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Appendix 1

Assumptions and selection of scenarios

(a) Choice of the response to landscape boundaries

Landscape edges were of marginal relevance for males and virgin females in our model because the selected landscapes had the highest points occurring within the landscape, thus leading individuals away from edges. However, edge effects were relevant for the dispersal of mated females. We considered four potential approaches to reduce boundary effects. One is a torus landscape, in which individuals passing the edges would re-enter the landscape from the opposite side. Such a scenario assumes that the distribution of resources is homogeneous across an infinite space, and therefore it overestimates the chances of long-distance dispersers to identify habitat patches (Hovestadt et al. 2000). Furthermore, in a topographically complex landscape, a torus landscape implies that the topographical patterns iterate periodically, and animals dispersing away from summits always reach other mountainous systems (and patches).

A second option is a reflective boundary, in which animals arriving at the landscape edges alter their directionality and move back into it. Similarly to a torus landscape, such an edge response underestimates the chances that animals can be lost in the matrix, and allow them to periodically encounter the same landscape attributes.

A third option is to extend the landscape and the distribution of patches, but with no topographical signal in the extended part of the landscape. This scenario allows animals to search for habitat patches over a larger homogenous area, thereby reducing the relevance of topographical signals. This scenario was therefore unfavourable.

The last option and the one chosen for simulations presented in this study, was to restrict the release locations and patches to a smaller area within a larger landscape map. Animals moving away from the system reach a buffer area where they still encounter topographical signals but no patches. If they continue onward on the same direction, they leave the buffer area, reach the landscape edges and die. Such simulations comply with the assumption that ecosystems are heterogeneous and therefore animals that move away from the patch systems are lost within a hostile “matrix”, or at least become irrelevant to that system. This scenario also complies with the high mortality rates that are usually associated with long-distance dispersal. While this scenario overestimates dispersal mortality (for mated females), we found it more plausible than overestimating dispersal success.

(b) Choice of a mortality scenario

Dispersal is often modelled using per-step mortality, leading the number of dispersing animals to decay exponentially with time. Such a procedure creates a 'type III' survivorship curve (after Pearl 1928), where most individuals die in the beginning of the simulation. However, it is far more likely that the survivorship curve of hilltopping butterflies is concave and not convex, complying with a 'type I' survivorship curve (Begon et al. 1996). First, adult insects often exhibit an increased mortality rate with time, due to rapid aging after the completion of copulation (in males) or egg-laying (in females) (Zalucki (1981) and Matsumoto (1985) for butterflies, Fox et al. (2003, 2006) for beetles. Second, one should expect only butterflies in good physical conditions to engage in hilltopping, and likely only after having 'fuelled up' (Shields 1967). Lastly, predation mortality during hilltopping seems negligible in comparison to predation when nectaring or egg-laying within patches. In fact, neither Shields (1967) nor G. Pe’er (unpubl.) ever observed any mortality during hilltopping. Finally, mortality could occur due to starvation (e.g. due to lack of resources on hilltops) or failure of females to find habitat patches, but these again support an abrupt, or type I, mortality scenario.

References

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(c) Patch-related processes

The hilltopping model ignores all processes that occur within patches, such as mating, egg-laying or competition. This is because the model is not intended to ask why animals engage in hilltopping but instead, what happens once they do so. Intraspecific interactions do certainly affect the propensity to engage in hilltopping or whether to remain in a patch once arriving, but they were not found to affect movement behaviour once hilltopping has been initiated (Pe'er et al. 2004).

The model further assumes that animals that recognize a patch move into it. A perceptual range of 50 m was determined in this study since empirical studies indicated on such a distance (Conradt et al. 2000, 2001, Schtickzelle et al. 2007). Preliminary tests further indicate that the qualitative results are only marginally affected by the perceptual range.

(d) Movement parameters: choice of the movement rules and a comparison with a more gradual CRW

The probabilistic movement rule taken here, where animals either move persistently straight, toward the steepest slope, or otherwise completely randomly, tend to create a slightly erratic pattern (straight, broken lines) which may seem somewhat unrealistic at small scales. An alternative strategy which is often taken in simulating correlated random (or non-random) walks is one which applies a gradual probability curve, using e.g. a wrapped Cauchy distribution or a power approximation of it. To explore whether such an approach may yield different results or should potentially be preferred in this study, we developed an alternative movement procedure where either the persistence probability (P_{up} or P_{down}) or the response to topography (Q_{up} or Q_{down}) obtain a gradual value. For the response to topography, the relative probability was determined by the difference in elevation between each of the 8 neighbours and the locality of the individuals. All values of the difference were corrected based on the minimum value (for Q_{up}) or the maximum value (for Q_{down}), and the absolute values were then weighted based on a power function followed by normalization so that the total probability of all 8 neighbours equals 1. We also enabled applying a more gradual probability to move persistently straight, by ranking the 8 directions from 5 (previous direction) to 1 (backwards) and assigning a power-value to these ranks. These values were then converted to a relative probability to move to each cell. To combine both, an additional weighing parameter *W* was added determines the relative contribution of *P* versus *Q*.

Preliminary simulations indicated that the resulting movement patterns are indeed somewhat smoother (Fig. A1). Analysis of the mating success and time until mating were qualitatively similar to those presented in the main body of this paper, indicating on an initial increase in mating success and decrease in time until mating with Q_{up}, followed by a decrease in mating success when the response to topography is too strong (compare Fig. A2 below to Fig. 3 in the body of the paper).

We nonetheless decided not to use the gradual movement rule within the body of the paper. First, field observations indicate that animals move either straight (ignoring topographical signals) or toward the steepest slope, and otherwise completely randomly with respect to topography (Pe’er et al. 2004) – likely because of other small-scale factors such as nectar sources, distraction by conspecifics or predators, etc. Secondly, the use of 'yes or no' probability values yields a linear increase in the strength of response with a given probability value, which is quite intuitive to understand and interpret. Third, applying a gradual movement rule on both *P* and *Q* requires exploring different weights for the two (as a replacement for dominance of *P* over *Q*), but this entails an additional parameter and hence increasing complexity. Furthermore, when comparing model parameters with observed patterns, a gradual probability distribution would require more complex equations, which may be less intuitive. Finally, Yackulic et al. (2011) suggested that despite the somewhat erratic nature of the movement patterns at small scales, such details may not be critical or even important at larger spatial scales. That said, we fully acknowledge that other movement rules, and especially a 'gradual approach', may be more suitable if small-scale movements are investigated, or if the distribution of turning angles is used as means to compare a model with observed movement behaviour.

Figure A1. Exemplary movements of 50 males and virgin females over a virtual landscape,(a) with the gradual movement parameter $Qgrad_{up}$ =1 (P_{up} = 0), and (b) with a $Pgrad_{up}$ =5 (Qup = 0)

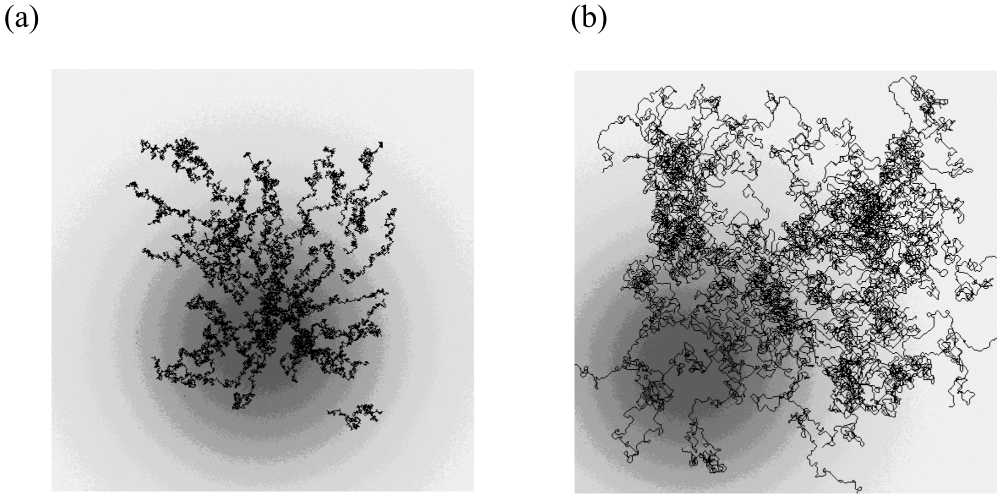
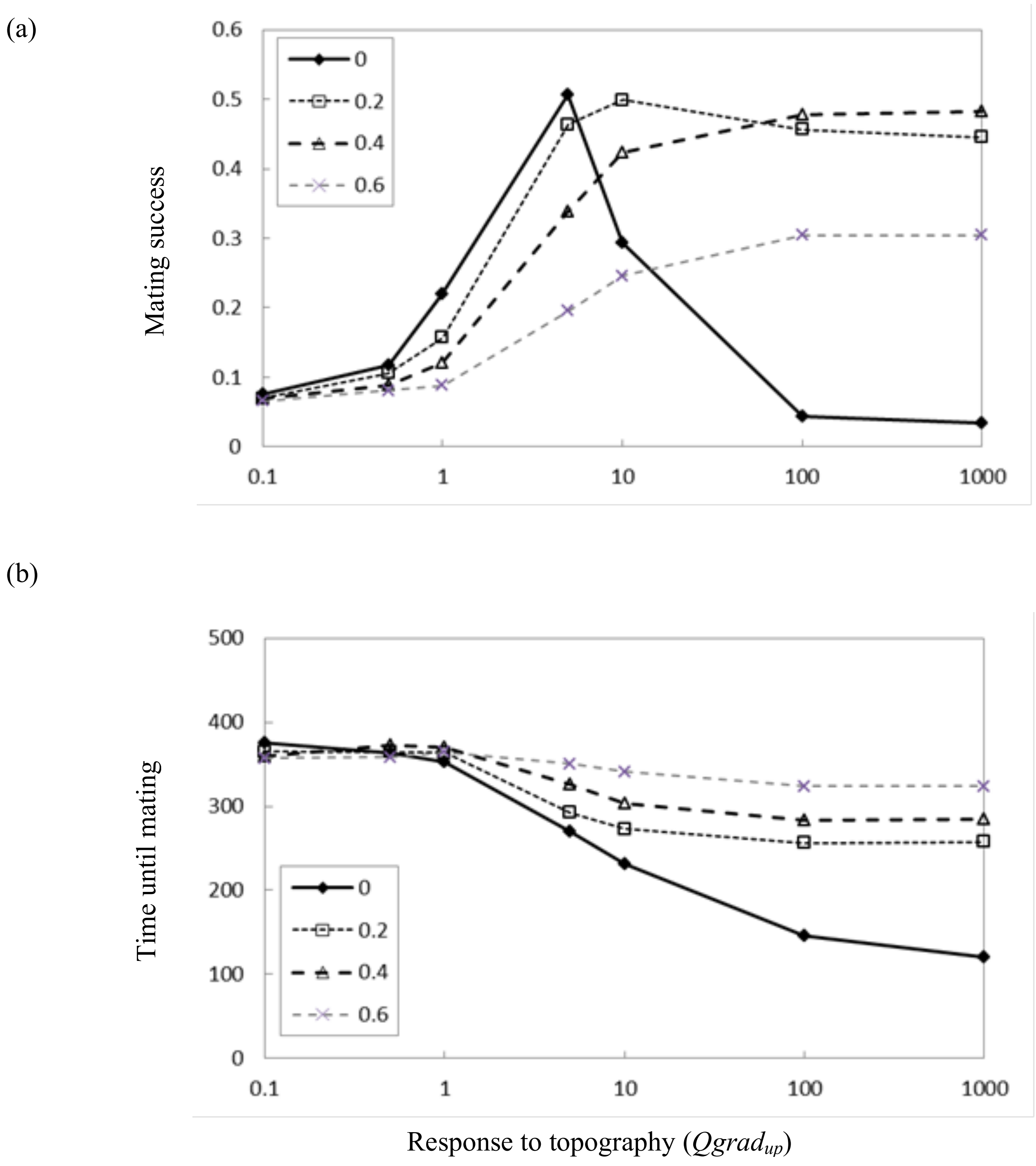


Figure A2. (a) Mating success and (b) mating time versus the gradual movement parameter *Qgrad*$_{up}$ with alternative values of P_{up} (not in its gradual option, for comparability with the result presented in the main text). Results are based on 20 simulation repeats.



(e) Choice of emergence scenario

Butterflies were released randomly across the entire landscape, assuming that they do not hatch in a limited number of well-defined patches, or at least assuming that they have already left them. This assumption was based on preliminary simulations, where we explored three possible scenarios for the release of individual butterflies over the landscape: 'Start in patches', 'One random release-point', and 'Random release'. Simulations were performed over a virtual landscape with one summit, and with five randomly-selected target patches. In each of the three release scenarios, we altered the response of males and virgin females (Q_{up}) and the response of mated females (Q_{down}) systematically from 0 to 1 in increments of 0.1, and assessed the chances of mated females to arrive successfully at the five habitat patches for every parameter combination. The first two scenarios yielded optimal parameter combinations that were not only unrealistic (males and virgin females should move always up; mated female strategy was unimportant) but did not even favour engagement of individuals in hilltopping (i.e., best strategy would be to remain in habitat patches).

We therefore chose the third scenario, 'Completely random release', for all further simulations in this study. This scenario forces individuals to engage in hilltopping, and allows investigating the patterns that result from hilltopping given that it occurs, rather than the question why hilltopping occurs from the first place.

An additional advantage of a random release scenario is that it substantially reduces the sensitivity of the model to population densities. Population density essentially affects the propensity of butterflies to engage in hilltopping (Pe’er et al. 2004) and the location of the mating event, especially if butterflies emerge in patches (– as were the results of our preliminary analyses). When butterflies emerge in patches, the model must utilize either very large time-gaps between butterfly emergences (thus adding complexity to the model) or exceptionally low population densities in order to invoke hilltopping. In a random-release scenario, however, the only intraspecific interactions in the model involves mating, and the optimal strategy identified therefore depends primarily on the success of animals to effectively reach hilltops – almost irrespectively of population density.

Appendix 2

List of model parameters and their values within this study

Input variables	Variable type and units	Values in this study
Behavioural variables		
Males and virgin females: persistence (P_{up})	single	explored (0-1)
Males: intensity of response to topography (Q_{up})	single	explored (0-1)
Mated females: persistence (P_{down})	single	explored (0-1)
Mated females: intensity of response to topography (Q_{down})	single	explored (0-1)
Butterfly release		
Number of individuals	integer	1111
State of individuals	choice between: males only; males and virgin females; all states	males and virgin females
Release scenario	choice between: one non-patch location; one patch; randomly in patches; randomly across the landscape	randomly across the landscape
Number of steps between emergences	integer	5
Landscape variables		
Landscape: upload or design	choice	explored
Landscape size	integer (number of cells along the length)	250
SD mountain width*	integer (number of cells)	120
Spatial noise	single (% of summit height, up to 100)	1.5
Number of summits	integer	1
Locality of summits	random or fixed	random
Expand map to reduce edge effects	boolean	yes
Summit Height	integer (arbitrary units)	2000
Patches		
Number of patches	integer	14
Spatial location of patches	choice between: Random; stratified-random (= lower, middle or upper third of elevation range); fixed to designated points; summits.	random
Who is allowed in patches	choice between: all, or mated females.	mated females only
Perceptual range of patches	integer	50
Processes until mating		
Females mate after X encounters		5
Mortality		
Type of mortality	choice between: per step; abrupt	abrupt
Per-step mortality	single	not applied
Maximum number of steps	integer	see Table 2
Landscape name	string	see Table 1 and Fig. 1

* Gaussian distribution

Appendix 3

Quantification of the effects of landscape parameters on the optimal behaviour identified

Below we present the outcomes of linear mixed effect model (LMM) for the behaviour of males and virgin females (M_{mvf}) and the behaviour of mated females (M_f), for simulations (a) with 600 time steps and (b) with 1000 time steps. We assumed the maximum model to contain the (random) main effect of landscape, the (fixed) main effect of the average landscape elevation, average patch elevation per simulation, the landscape complexity (*D*), and the interaction between the latter three. The rows provide performance indices for the maximum model compared to a model reduced by one factor (DF: degrees of freedom, REML: restricted maximum likelihood, ML: maximum likelihood, sd: standard deviation, p-value: significance level). Significance levels should be treated as means for ranking the effects rather than indicators of strength, as these values are affected by the number of simulation repeats. One of the most important outcomes of this analysis is that removal of either the parameter *D* or the average landscape elevation does not significantly reduce model performance, primarily due to the high correlation between the two.

(a) (600 steps)

Removed variable	Observed log-likelihood (DF, estimator)	Observed log-likelihood ratio	Random log-likelihood ratio (SD)	p-value
M_{mvf} (log-likelihood maximum model: REML = 516.6, ML = 520.9, DF = 9)				
Average patch elevation /sim (fixed)	507.7 (6, ML)	17.809	7.08 (3.099)	0.005
Landscape (random)	518.3 (9, REML)	14.734	0.402 (1.121)	<0.0001
Average landscape elevation (fixed)	514.3 (6, ML)	4.642	11.041 (3.104)	n.s.
D (fixed)	515.4 (6,ML)	2.534	10.633 (3.078)	n.s.
M_f (maximum model: REML = 425.8, ML = 425.6, DF = 6)				
Average patch elevation /sim (fixed)	379.75 (6, ML)	92.04	7.299 (2.99)	<0.0001
Landscape (random)	518.3 (9, REML)	45.21	0.353 (0.903)	<0.0001
Average landscape elevation (fixed)	417.05 (6, ML)	17.44	16.23 (2.92)	n.s.
D (fixed)	423.075 (6, ML)	5.399	13.31 (3.09)	n.s.

(b) (1000 steps)

Removed variable	Observed log-likelihood (DF, estimator)	Observed log-likelihood ratio	Random log-likelihood ratio (SD)	p-value
M_{mvf} (log-likelihood maximum model: REML = 329.7, ML = 331.8, DF = 9)				
Average patch elevation /sim (fixed)	315.60 (6, ML)	28.18	8.983 (3.01)	<0.0001
Landscape (random)	329.513 (9, REML)	15.76	0.34 (0.93)	<0.0001
Average landscape elevation (fixed)	323.82 (6, ML)	11.735	14.1 (3.00)	n.s.
D (fixed)	326.04 (6, ML)	7.303	12.41 (3.03)	n.s.
M_f (maximum model: REML = 425.8, ML = 425.6, DF = 6)				
Average patch elevation /sim (fixed)	379.75 (6, ML)	92.046	7.46 (3.06)	<0.0001
Landscape (random)	411.475 (9, REML)	45.21	0.40 (1.11)	<0.0001
Average landscape elevation (fixed)	417.05 (6, ML)	17.44	16.10 (2.85)	n.s.
D (fixed)	423.075 (6, ML)	5.399	13.11 (3.05)	n.s.