

# Virtual Corridors for Conservation Management

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**Abstract:** *Corridors are usually perceived as clearly visible, linear landscape elements embedded in a hostile environment that connect two or more larger blocks of habitat. Animal response to certain aspects of landscape heterogeneity, however, can channel their movements into specific routes that may appear similar to their surroundings. These routes can be described as "virtual corridors" (VCs). Here we contribute to the foundation of the concept of VCs and highlight their implications for conservation management. We used an individual-based model to analyze the formation of VCs in the case of hilltopping in butterflies—where males and virgin females ascend to hilltops and mate. We simulated butterfly movements in two different topographically heterogeneous landscapes. We analyzed the movement patterns with respect to one parameter, the intensity of response to topography. Virtual corridor structure depended on the behavioral parameter, landscape, and location of the source patch. Within a realistic range of the behavioral parameter and in a realistic landscape, VC structures may be complex and require individual-based models for their elucidation.*

**Key Words:** habitat gradients, hilltopping, individual-based model, landscape heterogeneity, landscape management, nonrandom dispersal, topography

Corredores Virtuales para la Gestión de la Conservación

**Resumen:** *Los corredores generalmente son percibidos como elementos lineales del paisaje claramente visibles que están embebidos en un ambiente hostil y que conectan a dos o más bloques extensos de hábitat. Sin embargo, la respuesta de los animales a ciertos aspectos de la heterogeneidad espacial puede canalizar sus movimientos hacia rutas específicas que pueden ser similares a su entorno. Estas rutas pueden ser descritas como "corredores virtuales" (CV). Aquí contribuimos a la establecer del concepto de CV y resaltamos sus implicaciones para la gestión de la conservación. Utilizamos un modelo basado en individuos para analizar la formación de CV en el caso de "hilltopping" en mariposas—las hembras vírgenes y los machos ascienden a las cimas de colinas para aparearse. Simulamos los movimientos de mariposas en dos paisajes heterogéneos topográficamente. Analizamos los patrones de movimientos con respecto a un parámetro, la intensidad de respuesta a la topografía. La estructura de los corredores virtuales dependió del parámetro conductual, el paisaje, y la localización del parche de procedencia. En un rango realista del parámetro de conducta y en un paisaje realista, la estructura de CV puede ser compleja y requerir de modelos basados en individuos para su dilucidación.*

**Palabras Clave:** dispersión no aleatoria, gestión de paisaje, gradientes de hábitat, heterogeneidad, "hilltopping," modelo basado en individuos, topografía, paisaje

## Introduction

Dispersal, the movement of animals out of habitat patches and between populations, is key to maintaining the via-

bility of populations in fragmented landscapes (Opdam 1990; Thomas 2000; Bullock et al. 2002). When movement between populations seems insufficient, efforts are made to enhance it artificially in order to improve the

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viability of isolated populations (Meffe & Carrol 1997). One approach for achieving this goal is to secure or provide corridors. Corridors are usually assumed to be linear habitats embedded in a dissimilar matrix (a hostile environment) that connect two or more larger blocks of habitat and enable animals to move between them (e.g., Tischendorf & Fahrig 2000).

The concept of corridors embraces a wide range of landscape elements that may be natural or artificial, protected or reclaimed habitats (e.g., hedgerows, fences, strips of forest within open landscapes, clearcuts within forests, cliffs, roads [Meffe & Carrol 1997; Rosenberg et al. 1997; Beier & Noss 1998]). Commonly used definitions and descriptions of corridors share, implicitly or explicitly, an underlying assumption that corridors have clearly visible spatial attributes. Additionally, the concept of corridors implicitly assumes that, in their absence, movements across the matrix are primarily random or at least not directed. This is despite growing evidence that dispersal is rarely random (e.g., Beier 1995; Palomares et al. 2000; Wiens 2001). Furthermore, nonrandom movements occur even when a directing element cannot be recognized (Conradt et al. 2000, 2001). Animals respond to various sources of habitat heterogeneity, being attracted to some habitat types while avoiding others. This can direct their movements and channel their routes into preferred pathways, which may not be clearly visible and may not even differ from their surroundings. These types of pathways lead to the concept of "virtual corridors" (VCs).

We analyzed the formation of VCs to characterize their structure and to draw conclusions on their implications for conservation management. To meet this goal, we focused on investigating the consequences of animal responses to topography. Topography is a source of landscape heterogeneity that is widely known to affect animal movement during dispersal (e.g., Nève et al. 1996; Shkedy & Saltz 2000; Lowe 2003). Animals respond to clearly visible linear characteristics of the topography, such as cliffs, ridges, ravines, and streambeds. Our contention is that animals may also respond to gradients of change in the topographical attributes (e.g., slope), forming corridors that cannot be visibly discerned (VCs). To this end, we examined a common and simple behavioral case study. We focused on hilltopping behavior in butterflies in which males and virgin or multiple-mating females seek topographic summits for the purpose of mating (Shields 1967). After mating, females descend from summits in search of host plants.

We used an individual-based, spatially explicit simulation model to analyze the formation of virtual corridors in the case of hilltopping butterflies in topographically heterogeneous landscapes. We characterized the spatial structure of the corridors formed, investigated the role of landscape complexity and the animals' movement behavior in this context, and compared the results with the char-

acteristics of corridors in the original sense. We discuss some implications for conservation management in general and the identification of areas of importance to connectivity in particular. We show that although the concept of VCs is straightforward their demarcation may be complex. Consequently, simple rules of thumb are insufficient for identifying VCs. Instead, knowledge of animal movement behavior and of decision-making processes during dispersal is crucial. We conclude that individual-based, spatially realistic simulation models can be powerful tools in this context.

## Methods

Individual-based models (IBMs) allow one to account for complex landscape structures and the behavioral response of individuals moving in them (DeAngelis & Gross 1992; Grimm et al. 1999). We used an IBM to simulate the movements of males and virgin females toward mountain summits in the process of hilltopping. This conceptual model is based on simple movement rules derived from field observations on the hilltopping butterfly lesser spotted fritillary (*Melitaea trivia*, Nymphalidae) (Pe'er et al. 2004). These observations indicated that males and virgin females move persistently, yet somewhat inconsistently, upward toward the steepest slope until reaching a summit. We constructed a simple model of this behavior that could serve in understanding the outcomes of hilltopping in terms of movement patterns and landscape utilization. In the model, males and virgin females were "released" individually at a specific point in the landscape (a source patch) to search for summits. We used grid-based maps (matrices of elevations) to introduce topographical heterogeneity. The response to topography was probabilistic. In each step, a butterfly could move upward with a probability  $q$  or move randomly with a probability  $1 - q$ . To obtain a general understanding of the outcomes of hilltopping without confining ourselves to a certain species, we varied the values of  $q$  throughout its range from 0 (totally random movement) to 1 (moving 100% of the time upward toward the steepest slope).

The probability  $q$  reflects the proportion of deliberate movements upward. It can be easily obtained from field observations with a simple conversion equation:  $q_{\text{model}} = q_{\text{obs}} \cdot 2 - 1$ , where  $q_{\text{obs}}$  is the proportion of movements upward observed in the field. This conversion equation reflects the fact that a random movement yields 50% of the movements upward in most topographic regimes (Pe'er et al. 2004).

To characterize the spatial patterns of the paths formed by the hilltopping process, we first simulated the movements of butterflies across a simple, virtual landscape with one randomly located mountain. Landscape extent was  $200 \times 200$  cells, and the mountain was bell shaped

(Pe'er 2003). To obtain a first impression of the resulting movement pattern, we depicted the movement routes of 100 individuals from a single source patch, with various values of  $q$ . We then altered  $q$  systematically from 0.1 to 1 in steps of 0.1 to evaluate how movement through the landscape changes as a function of  $q$ . In these simulations we used 500 individuals that moved 1000 steps. For each level of  $q$  we ran 20 simulation repeats.

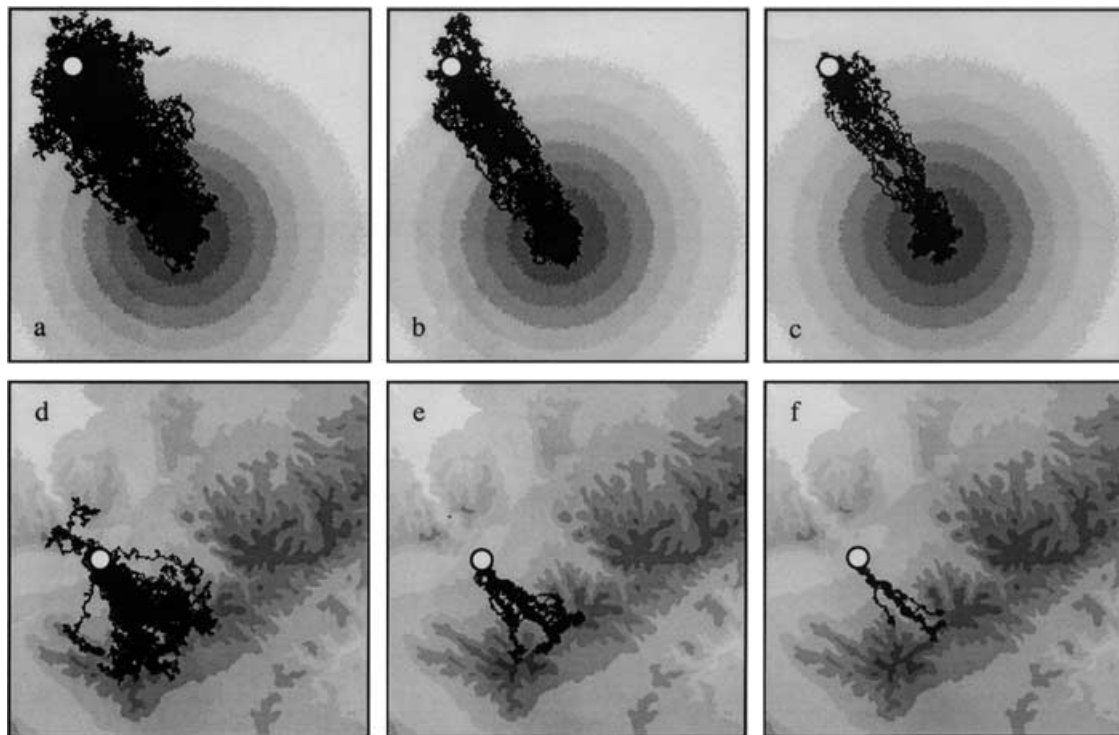
In the second step we assessed the impact of landscape complexity on the resulting movement patterns. We simulated butterfly movements across a realistic landscape with high topographic complexity. We used a map of a section of the Negev desert, Israel (31°05'N, 35°03'E), 300 × 300 cells in extent (cell side length = 25 m). The analysis followed the same procedure as above: we first depicted the movement paths of individuals over the landscape for several values of  $q$  and then performed a systematic analysis of the landscape-utilization pattern as a function of  $q$ .

## Results

Simulating butterfly movement through the simple, one-summit landscape showed that increasing the intensity of response to topography ( $q$ ) created a "channeling" ef-

fect that increased the concentration of movement paths along a single line connecting the source patch and the summit (Figs. 1a–c). The absence of any "classical" directing element in the landscape indicated the formation of a VC. To estimate the strength of the channeling effect as a function of  $q$ , we counted the number of cells visited by individuals during a given simulation and divided this number by the distance between the source patch and the summit. We called this measure "corridor width." Changing  $q$  systematically from 0.1 to 1 revealed a strong exponential-like decline in corridor width (Fig. 2a). This decline leveled off when the response to topography was medium or high. A sharp fall occurred when  $q$  increased from 0.9 to 1, indicating the formation of a deterministic path one cell in width.

In the one-summit landscape, the spatial orientation of the VC was self-evident, whereas its structure (characterized here by corridor width) depended on the movement parameter. When topography became complex, VCs were no longer obvious. Simulating butterfly movements over the realistic landscape indicated that the individuals are still channeled to certain routes so that VCs are formed (Figs. 1d–f). The individuals often took different routes, however, and ended up on several summits. In some cases several summits that seemingly could be reached were not reached at all. Here, both the movement pattern and



**Figure 1.** The trajectories of 100 individual butterflies (black marks) moving 1000 time steps from a single source patch (white circle) toward the mountain summit/s on (a–c) a virtual landscape with one summit and on (d–f) a realistic landscape of 7500 × 7500 m (cell size = 25 m). We used different probabilities of the butterflies moving upward ( $q$ ): (a,d)  $q = 0.2$ ; (b,e)  $q = 0.5$ ; and (c,f)  $q = 0.8$ . Gray shading reflects elevation (darker is higher).

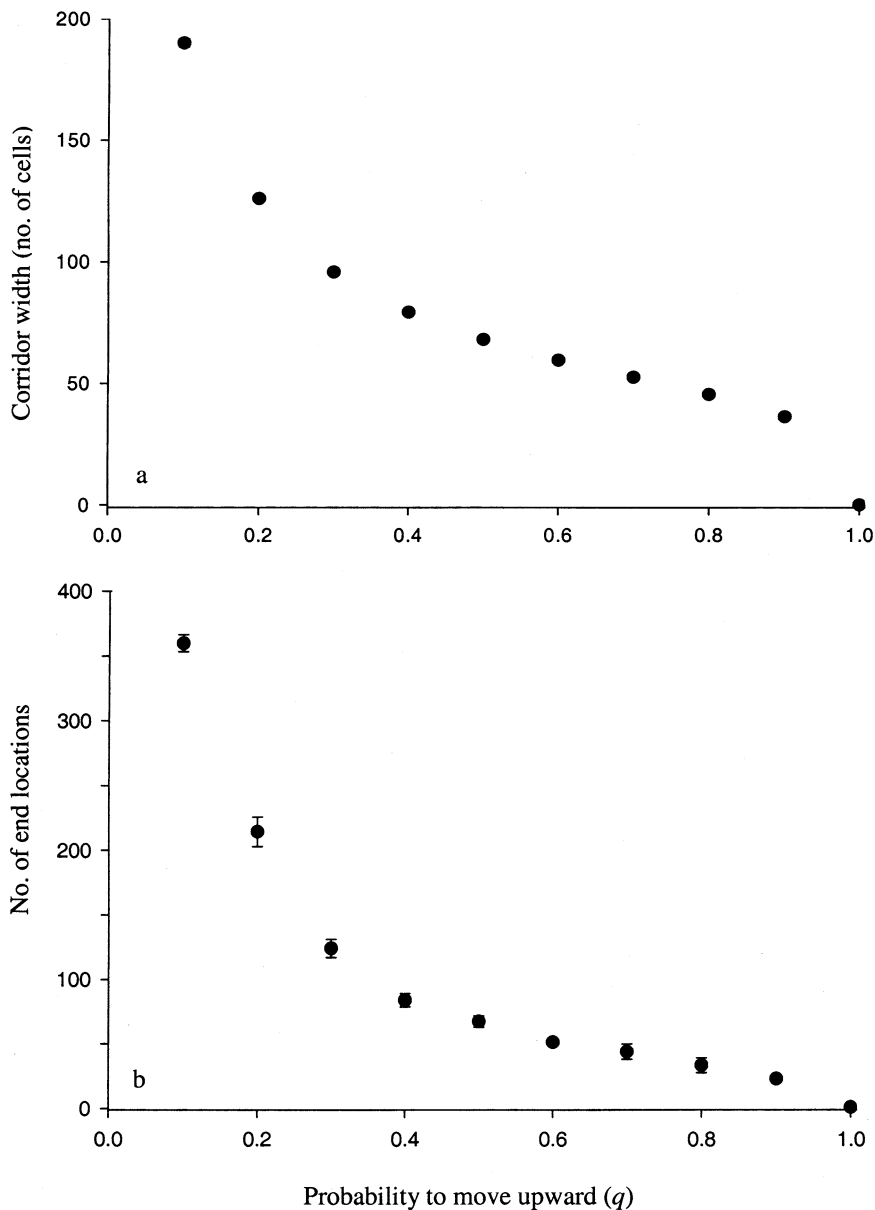


Figure 2. (a) Corridor width and (b) number of distinct end locations versus the intensity of response to topography (probability of butterfly to move upward,  $q$ ). Corridor width is evaluated as the number of visited cells divided by the distance from the source patch to the summit. The number of end locations is the number of cells occupied by individuals at the end of each simulation. When the final location of two or more individuals was  $<4$  cells away from each other, we considered them a single end location. Each value is the average of 20 simulations ( $\pm$  SE). In each simulation, 500 individual butterflies moved 1000 steps. Results are shown for two locations of the source patch but represent a consistent qualitative pattern.

the number of summits reached depended on  $q$ . Even when  $q$  was low, the movement paths were clearly confined to particular areas of the landscape (Fig. 1d). As  $q$  increased, a sharper movement pattern formed, yet a certain degree of complexity remained (Figs. 1e-f).

To characterize these results quantitatively, we analyzed the locations of the individuals at the end of each simulation. When the final location of two or more individuals was  $<4$  cells away from each other, we considered them as a single clump, which we term "end location." The number of distinct end locations provided an index of landscape utilization at the end of the hilltopping process. Potentially the index can range from the number of individuals (in the case of a totally random movement) to 1 (on a simple landscape and/or a completely directed movement).

Changing  $q$  systematically from 0.1 to 1 revealed that the number of distinct end locations declined strongly

with  $q$  and leveled off at moderate to strong values (Fig. 2b). The very high number of end locations obtained for low values of  $q$  was because many individuals did not reach a summit under the given time horizon. With moderate to strong values of  $q$  most of the end locations were summits, but still the number of end locations was high (several dozen). This indicates that in the given example even a strong response to topography resulted in a complex VC structure. Only when  $q = 1$  did all animals arrive at one end location (a single summit). The pattern of decline in corridor width and the decline in the number of end locations with  $q$  were similar (Figs. 2a & 2b).

Concerning the realistic range of response to topography ( $q$ ): field observations of the lesser spotted fritillary showed that the tendency to move upward was 0.775 for males and 0.818 for virgin females (Pe'er et al. 2004). These values converted to  $q = 0.55$  and  $q = 0.636$ , respectively. In this range of  $q$  values the model predicted a

high number of end locations (approximately 50) for the specific landscape chosen (Fig. 2b).

## Discussion

Animal responses to topography direct their movements, creating virtual corridors. Previous research indicates that animal dispersal can be channeled (e.g., Beier 1995; Ferreras 2001), and channeling effects are well known in connection with corridors (e.g., Wiens et al. 1993; Tischendorf & Wissel 1997; Haddad 1999). The current concept assumes, however, that corridors evolve along clearly visible, linear landscape structures. In our study such structures were absent, yet animals were channeled into specific routes (i.e., VCs). Our systematic analyses of landscape utilization with respect to the behavioral parameter ( $q$ , the intensity of response to topography) reveal that increasing the response to topography results in increasing channeling of individuals into a single, narrow route. Our results show how animal movements can be channeled into VCs and suggest methodologies for predicting the structure of VCs in a variety of landscapes.

### Lessons Learned about Virtual Corridors

Understanding the characteristics of VCs by comparing them with "normal" corridors contributes to a conceptual foundation of the VC approach.

1. In contrast to normal corridors, VCs do not necessarily form along visible directional landscape elements. They occur as a result of the animals' response to topography, even if this response is weak (e.g., our one-summit case).
2. The structure of VCs depends on the strength of the animals' response to topography, and it may be complex and unintuitive (e.g., complex-landscape case), especially for realistic values of the intensity of response to topography. Although a weak response channels animal movement even in complex landscapes, the number of routes taken may be high and may remain high even if the animals' response to topography is strong.
3. In contrast to normal corridors, the location of a VC is not fixed and depends on the location of the source patch. Thus, if the source patch shifts, so may the VC.
4. Although animal movements along normal corridors are expected to be in both directions (to and fro), movement along VCs may be unidirectional.

### Implications of Virtual Corridors for Conservation Management

Conservation-dependent animal populations often occupy a small number of relatively isolated patches. In such cases the number of movement paths, their structure, and the direction of movement along them become vital for the functionality of the system (Ferreras 2001). Some

movement paths maintain connectivity whereas others may lead animals away from patches to die in the hostile matrix. Thus routes that contribute to connectivity should be recognized and preserved, and the leakage of individuals into the matrix through dead-end routes should be prevented. Hence the ability to recognize priority areas for connectivity and to develop landscape-specific management plans becomes crucially dependent on our ability to identify VCs.

Because of their independence of visible habitat elements, their possible complex structure, and their dependence on the animals' behavioral parameters, VCs are not easily detectable. Consequently, intuitive decisions and simple rules of thumb (such as "go to the nearest summit" in the hilltopping case) are insufficient for predicting the location of VCs. Instead, other tools are needed for landscape analysis and for landscape-specific decision support. One approach is to use individual-based, spatially realistic simulation models (IBMs). One major advantage of such models is that they allow one to analyze the impact of the landscape on movement patterns through the eyes of the animals (Wiegand et al. 1999; Tischendorf & Fahrig 2000; Vos et al. 2001).

The use of IBMs does not exclude the need for field data. Such models must rely on a good understanding of animal behavior during dispersal and the elucidation of the relevant values of the behavioral parameters for the model. Tracking individuals, however, is a complex and exhaustive procedure that can provide data on the specific movement tracks of only several individuals in a single landscape. In contrast, IBMs enable extrapolation of these data and can provide generalizations and predictions on VC structure in a variety of landscapes and situations. Thus IBMs have the potential to handle VC complexity in a variety of landscapes.

Our IBM was simple, with a small number of parameters. Model simplicity served to highlight general features of VCs and their implications for conservation. Nevertheless the same model can also provide realistic prediction of movement patterns, once a specific, biologically sound parameter value for  $q$  has been chosen (Pe'er 2003). We therefore believe that simple IBMs, based on a few key behavioral parameters, may be capable of predicting specific patterns of landscape utilization by animals, namely VCs. This is in contrast to many IBMs that tend to be complex and case specific (Grimm 1999). Certainly, if species with a more complex movement behavior are considered or more detailed solutions are sought, then more sophisticated individual-based models are needed (Grimm et al. 1999), perhaps resulting in even more complex VCs.

Spatial scale and map resolution may also affect VC structure. The importance of these factors is addressed widely in landscape ecology studies (Turner et al. 1989; Obeysekera & Rutchey 1997). In the context of IBMs for identifying VCs, they may affect both the strength of landscape signals and their reliability, which, in turn, affects the predicted VC structure.

### Virtual Corridors in Other Contexts

We demonstrated that VCs evolve because animals respond to gradients of change in elevation. Many other landscape attributes present gradients to moving animals, for example, habitat suitability, temperatures, soil moisture, humidity, and human-produced factors such as noise, light, and pollutants. All these signals may direct animal movements and induce the formation of VCs in a wide variety of contexts.

The response to gradients plays an important role in homing birds (Phillips 1996; Wallraff 2000; Wiltshko & Wiltshko 2003) and in conspecific recognition in insects (Fadamiro et al. 1998; Yamanaka et al. 2003 and references therein). Wiens (1992) discusses aspects of animal response to gradients on the boundary between landscapes, but this discussion is limited to ecotones.

Although recently researchers have addressed connectivity in landscapes presenting continuous changes in habitat suitability (Malanson 2003), the response to gradients is still poorly represented in modeling animal dispersal, connectivity, and patch-recognition processes. A major reason for this may be the limitations of GIS maps: most current models of connectivity use maps with discrete habitat types in which the transition between habitats is abrupt (e.g., Gustafson & Gardner 1996; Schippers et al. 1996; Schadt et al. 2002). This dictates the assumption that animal movements inside a given habitat are random, so the interaction between the animal and the landscape is confined to the borders between habitats. Such models cannot account for animal responses to gradients and are expected to underestimate the proportion of channeled movements (Malanson 2003) and the formation of VCs. Also, it is possible that researchers revert to using a discrete-habitats approach partly because animal responses to gradients are not revealed easily in empirical studies. Thus we see a major challenge in recognizing how animals respond to gradients, depicting the gradients' spatial structure, and assessing the impact of gradients on movement and connectivity in fragmented landscapes. We suggest that whenever species' response to gradients can be sufficiently addressed, VCs are likely to be identified.

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