute to the local recreational disturbance of wildlife (Miller, Knight, & Miller, 1998; Reed & Merenlender, 2011).

Interestingly, our simulation results also revealed that trail design B was not necessarily an intermediate between trail designs A and C. For example, disturbance rates of the Downy Woodpecker, Carolina Chickadee, Brown Creeper (species of concern) and Hooded Warbler (species of concern) were not significantly influenced by trail design. Similarly, at low trail usage, disturbance rates experienced by Eastern Wood-Pewee, Acadian Flycatcher, Wood Thrush (species of concern) and Kentucky Warbler (species of concern) on all three trails were not significantly different. However, at moderate to high levels of trail use, disturbance among these four species was significantly lower at trail design A compared to trail designs B and C. In contrast, for the Ovenbird, trail design A was not significantly different from trail design B at low, moderate or high trail use. Thus, our multi-species study demonstrates that the selection a trail design that simultaneously keeps disturbance of wildlife to a minimum and increases recreational opportunities is highly species dependent, even among those species of concern (Blumstein et al., 2005). This study, therefore, highlights that modeling of multiple species at once provides a wider and more detailed picture in which to base management recommendations that are more relevant to the whole community (Montgomery et al., 2009).

Furthermore, our simulation results have demonstrated that the removal of invasive honeysuckle would likely not have a cumulative impact on recreational disturbance of the breeding bird

community in the Lawrence Creek Forest Unit. However, our study reveals that completely removing the honeysuckle is more likely to increase recreational disturbance of Ovenbirds. A likely mechanism underlying this is that the complete removal of honeysuckle brings more Ovenbirds in proximity to human recreational disturbance. Our results suggest the long-term benefits of removing invasive honeysuckle from the area will outweigh any negative implications of birds being exposed to disturbance caused by honeysuckle removal in the short-term (Boyce, Durtsche, & Fugal, 2012; McCusker et al., 2010; McEwan et al., 2010; McKinney & Goodell, 2010; Watling, Hickman, Lee, Wang, & Orrock, 2011). Overall, our simulation results minimize the logistical and biological concerns posed by the planned removal of invasive honeysuckle.

5. Conclusions

Our study highlights the importance of considering multi-species or wildlife communities when devising management strategies and designs for a site. We found that different species varied in their sensitivity to recreation and this sensitivity was not necessarily correlated with their conservation status (i.e., the most threatened species was not the most sensitive). Thus, we caution that implementing management strategies and site designs based on a single high profile species could have far-reaching implications for the survival and breeding success of other species within the local community. Identifying and comparing differences between individual species and populations within a wildlife community can therefore provide valuable insights in how we can devise more resilient long-term strategies that aim to preserve biodiversity (McIntire, Schultz, & Crone, 2007). This approach supports conservation practitioners' objectives to not only conserve species of concern, but also local biodiversity (McLane et al., 2011).

We acknowledge that determining disturbance thresholds that lead to the reduction in survival and/or breeding success or cause the displacement of individuals would be ideal for managers to optimize management decisions. However, acquiring such thresholds requires very specific empirical data, which were not available for this study. Nevertheless, there is evidence that disturbance to wildlife can have negative consequences on body condition, survival, breeding success, abundance and distribution (Amo, López, & Martín, 2006; Reed & Merenlender, 2008; Webber, Heath, & Fischer, 2013). From a conservation perspective, the most conservative option is to reduce wildlife disturbance to minimize the risk of a potential impact. Thus, managers should pursue reserve designs that cause little or no additional disturbance. In the past managers have had to rely on rational assumptions to choose the management strategies they need to implement. For example, it is rational to assume that increasing trail length or use would cause more disturbances. Yet without knowing the specifics of how birds respond to recreationists in time and space it is not a certainty that a longer trail will cause a significantly greater amount of disturbance.

The strength of our simulation modeling approach is that it makes it possible to rank the impacts of alternative management scenarios in a risk-free virtual environment (Knowlton & Graham, 2010; Nabe-Nielsen, Sibly, Forchhammer, Forbes, & Topping, 2010). For example, Ovenbirds were disturbed by humans 9 times more frequently along the new trail systems compared to the current trail system. By projecting the responses of wildlife to alternative scenarios before any action has been taken in situ, we can effectively explore park design, management strategies and habitat restoration efforts with no risk to the focal species (Merckx, Marini, Feber, & Macdonald, 2012; Moranz, Debinski, McGranahan, Engle, & Miller, 2012). A modeling approach therefore has great value as a management and planning tool on a case-by-case basis, supporting efforts by nature reserves, wildlife refuges and national

parcs to find a balance between wildlife preservation and conservation, and providing recreational opportunities (Hebblewhite et al., 2005). Nevertheless, we stress that follow-up surveys to monitor any management implemented should be a standard practice (Augusiak, Van den Brink, & Grimm, 2014). For example, the Indiana Department of Natural Resources continues to monitor the bird community at Fort Harrison State Park following implementation of the new bike trail. These data will enable us to assess the effectiveness of the trail system that was implemented at the park.

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Appendix A. Supplementary data

Supplementary data associated with this article and code for the SODA simulation can be found, in the online version, at <http://dx.doi.org/10.1016/j.landurbplan.2014.03.008>.

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