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RESEARCH ARTICLE

Cost analysis of remotely sensed foraging paths in patchy landscapes with plant anti-herbivore defenses (Patagonia, Argentina)

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Abstract We developed metrics at a landscape scale to evaluate the costs and rewards experienced by large herbivores while foraging in natural vegetation with patchy anti-herbivore plant structures. We show an application of these metrics to the analysis of 16,000 records of positions at successive 1 min intervals of free-ranging ewes (*Ovis aries*) harnessed with Global-Positioning-System (GPS) loggers, in a large paddock of the Patagonian Monte shrublands (Argentina). Dominant shrubs in the area display numerous anti-herbivore defenses (spiny-resinous leaves, thorny stems, etc.) protecting them from grazing and herbivore trampling. Preferred grasses and forbs constitute a minor part of aboveground plant biomass and grow in relatively open areas among or around shrub patches. We mapped the movement speed of ewes onto high-resolution aerial photographs of the grazed paddocks and estimated costs and rewards along their paths based on algorithms of surface cost theory. Ewes explored areas of sparse vegetation at low speeds compatible with predominant grazing, and increased their speed when crossing denser shrubby patches. The cost algorithm was applied to evaluate daily searching costs as well as grazing rewards in relation to the length of daily searching paths. The observed path lengths and search speeds were consistent with those that compensate costs and rewards of the grazing activities as estimated by the surface cost analysis. We conclude that the technique presented here constitutes a valuable tool to quantify the effect of landscape characteristics on behavioral traits of grazing animals in similar environments.

Keywords Cost model · Foraging · Large herbivores · Patagonian Monte · Remote sensing · Spatial analysis · Surface cost theory

Introduction

There is increasing interest in the study of spatial heterogeneity and its effects on ecological processes. In this context, landscape ecologists share interests with animal ecologists in developing parameters and metrics to characterize the movements of grazing animals. The effects of landscape heterogeneity on grazers and the effects of grazers on the landscape are relevant to ecosystem processes, management, and/or conservation (Lima and Zollner 1996; Farnsworth and Beecham 1999; Ropert-Couder et al. 2004; Kie et al. 2005; Prair et al. 2005).

Techniques of landscape ecology (animal telemetry, remotely sensed imagery) are increasingly used to understand the interactions between landscape heterogeneity and the behavior of free-ranging large herbivores (Ares et al. 2003a; Calenge et al. 2005;

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Ungar et al. 2005). Foragers, particularly large herbivores, respond to the spatial pattern of resources at a variety of scales and in turn influence the plant spatial patterns (Bisigato et al. 2005) and the structure and function of ecosystems (Hobbs et al. 1991; Pastor and Naiman 1992). In visually-oriented grazers, the time and costs of traveling between feeding stations can be substantial (Gross et al. 1995) and there is a need to identify the decision rules that animals use while foraging in order to develop and test ecological models that would operate at large scales (Judson 1994). A common assumption in addressing these issues is that animals would approach some optimal spatial behavior that would maximize their fitness or some related dimension of their biological cycle (fecundity, growth, survival) and be constrained by their cognitive abilities and the spatial pattern of forage resources (Viswanathan et al. 1999; Zollner and Lima 1999). Since fitness is usually difficult to assess, related currencies are taken as acceptable proxies for analysis provided they are amenable to quantification and variations in the proxies correlate with fitness variations. In foragers, energetic costs expended and the rewards obtained during foraging are commonly accepted proxies of reproductive success-fitness (Cuthil and Houston 1999; Lewison and Carter 2004).

Many empirical studies show that large herbivores exploit spatially heterogeneous vegetation through selective foraging, concentrating their activity in patches that offer high rates of intake or energy return (Bazely 1988; Laca 1992; Clark et al. 1995). Although the rate of energy intake is very relevant in considering the energy balance of herbivores, less attention has been devoted to energy losses experienced during searching for preferred feeding patches. Hulbert et al. (1998) estimated that an ewe weighing 50 kg would expend about 0.33 mJ/day (about 8% of fasting metabolism) when roving over 3,000 m/day and up to 0.77 mJ/day when climbing heights of 500 m (31% of fasting metabolism).

While the evaluation of energy losses directly related to mechanical work is relatively straightforward, estimating other terms of the energy balance might not be a simple task. Reduced energy intake can occur because the animal must share foraging time with other competing activities, like searching for food, escaping from predators, or maintaining visual contact with kin in intricate landscapes. Grazing over snow, muddy terrain, or intricate vegetation increases energy losses. Roving distances can be greatly increased due to sinuosity imposed by natural obstacles, including woody vegetation with anti-herbivore defenses. Theoretical analyses indicate that the length and geometry (London 1999) of the forager's paths depend on the spatial arrangement of resources (Viswanathan et al. 1999), the particular search strategy applied (Higgins and Strauss 2004), conspecific attraction, perceptual range (Lima and Zollner 1996), and forage depression effects (Stillman et al. 2000).

The similarity of the problem of spatial optimal foraging with economics has motivated interest in interpreting herbivore search tactics with models borrowed from the economic theory (Anderson 1983). Cramer and Gallistel (1999) found that vervet monkeys (*Cercopithecus aethiops*) approached the behavior of an efficient traveling salesman while searching for food patches in relatively simple arrangements. Grazers in shrubland landscapes (sheep (*Ovis aries*), goats (*Capra hircus*), guanacos (*Lama guanaco*), lamas (*L. glama*), etc.) must negotiate physical obstacles consisting of trees or shrubs of sizes in the range of their body size or greater. In addition, they must use complex forage patches where preferred forage is mixed with plants with anti-herbivore defenses (thorny stems, spiny leaves, resinous leaves, etc.). Following Lea (1979), several authors (Fantino and Abarca 1985; Goldschmidt and Fantino 2000; Orduña and Bouzas 2004) have conceptualized local foraging as successive choices which are reinforced by the balance of rewards/costs. A central point in interpreting the effect of heterogeneous environments on grazers is the evaluation of the cost/reward function (Gallistel 1999) in space.

In this study, we developed an application of a surface cost algorithm and illustrate its use with position data and travel speeds of sheep grazing paths at a free-ranging area in the Patagonian Monte. For those readers that might not be familiar with surface cost theory we present an introductory section in Appendix I. We further discuss applications of the technique to the analysis of the effects of landscape heterogeneity on foraging paths of large herbivores and in spatial explicit modeling of herbivore behavior in relation with landscape heterogeneity.

Methods

Introduction to the surface cost algorithm

The concept of surface cost finds application in automatic cartographic analysis of digitized images in defining the path of least cost between two locations, given the distance between them and a set of obstacles or facilities along the way. Eastman (1989) seems to have advanced the algorithm to compute surface costs that was adopted in some applications of spatial analysis (Douglas 1994; Eastman 2001; Basu et al. 2004). Ganskopp et al. (2000) used a cost algorithm to evaluate potential least-effort paths followed by cows on sloped terrain. Godard (2006) has recently made available a tutorial exercise on the subject at URL: http://www.ipt.univ- paris8.fr/vgodard/enseigne/sig/tuidrisi/tdi25sig.htm. An explanation of the theory, units of measurement and applications of the surface cost algorithm to studies on herbivore ecology at a landscape level is presented in Appendix I.

Study sites

Field data were obtained at a grazing range (1250 ha) of Smit's Ranch (42° 38'S, 65° 23′ W) in the Patagonian Monte (Chubut Province, Argentina). The area is characteristic of the Xeromorphic Tall Shrub floristic unit described in Ares et al. (1990) represented by the community of *Larrea divaricata*Cav. and *Stipa* spp. (León et al. 1998). Vegetation patches cover from 40% to 60% of the soil. The most frequent patch types are those dominated by *L. divaricata* (23–40% of all patches), *Atriplex lampa*Gill. Ex Moq. (14–23%), *Chuquiraga hystrix* Don. (4–32%), *Nassauvia fuegiana* Speg. (4–15%) and *Acantholippia seriphiodes* A. Gray (3–5%), with average patch sizes ranging from 42 to 346 dm^2 (Bisigato and Bertiller 1997). Most perennial shrubs display conspicuous anti-herbivore structures, such as resinous leaves in *L. divaricata* and *Larrea nitida* Cav., spiny leaves in *Chuquiraga avellanedae* Lorenz, and *C. hystrix*, thorny stems in *Lycium chilense* Myers ex. Bert, *Bougainvillea spinosa* (Cav.) Heimler and *Prosopis alpataco* Philippi. Because of spatial exclusion of dominant shrubs and preferred forbs and grasses (Bisigato et al. 2002), the former usually occupy the patch centers, with a crown of more preferred grasses and forbs that diffuses into sparsely covered interpatch spaces. Several field studies on the spatial distribution of plant biomass (Ares et al. 2003a), aerial photographs (Ares et al. 2003b, 2003c) and spatial-explicit modeling of the plant canopy (Bisigato et al. 2002) concluded that shrubs in the study area are randomly distributed. Under intensive grazing, relative grass cover declines while shrub cover increases (Bisigato and Bertiller 1997) attaining up to 99% of the total vegetation volume.

Sheep were introduced in the area at the beginning of last century (Defossé et al. 1992) and since then have been raised in large estancias (each 10,000 ha or more) like Smit's ranch, usually consisting of a few paddocks around a shared watering point. Under normal management, sheep would range freely within these large paddocks and eventually return to the central watering point. Studies on the diet composition (Baldi et al. 2004) of sheep in these environments indicate that annual and perennial grasses and forbs are the main components of the diet, with rare inclusions of some soft tissues of the dominant shrubs. Some observations indicate that free access of sheep to preferred plants is at places impeded by the presence of spines or thorny stems of neighbor shrubs. Most sheep paths run along longer ways around shrub patches rather than through them, and those herbaceous species (*Poa ligularis*, *Stipa tenuis*, *Elymus* spp.) that are highly preferred when growing at open spaces, are only occasionally consumed when they grow within shrub patches dominated by *C. avellanedae*, *P. alpataco*, *Schinus johnstonii* or *Larrea* spp.

Definition of surface costs to characterize plant anti-herbivore obstacles

We developed frictional surfaces to estimate the surface costs involved in sorting anti-herbivore structures by comparing the biomass of vegetation along sections of sheep paths with speeds compatible with predominant grazing with that along paths with speeds characteristic of predominant exploration. The underlying assumption in this procedure is that sheep would allocate time to stretches along foraging paths in proportion to the reward experienced when finding preferred patches (McNair 1982; Oom et al. 2002).

In order to describe the distribution of vegetation in the grazed area we used a low-altitude, high-resolution aerial panchromatic photograph, digitized to a pixel resolution of 0.1 m (Ares et al. 2003a). We call this image |T|. Such photographs of the Patagonian Monte, as in similar semiarid environments with patchy vegetation, shrubs appear as randomly spotted areas of dark optical density alternating with relatively light density areas corresponding to sparse vegetation, including grasses or even bare soil (d'Herbes et al. 2001). We used ranks of log transformed plant biomass volumes as supplied in Bisigato et al. (2002) to estimate a correlation ($R^2 = 0.78$, $P < 0.01$) with ranks of panchromatic optical density. This latter is conventionally expressed in terms of a nominal inverted scale of 256 gray tones (Fig. 1).

In order to obtain sheep path data, we retrieved 16,000 GPS-fixes corresponding to positions of two free-ranging ewes (weights: 38 and 37 kg respectively) in the field ranges, obtained at 1 min intervals during September 2003 and April 2004. The ewes were harnessed with standard GPS receivers (e-Trex, Garmin, KS, USA) on their fore-backs. The 2-strap harnesses also carried a solid-state memory and a programmable micro-controller (EEPROM-PIC16f84, Microchips Technology Inc. AR., USA), and six 1.5 V batteries. The total weight of the system was 1.2 kg, within the load range of telemetry equipment in similar studies (Rutter et al. 1997; Hulbert et al. 1998). After harnessed, the animals were first released in a small handling paddock among other non-instrumented specimens, and their behavior was observed during 30 min to check for signs of discomfort and harness acceptance. After this period, all animals were released to the foraging paddock. Ewe #1 was continuously sampled during 4 days and ewe #2 during 6 days.

The spatial precision of the GPS fixes was independently tested in the field at simulated sheep path sections (100 m) with 50 flagged, randomly spaced (0.3 m to 4 m) feeding stations. We obtained Latitude-Longitude fixes at the flagged positions while repeatedly (3×) walking along the simulated trail with a roving GPS receiver, each time pacing the walk at a different speed (1.75, 3.5, 7 m/min). The procedure was repeated 3 times at successive days. The GPS fixes were used to compute metric distances between successive flags. The absolute values of deviations of all estimates of a same distance respect to their average and the correlation of GPS-derived and tape-measured distances between consecutive flags were computed.

We estimated the ewes' movement speeds at 1 min intervals, overlayed (IDRISI v 14.02, Clark Labs., Worcester, MA, USA) the speed values onto the photograph image files and cross-tabulated the values of the image pixels and the speeds at which they were visited. After a preliminary inspection of the distributions of pixel values corresponding to various speed classes, we selected the speed ranges $0 < s \leq$

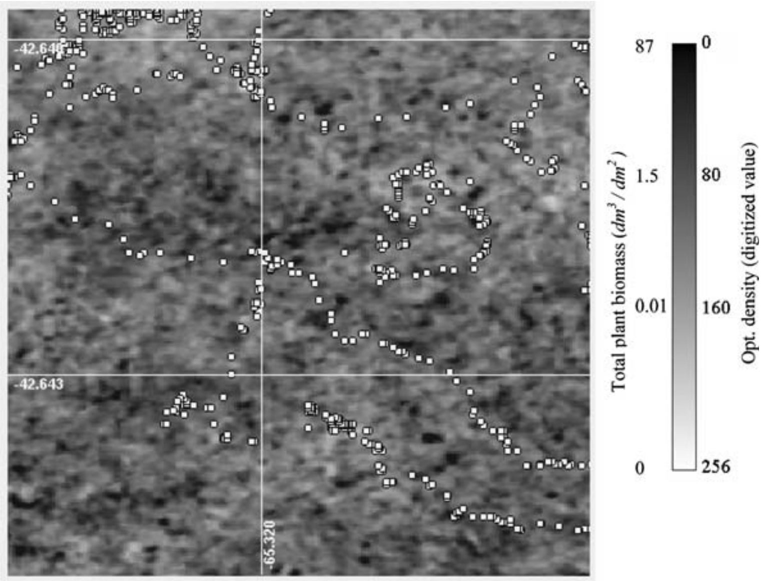

Fig. 1 Digitized (|T|) image of an aerial photograph of the study site with the conventional optical density coded in an inverted scale of 256 gray tones, and estimated rank correlated values of plant biomass at the Patagonian Monte. The dots correspond to some of the positions of free-ranging ewes at 1 min intervals retrieved in this study

2.5 m/min and $s > 2.5$ m/min as adequate to characterize predominant grazing activity (Hester et al. 1999) or predominant exploring activity, respectively. We extracted the frequency distributions of the image pixel values corresponding to each speed class. We made statistical comparisons of the frequency distributions by fitting bell-shaped, 3-parameter probability distribution functions (PDF) functions ($\boldsymbol{a}_0$:amplitude; $\boldsymbol{a}_1$: mean; $\boldsymbol{a}_2$: spread):

$$y = \boldsymbol{a}_{0,T,G,E}/(1 + ((x - \boldsymbol{a}_{1,T,G,E})/\boldsymbol{a}_{2,T,G,E})^2), \qquad (1)$$

to the observed histograms, where the parameter subscripts refer to the distribution of pixels visited at grazing and exploring speeds ($_{G,\ E}$, respectively) or those of the total range area ($_T$) represented by the |T| image. Statistical tests of differences between the PDFs were performed on their mean value $\boldsymbol{a}_{1}$, ($P < 0.05$). Fits were obtained through the Marquardt-Levenberg's algorithm implemented with the application package Peakfit v3.0 (Jandel Scientific, CA, USA).

We defined frictional images for cost analysis of the grazing and exploring paths ($|\mathrm{F_G}|$ and $|\mathrm{F_E}|$, respectively) through the following algebraic operations on digitized image files:

$$|\mathrm{G}| = \boldsymbol{a}_{1,G}/\boldsymbol{a}_{1,T} \times |\mathrm{T}| \qquad (2)$$

$$|\mathrm{E}| = \boldsymbol{a}_{1,E}/\boldsymbol{a}_{1,T} \times |\mathrm{T}| \qquad (3)$$

$$|\mathrm{F_G}| = |\mathrm{G}|/|\mathrm{T}| \qquad (4)$$

$$|\mathrm{F_E}| = |\mathrm{E}|/|\mathrm{T}| \qquad (5)$$

where the first right-hand product terms in eqs. 2 and 3 are scalar quantities, |G| and |E| are digitized images, |T| is the image of the total range area (null selectivity model) and the algebraic operations are applied on a pixel-by-pixel basis.

Surface cost model

We estimated the following surface costs along paths of ewe #1 and #2 by means of the application IDRISI v 14.02:

$\boldsymbol{C}_{d,d}$: Distance cost, expressed as the daily average cost of traveling over a unit-valued friction image ($f(x, y) = -1.0$). This was obtained by overlaying the ewe's daily paths on an image of the same size of the study area, with all negative, unit-valued pixels (distance image).

$\boldsymbol{C}_{d,v}$: Frictional cost, expressed as the daily average cost for an ewe that would travel over a vegetated surface at exploring speeds. This was obtained by using friction image $|\mathrm{F_E}|$.

$\boldsymbol{C}_{d,gv}$: Reward cost, expressed as the daily average cost for an ewe roving along the vegetated surface at speeds compatible with predominant grazing. This was obtained by using the friction image $|\mathrm{F_G}|$.

We calculated the daily reward ($\boldsymbol{R}_g$) obtained during predominant grazing as:

$$\boldsymbol{R}_g = \boldsymbol{C}_{d,gv} - \boldsymbol{C}_{d,v}. \qquad (4)$$

.

We further performed linear regression analyses of $\boldsymbol{R}_g$ and $\boldsymbol{C}_{d,gv}$ vs. $\boldsymbol{C}_{d,d}$ by extracting boot-strapped average samples of combined paired $\boldsymbol{C}_{d,d}$, $\boldsymbol{C}_{d,gv}$, and $\boldsymbol{R}_g$ values from ewes #1 and #2 (4 × 6 = 24 day estimates).

Results

Ewe's path data and spatial selectivity

The GPSs used in this study yielded unbiased estimates of the distances among points spaced in the range 3 to 40 dm on the simulated sheep trails (Fig. 2). The mean deviation (absolute value) of all fixes (3days × 3speeds, × 50 positions, $n = 450$) respect to the mean at each flagged position was

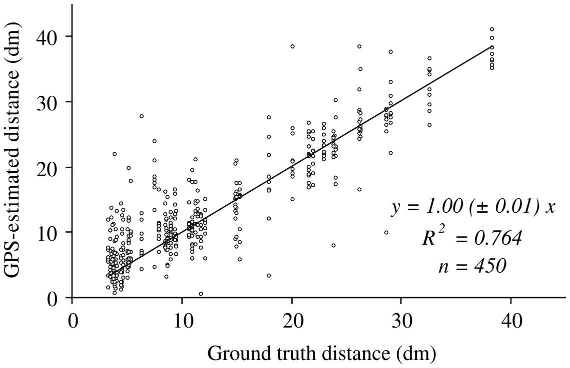

Fig. 2 Ground truth vs. roving GPS estimates of distances between successive stations randomly spaced along a simulated sheep path (3 speeds × 3days × 50 positions = 450)

4.04×10^{-6} degrees of Latitude (or 4.4 dm), and 9.02×10^{-6} degrees of Longitude (or 8 dm), implying a mean relative spatial accuracy of 35.2 dm^2.

The ewes explored subsets of the range area at varying speeds depending on the encountered density of vegetation biomass (Fig. 3). The frequency distributions of pixel values corresponding to the paths used by the ewes were shifted ($P < 0.05$) with respect to that of the null model |T| ($a_{1,T} = 177.2 \pm 1.7$, see Fig. 3a). Ewes moved over relatively open areas at speeds compatible with predominant grazing ($0 < s \leq 2.5$ m/min, $a_{1,\,G} = 187.6 \pm 2.1$, Fig. 3b) and adopted speeds compatible with predominant exploration ($s > 2.5$ m/min) when moving over more dense areas ($a_{1,\,E} = 180.2 \pm 1.1$, Fig. 3c).

Surface cost model

Ewes obtained variable daily $\boldsymbol{R}_g$,with different $\boldsymbol{C}_{d,d}$ and $\boldsymbol{C}_{d,gv}$ costs along searching stretches (Fig. 4). At daily paths with high $\boldsymbol{R}_g$ values corresponded low $\boldsymbol{C}_{d,d}$ costs (note that because of conventional expression of costs as negative quantities, decreasing absolute values along the cost axes correspond to lower costs). $\boldsymbol{C}_{d,d}$ measures exploring effort, in terms of how long stretches at 1 min intervals are (See also example in Appendix Table I-1a). Low $\boldsymbol{C}_{d,d}$ values implied that ewes walked shorter paths at 1 min intervals, when over better rewarding vegetation patches. Low $\boldsymbol{C}_{d,d}$ costs corresponded to high $\boldsymbol{C}_{d,gv}$ costs indicating higher costs of selecting preferred vegetation with lower searching-exploring effort (Fig. 4). When costs and rewards are plotted with their respective signs and scaled on a same graph, a compensation point can be estimated at daily path lengths equivalent to $\boldsymbol{C}_{d,d} \approx -2.48\ eq.pixel/pixel$. Beyond this point (right side of Fig. 4), increases in grazing reward $\boldsymbol{R}_g$ are obtained at the expense of increasing grazing costs $\boldsymbol{C}_{d,gv}$.

Discussion

Our findings about the assignation of varying times to foraging paths depending on the quality of the plants encountered by ewes (low-speeds at relatively open areas with low biomass, high speeds at more dense areas with predominant shrub biomass) are consistent

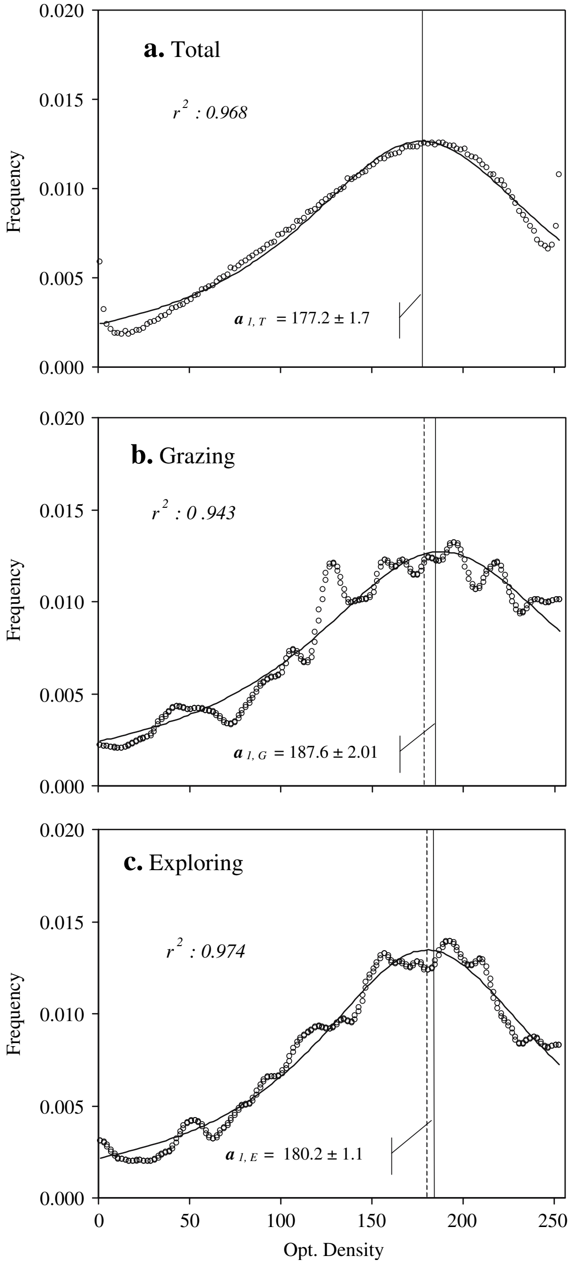

Fig. 3 Frequency of pixel values (dots) corresponding to (**a**): image |T| of the total grazed area, and subsets corresponding to pixels along ewes' paths traveled at speeds: (**b**), $0 < s \leq 2.5$ m/min and (**c**), $s > 2.5$ m/min. The bell-shaped curves indicate the best fitting continuous distribution (PDF, see text, eq. 1). Mean values ($\boldsymbol{a}_1$) are indicated with vertical solid lines and are reported along with 95% confidence intervals. The line for the mean from inset (**a**) is indicated with dotted lines in the other insets for comparison (also see Methods, eq. 1). Note that high pixel values correspond to areas with sparse vegetation, low values to dense, shrubby patches (also see Fig. 1)

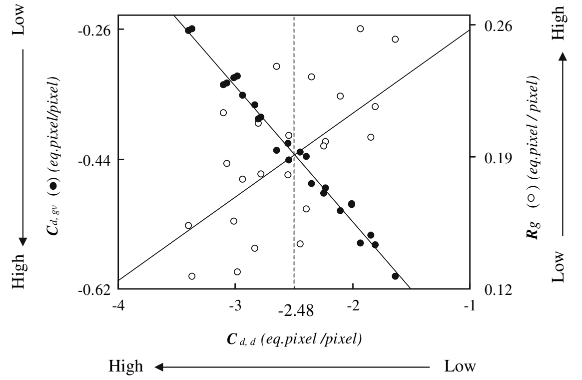

Fig. 4 Relations between distance costs ($\mathbf{C}_{d,d}$), costs of paths at $0 < s \leq 2.5$ m/min ($\mathbf{C}_{d,gv}$) and grazing rewards ($\mathbf{R}_g$) along daily ewe's paths. Regression $\mathbf{C}_{d,gv}$ vs. $\mathbf{C}_{d,d}$: $y = -(0.14 + 0.12\, x)$, $R^2 = 0.6$, $P = 0.002$; Regression $\mathbf{R}_g$ vs. $\mathbf{C}_{d,d}$: $y = 0.007 + 0.71\, x$, $R^2 = 0.99$, $P = 6.2 \times 10^{-21}$. Dots correspond to values of boot-strapped samples of 2 ewes during 4 and 6 days respectively

with the bulk of optimal spatial foraging models (Noy-Meir 1973; Charnov 1976). These assume that patch residence time would increase with patch quality particularly when all patches are of low quality (McNair 1982). Such a hypothesis might be considered a component of MacArthur and Pianka's (1966) optimum foraging theory, whereby animals are expected to minimize energy expenditures while maximizing energy gains in their daily endeavors.

The pattern in this study is also consistent with observations on similarly structured vegetation like in heather (*Calluna vulgaris* (L.) Hull). Based on defoliation observations in these systems, Oom et al. (2002) reported that sheep grazed intensively in relatively small areas where preferred grasses were dominant. Frequent (1 min-intervals) standard GPS fixes might be necessary to detect patch-related movement speeds. Faster animals than sheep might require even shorter sampling intervals, as suggested by negative results in detecting elk (*Cervus elpahus*) speed-related patch selection when logged at about 1 hour intervals in Oregon (USA) ranges (Kie et al. 2005). At some days, the balance of relative rewards and costs experienced by the ewes favored rewards over costs, in some other days this same balance was reversed. It is not clear whether sheep in our experiment maximized their grazing effort, as would be expected from general grazing theory (Stephens and Krebs 1986) or just satisfied their needs. The cost surface paradigm here proposed could motivate further use to examine these and related hypotheses on the effects of landscape heterogeneity on foraging tactics and population fitness in similar foraging systems with patchy vegetation pattern (Tongway et al. 1990).

Application of the cost algorithm in herbivore ecology at a landscape scale

The surface cost metrics ($\mathbf{C}_d$ and $\mathbf{R}_g$) presented in this study allowed the relative quantification of the daily foraging paths of ewes in terms of the costs-rewards obtained when negotiating anti-herbivore obstacles while searching for preferred plants. This is to our knowledge the first study in using the cost theory approach to pursue this type of objective.

The concept of surface cost and the resulting form of expressing travel rewards seems promising in the analysis of herbivore behavior at a landscape scale. Similar metrics can be used to test hypotheses related to foraging tactics in landscapes with patches of plants with different preference by herbivores. Herbivores select paths through the landscape, and most evidence indicates that path selection is dictated by successive, instantaneous evaluations of the environment at various scales of perception. The application of the cost algorithm to the analysis of herbivore paths requires a definition of the frictional and reward surfaces at a landscape scale. In this study, we related the frictional field to the abundance of plants with anti-herbivore defenses as inferred from digitized aerial photographs. Other frictional costs relevant to herbivore ecology could be also assessed by similar metrics. Ganskopp et al. (2000) using cost analysis showed that free ranging cows do follow paths of least effort in relation to terrain slopes. Further frictional costs related to patchy primary productivity, terrain geomorphology, thermal fields, wind regime, and distance to water sources could be evaluated with the procedures here presented. These attributes can be inferred from available remotely sensed data at a regional scale.

Application of the surface cost algorithm to herbivore spatial explicit modeling

We developed interest in the surface cost theory within the frame of current efforts to develop validation metrics for spatial explicit simulation models of sheep behavior in the Patagonian Monte. The development of individual-based models that operate on large spatial scales requires identifying animal foraging rules (Turner et al. 1993; Gross et al. 1995). The grazing environment can be conceived as a multi-frictional surface where factors like food availability, nearness to water sources and places to hide from predators contribute to model animal spatial behavior. This implies that the space between patches cannot be treated as isotropic uniform such that movements in any direction would be equally feasible (i.e. at equal cost), as assumed in earlier treatments of herbivore movement rules (Gross et al. 1995; Cramer and Gallistel 1999). Rather, both preferred and non-preferred patches would present varying degrees of resistance-facilitation to movement in various directions (Beecham 2001; Oom et al., 2005). In developing spatial explicit grazing models, adequate metrics are needed to describe the activity of grazers in relation to the spatial heterogeneity of the factors that influence herbivore behavior, including the spatial distribution of plants (Kohler et al. 2006). The cost algorithm constitutes a tool for quantitative validation of such models.

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APPENDIX I

Introduction to the surface cost algorithm

The principle in surface cost analysis is that energy must be expended during travel to do mechanical work, in amounts related to the travel length. Cost values are assigned to points in space according to its distance to a defined target. In a simple case, the surface cost value at a point O (origin, ten distance units from another point T (travel target), is 10. The cost value of a travel starting at T is 0 when T is defined as target, or 10 if O is the target. Costs for all points in space are measured in distance units (*du*, with length dimensions) respect to a target. Several cost values can be assigned to a single origin, each one with respect to alternative targets.

Table I-1 Examples of calculation of the surface cost metrics for travel to targets 10 pìxels from each other. (a) Movement to A or B is over a flat surface, where only the energy expended in mechanical work for transportation is relevant (unit distance/pixel, unit frictional factor/pixel). (b) Movement over pixel 3 at stretch C–D demands three-fold extra energy because of deep snow, while an energy bonus of 0.5 at pixel 4 occurs because of down-slope, resulting in higher $\mathbf{C}_d$ than in a). (c) Movement to E or F occurs with energy rewards in the form of backwind, down-slope and food at pixels 3, 4, 7, 9 resulting in $\mathbf{C}_d > 0$

Pixel	1	2	3	4	5	6	7	8	9	10	($\mathbf{C}_n$)	($\mathbf{C}_d$)
											(*eq. pixel*)	(*eq.pixel/pixel*)
a)	**A**									**B**		
d_i	0	1	2	3	4	4	3	2	1	0		
f_i	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0		
$\mathbf{c}_i$	***0.0***	***−1.0***	***−2.0***	***−3.0***	***−4.0***	***−4.0***	***−3.0***	***−2.0***	***−1.0***	***0.0***	−20.0	**−2.00**
b)	**C**									**D**		
d_i	0	1	2	3	4	4	3	2	1	0		
f_i	−1.0	−1.0	−3.0	−0.5	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0		
$\mathbf{c}_i$	***0.0***	***−1.0***	***−6.0***	***−1.5***	***−4.0***	***−4.0***	***−3.0***	***−2.0***	***−1.0***	***0.0***	−22.5	**−2.25**
c)	**E**									**F**		
d_i	0	1	2	3	4	4	3	2	1	0		
f_i	−1.0	−1.0	3.0	2.0	−1.0	−1.0	4.0	−1.0	2.0	−1.0		
$\mathbf{c}_i$	***0.0***	***−1.0***	***6.0***	***6.0***	***−4.0***	***−4.0***	***12.0***	***−2.0***	***2.0***	***0.0***	15.0	**1.50**

Notes: d_i, f_i, $\mathbf{c}_i$ as in eq. *I*−1; $\mathbf{C}_n$, $\mathbf{C}_d$ as in eq. *I-2. I-3*,respectively

In most situations, the energy required for transportation is only partially related to the traveled distance, because at some points along the path energy could be obtained or alternatively, extra energy might be required to overcome resistance. Energy can be obtained along the way in the form of back-winds, down-slopes, or energy sources that can be tapped (fuel-tanking places in the case of cars, food in walking animals). Resistance to movement can occur in the form of deep snow, front winds, up-slopes, or any other factor obstructing or deterring movement. In Eastman's (1989) concept, there is a cost component dependent on the distance traveled, and another component dependent on the relative ''friction'' encountered along the route. Note that the term ''friction'' is used in a generalized way and includes both retarding and enhancing effects on the travel energy cost. In order to account for the extra energy expenditures or bonuses occurring at each point in space, costs are expressed in Equivalent Distance Units *(eq.du*, length dimensions), i.e. the equivalent cost that would result if the travel were performed along a ''flat'', no-frictional surface. When costs are computed over digitized images, costs can be conveniently measured in Equivalent Pixels (*eq.pixel*). Accordingly, costs values at any point in space ($\mathbf{c}_i$) are expressed as:

$$\mathbf{c_i}(\mathbf{eq.pixel}) = (\mathbf{d_i} \times \mathbf{f_i}), \qquad (\mathrm{I}-1)$$

where $d_i > 0$ is the number of pixels between pixel i to the target pixel, and fi is a so-called frictional, unitless coefficient characterizing extra demands ($fi < 0$) of energy to travel over pixel i, or $fi > 0$ if energy gains exist over the same.

Some extensions of the cost algorithm are of interest in landscape ecology applications. In this study, we further define the total cost ($\mathbf{C}_n$) of all possible travels started at any point between two alternative targets (i.e. A, B) as:

$$\mathbf{C}_n(A-B)(eq.pixel) = \Sigma_{i=1\ldots n}\mathbf{C}_i \qquad (\mathrm{I}-2)$$

where n is the number of pixels between the targets, with average surface cost ($\mathbf{C}_d$) :

$$\mathbf{C}_d(eq.pixel/pixel) = \mathbf{C}_n/n \qquad (\mathrm{I}-3)$$

Note that C_d quantifies the average cost value per unit distance along the stretch A-B, independently of the distance between them. Consider the examples on digitized paths displayed in Appendix Table I-1. In a), a subject is assumed to travel along a homogeneous non-frictional area, from any point between two target pixels (A-B) towards either of the extremes, depending on which is closer. Since no energy demand to travel other than the corresponding to mechanical work exists over such area, the $\mathbf{c}_i$ value of pixels 1 to 10 strictly depends on the distance to the nearest possible target, which implies that $f_i = -1$, for all i. $\mathbf{C}_n$ and $\mathbf{C}_d$ are computed like in eqs. I–2, I–3 above.

Let us now consider the case in Table I-1- b) along a stretch C-D where pixel no. 3 might be covered with deep snow that would require a 3-fold energy expenditure respect to a flat surface, and pixel 4 would have a down-slope that would reduce the requirement of mechanical work by 1/2. This is introduced by modifying f_3 and f_4 accordingly. Since extra demands of energy occur over the path, the average cost per pixel along C-D is (negative) greater than in case a).

In the case of the stretch E-F, (Table I-1- c) where several pixels along the path are characterized by $f_i >$ 0 because of down-slopes, food or backwind, the sum of all energy bonuses exceeds the distance cost, and $\boldsymbol{C}_d>0$ characterizes a travel along which net energy is obtained.

Consider now a subject seeking to maximize the energy balance at the end of a travel of 10 pixels. In this case, the moving subject would choose the path E-F. Since the cost involved in mechanical work (Appendix Table I-1a) cannot be avoided, the reward function (R) associated with the choice, measured in terms of saved costs, can be defined as:

$$\boldsymbol{R}(eq.pixel/pixel) = \boldsymbol{C}_{d,(E-F)} - \boldsymbol{C}_{d,(A-B)}, \qquad (\mathrm{I}-4)$$

where the sub-indexes indicate the corresponding stretches in Table I-1.

The cost-reward concepts can be applied to issues of interest in studies on herbivore ecology at a landscape scale. Recent GPS technological developments allow locating the successive positions of GPS-collared animals in space. Consider that A, B, C, D, E,...F in Table I-1 were the successive positions of a collared herbivore, recorded at successive time intervals. Consider overlaying the positions over digitized, remotely sensed landscape images where pixels values would correspond to friction coefficients related to the availability/scarcity of biomass of preferred plants, the thermal field, wind field, geomorphology, distance to water source, etc. or in general any other habitat variable that would be influential in herbivore's energy balance. Since at any point along the path the animal could decide to continue moving towards the next target or to any other target point in space (including a non-move) the surface cost $\boldsymbol{C}_d$ along the whole path A-F would quantify the average value of the instantaneous choices. At the end of a recorded period, the average reward $\boldsymbol{R}$ along the chosen stretches would indicate how efficient the succession of choices was in maximizing the performance with respect to the particular type of friction considered.

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