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Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes

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ABSTRACT

Most rare and endangered large carnivores such as tiger (*Panthera tigris*) exist in human-dominated landscapes as small, fragmented and isolated populations across their range. Connectivity between the remaining populations in the habitat fragments is essential for their long-term persistence and focus of management initiatives. We describe an individual-based, spatially explicit model of tiger movement behavior based on previously developed habitat models to (i) quantify inter-patch connectivity among major (protected) habitat patches in the Terai Arc Landscape of India and Nepal and (ii) investigate the effect of potential management initiatives, e.g. restoring corridors, on enhancing connectivity among fragmented protected habitats. Connectivity was not solely a function of distance between patches, but an outcome of the interplay between movement behavior and landscape composition, with asymmetric connectivity explained by canalizing or diffusing effects of the landscape, and depending on the landscape context of the starting patch. Patch connectivity was mostly determined by autocorrelation in tiger movement, the daily movement capacity, landscape structure, and the amount of matrix habitat. Several habitat patches were likely to be island-like and already effectively isolated. However, simulating scenarios of corridor restoration showed that most habitat patches in India and between India and Nepal could recover connectivity, which may mitigate negative genetic consequences of small population size and effective isolation on tiger populations in this landscape. Combining habitat models with individual-based models is a powerful and robust approach that could be widely applied to delineate dispersal corridors of large carnivores and quantify patch connectivity even if data are scarce.

1. Introduction

Studies on habitat connectivity have become a central issue in conservation biology and are of vital importance to the conservation of threatened species world-wide especially in fragmented landscapes (Crooks and Sanjayan, 2006; Revilla and Wiegand, 2008; Simberloff, 1988). Landscape or structural connectivity is defined as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993), however "without any requisite reference to the movement of organisms or processes across the landscape" (Crooks and Sanjayan, 2006). Depending on the spatial scale and the management question, connectivity may be assessed with regard to the entire landscape as typically done in landscape ecology (e.g., Tischendorf and Fahrig, 2000), or with regard to specific patches (i.e., "inter-patch connectivity") in metapopulation studies (e.g., Moilanen and Hanski, 2001).

However, movement or dispersal success and, therefore, functional connectivity depends on both, the spatial structure of the landscape and the behavior of the dispersing species in response to landscape heterogeneity (Revilla et al., 2004; Kramer-Schadt et al., 2011). An assessment of dispersal success is especially complicated in intensively used landscapes due to movement barriers imposed by humans (Graf et al., 2007; Kramer-Schadt et al., 2004). Additionally, field studies on dispersal are very time consuming and expensive, especially for large carnivores because of high tracking-costs of individual animals. As a result, our current understanding on movement behavior of such species is limited and alternative approaches are required to complement the assessment of connectivity (Graf et al., 2007; Revilla et al., 2004; Zollner and Lima, 1999).

Abbreviation: TAL, Terai Arc Landscape.

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One approach to estimate inter-patch connectivity is to use models. Depending on the landscape structure, the scientific question and the organism of interest, several approximations to this complex problem have been proposed. For example, the incidence metapopulation model (Hanski, 1994; Moilanen and Nieminen, 2002) describes connectivity between two patches as a declining function of distance between the patches without taking into account details of landscape structure. Similar simplifying assumptions are made in graph-based landscape connectivity indices (e.g., Keitt et al., 1997; O'Brien et al., 2006; Pascual-Hortal and Saura, 2006; Urban and Keitt, 2001; but see Saura and Rubio, 2010). In contrast, least-cost path analysis explicitly considers the impact of landscape structure to find the optimal movement path between two patches that minimizes a given cost criterion (e.g., Adriaensen et al., 2003; Gonzales and Gergel, 2007; Klar et al., 2012; Nikolakaki, 2004; Wikramanayake et al., 2004). Friction values that represent the resistance to movement through different landscape elements (i.e., the cost) implicitly represent behavioral decisions regarding movement through particular landscape features (Schadt et al., 2002). However, this method cannot directly include dispersal behavior and is only able to assess structural connectivity and therefore often lacks biological realism (Calabrese and Fagan, 2004; Crooks and Sanjayan, 2006). Although least-cost path analysis can identify potential corridors, additional information on the movement behavior and dispersal ability of the species is required to assess if the identified corridors provide indeed functional connectivity, and if the animals may actually find them. Behavior and the landscape context of the start patch become especially important in complex landscapes comprising for example narrow passages of dispersal habitat and dead ends. In this case asymmetrical inter-patch connectivity is likely to occur (Ferreras, 2001; Gustafson and Gardner, 1996; Revilla et al., 2004; Schippers et al., 1996) because the landscape structure surrounding the start patch can have both canalizing and diffusing effects on movement. Thus, assessment of functional connectivity that considers the movement capacity and the behavioral response of the target species to the physical landscape structure (i.e. spatial information about habitats or landscape elements) (Crooks and Sanjayan, 2006) is required for planning conservation efforts in complex fragmented landscapes.

Individual-based spatially explicit simulation models (Dunning et al., 1995; Grimm and Railsback, 2005; Revilla and Wiegand, 2008; Wiegand et al., 2004b) overcome the limitations of landscape connectivity indices and cost-path analysis. They simulate dispersal explicitly and behavioral movement rules describe how organisms interact with landscape structure; this type of models is therefore especially suitable for evaluation of dispersal success and connectivity between specific habitat patches in situations where details of landscape structure and behavior matter (Kramer-Schadt et al., 2011; Nathan et al., 2008; Schick et al., 2008; Tracey, 2006). This type of model has been successfully used in several studies on animals and birds (e.g., Iberian lynx (*Lynx pardinus*; Revilla et al., 2004; Revilla and Wiegand, 2008), Eurasian lynx (*Lynx lynx*; Kramer-Schadt et al., 2004), capercaillie (*Tetrao urogallus*; Graf et al., 2007), red-cockaded woodpecker (*Picoides borealis*; Bruggeman et al., 2010) and tortoise (*Testudo graeca*; Anadón et al., 2012) to analyze dispersal behavior and/or estimate connectivity between habitat patches.

Large carnivores are particularly vulnerable to extinction in fragmented landscapes because of their low population density, wide ranges, low fecundity, and direct persecution by humans (Dinerstein et al., 2007; Noss et al., 1996). A typical example is the fragmented populations of tiger (*Panthera tigris*) that exist in the Terai Arc Landscape (TAL), which consists of twelve protected areas and covers ca 78,000 km^2 area in the Himalayan foothills in India and Nepal (Dinerstein et al., 2006). The TAL is one of the top priority landscapes for tiger conservation (Sanderson et al., 2006) that was once continuous across the Himalayan foothills but is now highly fragmented and most of the remaining large, intact habitats are located within protected areas (Wikramanayake et al., 2004). As tigers cannot sustain viable populations in small habitat fragments (Johnsingh and Negi, 1998; Sanderson et al., 2006) a conservation project was initiated in the TAL by the World Wildlife Fund that implemented the concept of metapopulation management to restore, reconnect, and manage wildlife corridors to link 11 important protected areas that harbor wild tigers (Dinerstein et al., 2007; Smith et al., 1998; Wikramanayake et al., 2004). Consequently, potential connectivity among habitat patches was assessed based on a least-cost pathway model (Wikramanayake et al., 2004). However, least-cost analyses cannot assess functional connectivity, and hence this study could not establish a quantitative measure of potential corridors (links) that is an important property of effective conservation methods (Jordán, 2003).

Here, we provide the next step required for corridor assessment in the TAL using a dynamic individual-based simulation model that incorporates behavioral details of movement within real landscapes. More specifically, we present a simple spatially explicit and individual-based dispersal model to (i) quantify the inter-patch connectivity among the major (protected) habitat patches in this heterogeneous landscape and (ii) investigate the effect of potential management initiatives, by restoring corridors, on enhancing connectivity among fragmented protected habitats. Previous studies stressed the importance of these corridors for maintaining landscape-level connectivity, but also highlighted the uncertainty surrounding successful usage of these corridors by tigers (Johnsingh et al., 2004; Wikramanayake et al., 2004). This exercise was motivated by two purposes: to assess the consequences of our uncertainty about the movement and habitat use of tigers for predicting patch connectivity and to test the effectiveness of potential landscape restoration measures by providing undisturbed corridors for tiger. To overcome the problem of uncertainty arising from scarce data in parameterizing the dispersal model, which is common in endangered species (Kramer-Schadt et al., 2007; Wiegand et al., 2003, 2004b), we conducted exhaustive sensitivity analyses. Finally, we discuss our results in respect of tiger management in the TAL.

2. Materials and methods

2.1. The habitat map

We used probabilistic habitat suitability (HS) maps with a cell size of 500 m × 500 m derived for tiger in the TAL by logistic regression and ecological niche factor analysis as described in Kanagaraj et al. (2011); their Fig. 3) (see also Appendix A and Table A1). We divided the TAL into four functional habitat types: breeding habitat, dispersal habitat, matrix and barrier (e.g., Kramer-Schadt et al., 2004; Revilla et al., 2004; Revilla and Wiegand, 2008). In our model, the movement decisions of tigers depended directly on these four categories (see Section 2.3). The four habitat types were defined by three threshold values 0.9, 0.5 and 0.01 dividing the probability-of-use given by the logistic regression equation into four classes (Appendix A). Because the predicted probability of occurrences in our habitat map (hereafter 'landscape map' *l*) was an almost binary function with either a high (>0.9) or a low (<0.25) probability of tiger occurrence (Fig. 3 in Kanagaraj et al., 2011), we only changed the central threshold of 0.5 in our original