are working to increase simulation accuracy while reducing the computational burden. A central challenge concerns simulation of interacting processes that occur on different time scales; the fast scale imposes a short simulation time step, but that makes the simulation too slow to observe the slow scale. This is being met with new algorithms and hybrid simulations that treat space and stochasticity only as required. Also, given the size and the possible nonlinearity and non-determinism represented by biological models, tools for analysis of models, such as those that provide parametric sensitivity analysis, and for comparing models to data for parameterization and (in)validation are both profoundly needed and in a relatively primitive state.

It is easy to describe the ideal simulation tool: it should be able to simulate reactions and diffusion as accurately as needed, account for all relevant mechanical processes, help with model parameterization, validate and discriminate between models using data, and be easy to use. Many modeling tools are aiming towards this goal but it remains elusive, in part because of the extraordinary speed with which improved analysis methods and cellular measurements are being developed.

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Elephants avoid costly mountaineering

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Understanding the behavioural decisions underlying animal movements is a major challenge. Here we report evidence for the importance of the abiotic terrain feature ‘gradient’ in guiding the movements of African savannah elephants (*Loxodonta africana*). Global Positioning System (GPS) tracking data overlaid onto digital elevation and surface gradient models show that elephants tend to avoid steep slopes. Energy calculations suggest that even minor hills are considerable energy barriers for heavy animals.

Elephants are keystone animals in Africa and Asia [1], and effective conservation planning strategies must integrate a thorough knowledge of the range use and spatial requirements of these magnificent animals. Only with such knowledge can we ensure that elephants will be able to survive despite increasingly aggressive human encroachment into their traditional territory [2]. Moreover, there is much to be learned scientifically from understanding the ecological requirements — as well as limitations — of the last remaining representatives of a once cosmopolitan and ecologically critical megafauna.

Early studies of elephant movements deployed radio tracking from the air and provided rather infrequent ‘fixes’ which painted an incomplete picture of spatial utilisation [3]. Modern GPS collars using a satellite and/or cell-phone link allow us to collect movement data with high temporal and spatial resolution [4], reflecting true range use by also mapping areas not visited. Long-term elephant tracking studies are beginning to show

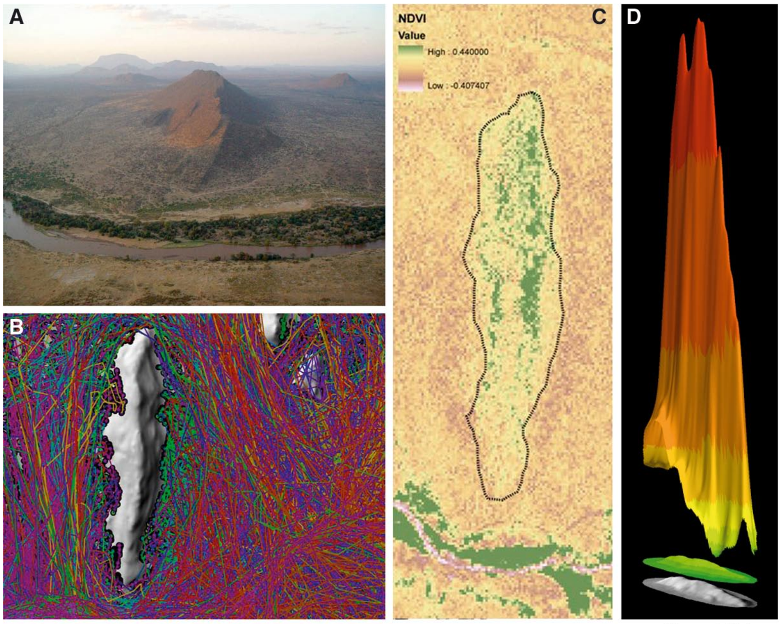

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Figure 1. Koitogor and the Samburu elephants.

(A) Koitogor Mountain – a prominent feature of the Samburu Landscape rising 300 m above the adjacent plain. (B) Three-dimensional model of Koitogor with individual elephant tracks shown as coloured lines. (C) NDVI image (February 2000) demonstrating that even in the dry season (February 2000) the hill (outlined) is greener than the plains although not the river banks (bottom). (D) Energy calculations for the costs of ascending Koitogor (grey, map topography) for a 100 kg animal (middle) and a 5000 kg elephant (top) with the colour coding indicating the basic cost of ascent from green to red (for details see text and Figure 2 legend, and the Supplemental data).

how regions of high elephant density are linked by a network of corridors cutting through localities that are otherwise avoided [3]. Understanding what makes a density 'hot-spot' as compared to a corridor (and what distinguishes either from a no-go area) will be crucial for securing safe niches for elephants in the face of ever expanding human influence [5].

The Samburu/Isiolo/Laikipia districts in northern Kenya cover a combined area of 32000 km^2 of mostly unprotected habitat and are home to ~5400 elephants. GPS tracking data give insights into the requirements of this population [6] which are important both ecologically as well as scientifically. In order to understand and explain the ecology of this population, we are studying the various factors that might affect elephant movements, such as geography, hydrology, vegetation cover and land use, as well as the demographies of elephants, humans and livestock. Regional topography affects variables such as soil moisture, nutrient concentrations and vegetation, and may thus affect local elephant ecology indirectly [7]. Here we show that terrain may also directly affect elephant movements by imposing considerable energetic costs on travel.

By overlaying the elephant tracking data onto a digital elevation model (DEM) covering 237km^2 centered on our study region, we found that elephant density decreased exponentially on increasing hill-slopes ($R^2 = 0.90$; for details see the Supplemental data available on-line with this issue). Elephant avoidance of an isolated, prominent hill, Koitogor (Figure 1A), serves to illustrate this general behaviour pattern (Figure 1B), showing that the elephants even ignore Koitogor's substantial vegetation cover (Figure 1C). While in addition to slope there may be other important reasons for the elephants' general avoidance of climbing this hill — such as overheating, risk of injury, lack of water or unsuitability of forage — we suggest that energetic considerations could be one of the main factors for the following reasons.

Shifting 1 kg of bodyweight vertically upward 1 meter increases its potential energy by 9.8 J. Thus, at a typical muscle efficiency of ~25% [8,9], moving upwards would in principle add an estimated extra 39.2 J kg^{-1} to the basic metabolic cost of level movement. Thus climbing might cost a 4 ton elephant an additional 160 kJ m^{-1} over and above the estimated 4 kJ m^{-1} of level walk (~1 J kg^{-1} m^{-1} at 2 m sec^{-1} [10]). Apparently muscles are a third more efficient when climbing [9], thus working at 33% efficiency a 4000 kg elephant would incur extra expenses of about 100 kJ (or 25 kcal) for every meter climbed [9,11]. This computes to ~2500% of the cost of level walking, which is not unlikely [12] because the low basic metabolism of the large animal makes 'working' relatively costly [8].

The calorific value of a savannah elephant's forage is about 10,000 kJ kg^{-1} (2,500 kcal kg^{-1}) dry [13]. Daily the animal consumes about 1% of its bodyweight of dry food [14], with a 4 ton elephant eating 42 kg dry (or 162 kg wet) vegetation [15]. Hence in its average 16–18 hours of daily foraging [16] this animal would have an hourly intake of ~2 kg dry forage or 20,000 kJ. Climbing 100 m would 'burn' 10,000 kJ which would have to be either replenished by an extra half hour of foraging or paid for by using up body reserves. Clearly, climbing is something that an elephant should not do lightly. Figure 1D depicts dramatically the extra energy costs that a 5 ton elephant would likely incur climbing Koitogor. These costs might explain why, in our map of tracked movements, Koitogor represents a largely 'white' no-go area (Figure 1B) for the local elephants, bulls (~6 tons) as well as females (~4 tons) leading their herds.

We conclude that megafauna probably take a rather different view of their surroundings (Figure 2) than more lightweight animals. This is especially true if the heavyweights, like elephants, are herbivores for which energy replenishment is so much more time consuming than it is for carnivores.

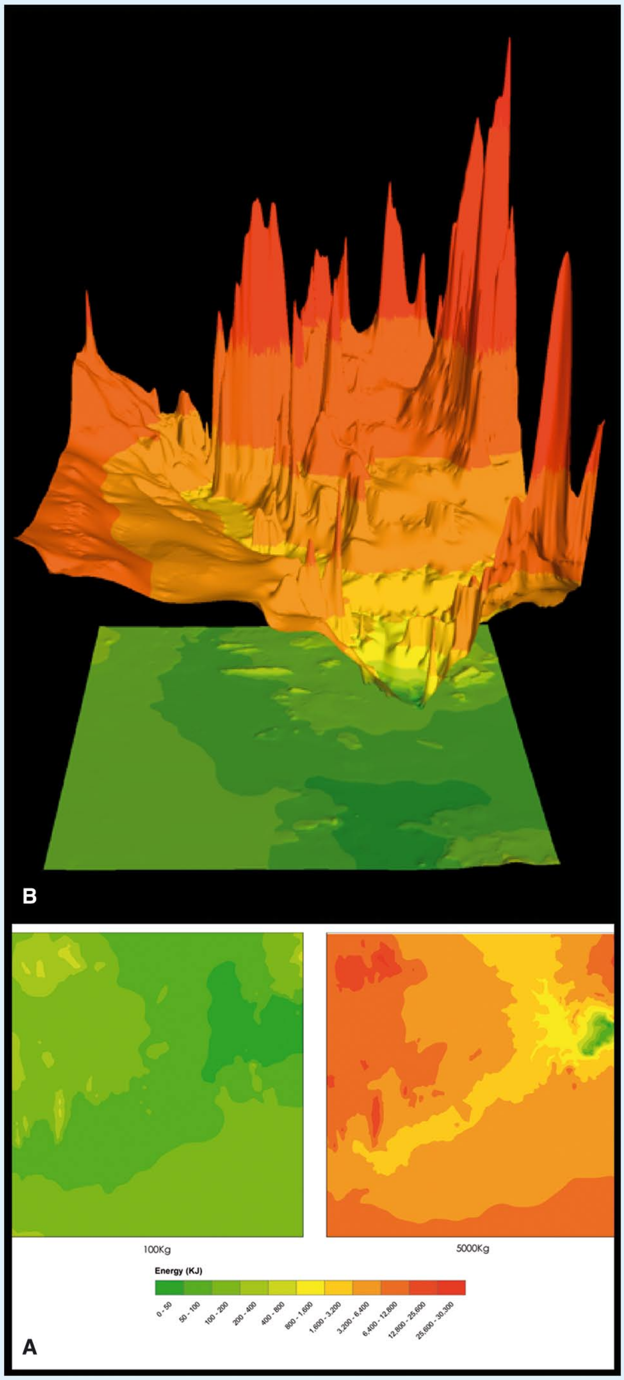

Figure 2. Energy ‘scapes’ depicting the predicted costs of climbing for a lightweight (100 kg) and a heavyweight (5 ton) mammal moving in the Samburu environment.

(A) Topographical two-dimensional map showing energy expenditure required to lift the animal’s weight. (B) Three-dimensional energy maps illustrating how costly the 5 ton elephant (upper map) would find the terrain.

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Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/16/14/R527/DC1/

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