Ecological Modelling 282 (2014) 44–58

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Activities, motivations and disturbance: An agent-based model of bottlenose dolphin behavioral dynamics and interactions with tourism in Doubtful Sound, New Zealand

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ARTICLE INFO

Article history:
Received 22 January 2014
Received in revised form 5 March 2014
Accepted 6 March 2014
Available online 2 April 2014

Keywords:
Agent-based model
Animal behavior
Bayesian
Human disturbance
Multi-state model
Wildlife tourism

ABSTRACT

Agent-based models can be used to simulate spatially-explicit animal behavioral processes and their interactions with human activities. This approach can be applied to predict the potential effects of such activities on animal behavior and individual condition that could lead, in turn, to alterations in vital rates and, ultimately, long-term population change. We developed an agent-based model to describe the effect of interactions with tourism on the behavior of bottlenose dolphins in Doubtful Sound (New Zealand). The model describes the temporal variation of the individuals' hidden motivational states, the way in which these states interact to determine the activity of groups of dolphins, and the feedback influence of the group's activity on individual motivations and condition. Moreover, it realistically simulates the movement of dolphin groups in the fiord. The model also includes tour boat behavior, incorporating the way key geographical features attract these boats. In addition to tourism effects, we accounted for the spatial heterogeneity in both dolphin activities and shark predation risk. The final simulation platform generated a realistic representation of the social and behavioral dynamics of the dolphin and boat populations, as well as observed patterns of disturbance. We describe how this tool could be used to ensure effective management of the interactions between anthropogenic factors and bottlenose dolphins in Doubtful Sound, and how it could be adapted to evaluate the effects of human disturbance on other comparable populations. We then fitted the dolphin component of the model to data collected during visual studies of the Doubtful Sound dolphin population between 2000 and 2002 using a Bayesian multi-state modeling framework. However, when the parameter estimates from this fitting process were used in the agent-based model, biologically realistic representations of the population were not generated. Our results suggest that visual data from group follows alone are not sufficient to inform such agent-based models. Information on the spatial structure of the animals' activities and an appropriate measure of individual condition are also required for successful model parameterization.

1. Introduction

A framework for the analysis of behavioral dynamics is important when evaluating the potential effects of the interactions between wildlife populations and anthropogenic activities. The extent of human activities is constantly increasing in both the terrestrial and the marine environment (Inger et al., 2009; McKinney, 2002). Nevertheless, we lack suitable tools to interpret the consequences of these activities for wildlife and to allow for a sustainable use of natural resources. It is relatively easy to predict the effects of direct mortality events on the viability of a population (e.g. Wade, 1998), but exposure to anthropogenic disturbances can influence population dynamics even in the absence of such events. The estimation of these sub-lethal effects is more challenging, since the connection between short-term disruptions of the activity of individuals and a biological significant long-term effect on the population (i.e. one that is relevant to management and conservation) is indirect (Gill et al., 2001). In order to estimate these indirect relationships, we need to understand how behavioral responses are translated into changes in the individual vital rates (such as survival or reproductive success), which determine population dynamics

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http://dx.doi.org/10.1016/j.ecolmodel.2014.03.009

(New et al., 2013). For example, changes in activity budgets need to be converted into changes in energy acquisition and expenditure, so that we can calculate the impact of a shift in the amount of time allocated to a given activity (e.g. foraging, resting or socializing) (Duchesne et al., 2000; Galicia and Baldassarre, 1997; Lusseau, 2003a) on the condition of the individuals involved (McClung et al., 2004; New et al., 2013).

Agent-based models offer an effective framework to simulate the spatial and temporal dynamics of animals' behavior, as well as their interactions with spatially-explicit human activities (Bousquet and Le Page, 2004; McLane et al., 2011). Different components of the system (or 'agents') are integrated in a complex spatio-temporal context, where they move autonomously. Animals integrate stimuli from their perception of the external environment and their internal physiology, and this determines their motivational states (McFarland and Sibly, 1975; Schliehe-Diecks et al., 2012). Observable activities arise from the interactions among this unobservable set of competing motivations (McFarland and Sibly, 1975). In turn, a specific activity will have a feedback influence on an individual's motivational states (Zucchini et al., 2008). The drive to perform a given activity also affects animals' movements in the environment, which respond adaptively to the encountered conditions and to changes of the environment through time. Likewise, anthropogenic agents can act and move in space as the result of their own motivations. Agent-based models can therefore describe the time series of agents' activities and motivational states, and how reciprocal interaction between agents might alter these states (McLane et al., 2011). Understanding how individual activities and motivations respond to a changing ecological landscape is integral to successful management of any human activity.

Previous studies have used these concepts to predict the consequences of disturbances (Ahearn et al., 2001; An et al., 2005; Anwar et al., 2007; New et al., 2013). New et al. (2013) outlined a mechanistic model detailing the dynamics of a bottlenose dolphin (*Tursiops truncatus*) population in the Moray Firth, Scotland, exposed to interactions with boats that are perceived as a risk by individual dolphins (Frid and Dill, 2002; Laundré et al., 2001; Wirsing et al., 2008). Their model simulates social, spatial, behavioral and motivational interactions that evolve across discrete time steps, and provides predictions of how dolphin condition changes in response to different boat exposure scenarios. However, the model does not simulate the dynamic interplay with such anthropogenic agents, and boats are included only as a layer of exposure probability.

While agent-based models can be informed using the available literature, the question remains whether suitable data can be collected to directly fit their components to real observations. Traditional visual observation techniques (Altman, 1974) have generated large datasets on animal behavior and interactions with human activities across the world. Therefore, they could provide a useful source of information to parameterize these models.

A geographically isolated population of bottlenose dolphins inhabits Doubtful Sound, New Zealand (Currey et al., 2007; Williams et al., 1993a). This population is the target of an increasingly intense dolphin watching industry that includes dedicated wildlife watching trips, scenic cruises in the fiord, and kayak experiences (Lusseau, 2005). Interactions between dolphins and this industry have been shown to significantly alter dolphins' activity budgets (Lusseau, 2003a), and to be a dominant factor leading to the population's current IUCN status of 'critically endangered' (Currey et al., 2007, 2011).

The objectives of our study were:

(1) To develop an agent-based model for the Doubtful Sound scenario.
(2) To investigate how the dolphin component of this mechanistic model might be fitted to traditional observational data in a multi-state modeling framework.

2. Materials and methods

We first developed an agent-based model for the behavioral, social and spatial dynamics of the bottlenose dolphin population in Doubtful Sound and the tourism boats with which they interact (Section 2.1). We then used the data collected in Doubtful Sound (Section 2.2) to parameterize simplified versions of the dolphin submodel in a multi-state modeling framework (Section 2.3). The biological soundness of both the agent-based model and of the estimated parameters was assessed through the results of the simulations (Fig. 1).

2.1. Agent-based model

Our model builds on the one elaborated by New et al. (2013) for a comparable small, resident population of coastal bottlenose dolphins exposed to boat traffic (Fig. 2). It differs from that model by incorporating (1) a quantitative approach to define the complex spatial structure of the environment that determines dolphin movement, (2) a gradient of predation risk, (3) a dynamic model for boat behavior, (4) a time step that is more appropriate to the temporal scale of dolphin behavior and the data collected at Doubtful Sound (Section 2.2), and (5) a measure of body condition (in this case, respiration rate) that can be observed directly.

Modeling the actual distribution of observed activities in the study area, as opposed to using a simple depth range to define the suitable areas for foraging (New et al., 2013), offers an empirical characterization of the spatial structure of the environment, while allowing for a realistic degree of stochasticity. Dolphins in Doubtful Sound are also subject to low levels of predation from sharks (Schneider, 1999), which can play a large role in shaping animals' distribution (Fortin et al., 2005; Heithaus and Dill, 2002; Semeniuk et al., 2012, 2014). Other environmental gradients could affect dolphin behavior, but we decided to focus on the effects of predation risk to exemplify how natural or anthropogenic gradients (e.g. the distance from an anthropogenic source of disturbance) could be incorporated in the model. Our inclusion of a dynamic model to describe boat behavior in the fiord allows the various types boats to move and interact in different ways with the dolphins, and introduces stochasticity in the boats' behavior that was lacking in New et al. (2013). The boat model can be easily extended to match any expansion of the industry and the introduction of new types of boats.

The model description follows the updated ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010). The annotated R code (R Development Core Team, 2013) for the agent-based model is provided in Appendix A, together with the input data.

2.1.1. Purpose

The purpose of our agent-based model was to provide a realistic simulation of the effects of boat disturbance on the behavior and body condition of bottlenose dolphins, in order to investigate how such a mechanistic model might be fitted to traditional observational data.

2.1.2. Entities, state variables and scales

The model comprised three low-level entities (Table B.1 in Appendix B): individual dolphins, individual boats and grid cells. Individual dolphins were characterized by the state variables: motivational states (hunger, fear, inclination to socialize and condition), age class (adult, juvenile, female with calf), respiration rate, and a