

Patch density determines movement patterns and foraging efficiency of large herbivores

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Few experimental studies have tested theoretical predictions regarding the movement strategies of large herbivores and their consequences for foraging efficiency. We therefore analyze how the movement and foraging behavior of goats are related to patch density, with patches being trees and bushes. We show that their movements become slower and more tortuous when patch density increases, resulting in shorter steps, more acute turns, and a lower net displacement. Furthermore, the movements of the goats can be well described by Lévy walks (LWs). In agreement with hypotheses generated by LW models, the goats move with $\mu \approx 2$ at low patch density but with $\mu \approx 3$ when patches are abundant. However, simplified statistical descriptors of movement patterns like the shape of the step/flight length and turn angle distributions become insufficient in predicting foraging efficiency when patch density is high because then the sequence of steps and turns becomes an important determinant of foraging efficiency. By changing their movements and behavior with increasing patch density, the goats intensify their utilization of resources and consequently are able to raise the efficiency of the foraging process more than proportional to the increase in patch density. This resembles the concept of area-restricted search, stating that animals concentrate their foraging effort in areas with high reward, thereby increasing the efficiency of foraging. The findings as presented in this paper provide support for theoretical expectations on the movement and foraging behavior of large herbivores in relation to resource density. *Key words:* foraging behavior, Lévy walk, movement strategy, patch density. [*Behav Ecol*]

Spatial variation within landscapes results in a heterogeneous distribution of animals' food resources. Hence, the movement strategy that animals use while foraging on spatially dispersed resources is crucial to their success in exploiting them (Bell 1991; Viswanathan et al. 1999; Zollner and Lima 1999; Bartumeus et al. 2005). Because the interplay between environmental heterogeneity and movement of individual foragers is an extremely important aspect of ecological dynamics (Turchin 1998), the movement strategies of foraging animals have been a central focus in ecology (e.g., Schoener 1971; Pyke et al. 1977; Stephens and Krebs 1986; Bell 1991; Turchin 1998; Viswanathan et al. 1999; Zollner and Lima 1999; Bartumeus et al. 2005). Ecologists have therefore invested a lot of effort in quantifying movement patterns of organisms (Turchin 1998). This is mostly done within the realm of microorganisms, insects, birds, and small mammals (e.g., Kareiva and Shigesada 1983; Turchin 1991; Crist et al. 1992; Cole 1995; Viswanathan et al. 1996, 1999; Levandowsky et al. 1997; Atkinson et al. 2002; Bartumeus et al. 2003; Austin et al. 2004; Ramos-Fernández et al. 2004). However, experimental studies of the movement strategies and the efficiency thereof in large mammalian herbivores are rare (but see Gross et al. 1995; Bergman et al. 2000; Mårell et al. 2002). Consequently, the movement behavior of large herbivores is still poorly understood (Morales et al. 2005). In order to increase our understanding of the movement and foraging behavior of large herbivores, experiments need to be carried out to test

theoretical predictions. In this paper, we therefore analyze the movement behavior of a large mammalian herbivore species (the goat, *Capra hircus*) in relation to the density of resources and the effect of these movements on foraging efficiency.

Several studies showed that animals often adjust their decision making in relation to the density of food resources (Benhamou and Bovet 1989; Bell 1991; Turchin 1998; Farnsworth and Beecham 1999; Nolet and Mooij 2002; Benhamou 2004; Newlands et al. 2004). A general hypothesis in foraging ecology is that animals, in order to increase the efficiency of foraging, increase the tortuosity of their movement paths and decrease the speed of movement when resource density increases (e.g., Kareiva and Odell 1987; Bell 1991; Turchin 1991, 1998; Focardi et al. 1996; Viswanathan et al. 1999; Bartumeus et al. 2005). By doing so, animals foraging in an area with high food abundance have a lower net displacement and decrease the chance of leaving the high resource density area, thereby increasing the utilization of resources (Kareiva and Odell 1987; Turchin 1991; Focardi et al. 1996; Bartumeus et al. 2005). On the other hand, when resources become scarce, straighter and faster movements become more efficient than highly tortuous ones, as they result in high net displacement, thereby minimizing the chance of revisiting an already visited resource and increasing the chance of finding new resources (Turchin 1991; Crist et al. 1992; McIntyre and Wiens 1999; Viswanathan et al. 1999; With et al. 1999; Zollner and Lima 1999; Bartumeus et al. 2005). These mechanisms lead to area-restricted search by concentrating foraging effort in areas with high reward and hence lead to an increase in foraging efficiency (Kareiva and Odell 1987; Mårell et al. 2002).

Considering animal movement as a discrete series of displacement events separated by successive reorientations provides a very powerful approach to study movement paths

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(Turchin 1998). It allows for the characterization of movement paths by few parameters and provides a mathematically tractable way for analyzing them (Benhamou 2004). Discretization of movement paths can determine the statistical distributions of displacement lengths (i.e., step lengths) and of changes of direction (i.e., turn angles) (Bartumeus et al. 2005). These distributions are key elements in many models of the movement of organisms, and modulation of these distributions results in modulation of movement path tortuosity. To shift movements from straight to tortuous, animals can increase the frequency or magnitude of turning, decrease the proportion of long steps, or do both (Ward and Saltz 1994; Bartumeus et al. 2005). A special class of random walk models known as Lévy walks (LWs) provides hypotheses regarding the proportion of long steps in relation to resource density, especially when these resources are distributed in few patches (Viswanathan et al. 1999). These LWs are scale-free movements that are characterized by an exponentially decreasing frequency distribution $P(l) \sim l^{-\mu}$ of flight lengths (l) with $1 < \mu \leq 3$. The flights are episodes of approximately straight locomotion and can be interpreted as the aggregation of steps in more or less the same direction. A movement strategy with $\mu \approx 2$ is hypothesized to be optimal for exploiting scarce resource patches, whereas $\mu \approx 3$ results in highly tortuous movements (essentially corresponding to Brownian movement) that are considered optimal at high patch density (HPD) (Viswanathan et al. 1999; Bartumeus et al. 2005).

The shape of movement paths is a fundamental determinant of the efficiency of movement strategies (Bartumeus et al. 2005). This paper therefore focuses on the movement pattern and foraging efficiency of goats foraging on spatially dispersed resource patches. We analyze their movement and foraging behavior in 2 different patch densities to address a set of consecutive hypotheses. We hypothesize that as patch density increases, the movement paths become more tortuous, resulting in shorter steps and larger turning angles. In accordance with results of LW models, movement paths are converted into flights and, if the distribution of flight lengths fits a Lévy distribution, we hypothesize a shift in the slope μ of the Lévy distribution of flight lengths from $\mu \approx 2$ at low patch density (LPD) toward $\mu \approx 3$ at HPD. To test whether the efficiency of movement of the foraging goats can reliably be characterized by the statistical distributions of step or flight lengths and turn angles, we conduct a modeling exercise and compare observed movement paths with statistically equivalent bootstrapped pseudopaths. Because we expect the movement strategy of the goats to involve more than solely a random draw of the statistical distributions of step or flight lengths and turn angles, for example, through the use of visual cues, we hypothesize that the goats encounter more browse while moving than simulated ones moving with the same statistical distributions of step or flight lengths and turn angles. We then test our last hypothesis that, due to adaptations of their movement strategy to changes in patch density, the efficiency of foraging increases more than proportional to an increase in patch density. We define foraging efficiency by means of the sampling efficiency (number of visited patches per meter traversed) and the browsing efficiency (time spent browsing divided by time spent walking). We test these hypotheses in an experimental setup by analyzing the differences in movement and foraging behavior of goats between a high and a low resource density plot and by comparing computer-simulated pseudopaths with the observed paths. While testing these hypotheses, we aim at finding empirical evidence for theoretical predictions of the behavior of foraging animals and hence contributing to a better understanding of the foraging behavior of large mammalian herbivores.

MATERIALS AND METHODS

Study species and study site

We selected goats (*Capra hircus*) because in our study area, they mainly forage on easily recognizable *Acacia* trees and bushes (Breebaart et al. 2002) and thus visit clearly delimited patches, enabling us to avoid the common problem of herbivores that forage on patches that are very diffuse (Senft et al. 1987; Bailey et al. 1996).

We conducted fieldwork at Ukulinga Research Farm, Pietermaritzburg, South Africa (29°67'E, 30°40'S). Two adjacent plots with savanna vegetation were used. Both plots were similar regarding vegetation structure and composition because both were influenced by the same management practices and abiotic conditions. Both plots were composed of a homogeneous grass layer with randomly scattered trees and bushes, which we will further refer to as *patches*. The dominant tree species was *Acacia nilotica*, making up more than 90% of the patches. *Acacia sieberiana*, *Lippia javannica*, *Lantana camara*, and *Rhus pyroides* also occurred. Within each plot, 3 release areas (20 × 20 m) were selected in which the goats were released for observations. The 2 plots are called plot LPD and plot HPD. Plot LPD covered 1.3 ha and contained 239 patches, whereas plot HPD covered 2.0 ha and contained 594 patches, respectively 178 and 294 patches/ha.

With an aerial photograph and a global positioning system, we surveyed both plots and drew detailed maps (scale 1:500) showing all patches and plot boundaries. At each patch, we recorded species, x and y coordinates, patch height, canopy bottom height, and average canopy radius. With these measurements, the browse availability per patch below the upper browse height of goats (1.5 m) was estimated following Camp and Hardy (1999).

There were no significant differences in patch characteristics between the plots (canopy height: Mann–Whitney, $U_{239,594} = 70058.5$, $P = 0.768$; canopy bottom height: Mann–Whitney, $U_{239,594} = 67882.5$, $P = 0.321$; canopy radius: Mann–Whitney, $U_{239,594} = 67642.5$, $P = 0.288$; browse availability per patch: Mann–Whitney, $U_{239,594} = 69793.5$, $P = 0.705$). The distribution of the patches in both plots did not significantly deviate from a random distribution (LPD: nearest neighbor ratio = 0.935, $z = -1.930$, $P > 0.05$; HPD: nearest neighbor ratio = 0.982, $z = -0.855$, $P > 0.05$; calculated using ArcMap 9.1, ESRI Inc, Redlands, CA). Daily air temperature and rainfall were recorded during the fieldwork period, but no significant differences were found between observation weeks (rainfall: analysis of variance [ANOVA], $F_{5,24} = 0.936$, $P > 0.05$; daily air temperature: ANOVA, $F_{5,24} = 2.392$, $P > 0.05$).

Observations

Fifteen goats were divided into 3 groups of 5 goats. For 5 consecutive days, one group of goats was selected and released at a random position in a randomly chosen release area of a plot. From this group, we randomly selected one goat that was observed at short distance for a period of 15 min. The behavior of the observed goat was recorded in space and time. At regular intervals (5 s), we recorded the location of the observed goat on the plot map. Our fine-scale maps and close focal observation allowed us to achieve mapping accuracy of 0.5 m. For the temporal measurements, we used a Psion Workabout portable computer and the program Observer (V3.0, Noldus Information Technology, Wageningen, The Netherlands) to record the activity of the goat at a 1-s resolution, simplified with the classes *browsing*, *grazing*, *walking*, *standing*, *lying*, and *other*. Because the grass layer in both plots was visually homogeneous and did not differ between the plots, we cannot relate characteristics of movement paths or foraging

behavior to grazing. In this paper, we therefore focus on browsing and walking. On average, 8 observations were carried out per day. The observations per day were lumped to have a sufficient number of steps and turns to be able to determine the statistical characteristics of the movement paths and because we could not find significant differences in behavior between individual goats. At night, the goats were kept in a stable without access to food. We observed the goats for 6 weeks, each week with one group in one plot, so that after 6 weeks each group was observed in both plots.

Discretization and analyses of movement paths

To test our first hypothesis that the steps become shorter and the turn angles become larger when patch density increases, we calculated the distances between all successive positions (i.e., step lengths) and the turn angles between successive steps, using all recorded positions. The turn angles were calculated as deviation angles from straight locomotion with the interval $(-180^\circ, 180^\circ)$, where negative angles were turns to the left, positive angles were turns to the right, and 0° corresponded with straight locomotion. We then analyzed the distributions of step lengths for differences between the plots. We analyzed the turn angle distributions with Oriana, a circular statistics program (V2.0, Kovach Computing Services, Anglesey, Wales, United Kingdom), based on the methods described by Fisher (1993). For both plots, we calculated the orientation and length (r) of the mean resultant vector. The orientation of the mean resultant vector expresses the angular mean (i.e., the mean turn angle), and the length of the mean resultant vector expresses the concentration of the distribution around its mean, between $r = 0$ (uniform, fully dispersed circular distribution) and $r = 1$ (punctual distribution, all angles being equal) (Benhamou 2004). Hence, the length of the mean resultant vector is a measure of the strength of directionality of the turn angles, that is, the tendency of the forager to maintain a similar heading from one time step to the next.

Based on the discretized movement paths, we also calculated and analyzed the total distance traversed per movement path, the average speed while traversing, and the net displacement, that is, the beeline distance between the first and last point of an observation. Furthermore, we calculated the “searching intensity” index, expressing the searched area per distance unit traversed, calculated as the ratio between the area of a movement path with width x (with $x = 0.5$ m, see below) divided by the total length of the movement path. This area:length ratio expresses the level of overlap in searched area. High values indicate that a large proportion of the searched area is scanned only once, whereas low values indicate a large overlap in searched area so that a larger proportion of the searched area is scanned more than once. Reversely, the area:length ratio can also be interpreted as a measure of the tortuosity of the movement paths, with high values indicating straighter movements and low values indicating a high level of tortuosity, because an increasing frequency or magnitude of turning results in an increase of the searched area that overlaps with each turn.

Path aggregation and Lévy flights

To be able to test the hypotheses from LW models that animals move with $\mu \approx 2$ in LPD environments and toward $\mu \approx 3$ when resources are abundant, we converted the movement paths into flights. Following Bartumeus et al. (2005), the flights of the LW can be interpreted as an aggregation of steps in more or less the same direction, separated by acute turns. We aggregated a variable number of steps into flights using

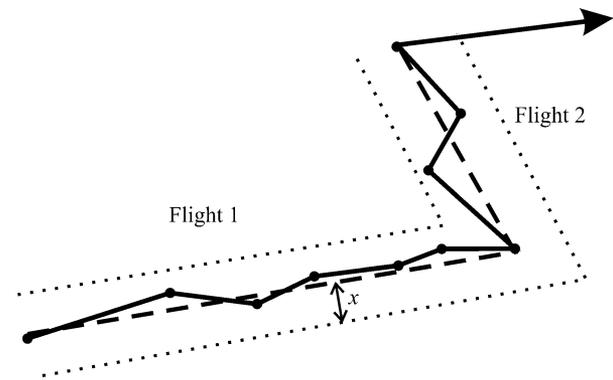


Figure 1

Aggregating N positions of an animal’s movement path into one flight if all intermediate positions are no more than x m away from the line connecting the first point with point N (after Turchin 1998). We used $x = 0.5$ m.

the approach suggested by Turchin (1998). N positions were aggregated into one flight if all intermediate positions were no more than x m away from the line connecting the first point with point N (Figure 1). For x , we used 0.5 m because this is the approximate step size of the goats and the accuracy of observation. Oversampling was avoided because serial correlation of turn angles vanished (Pearson product-moment correlation coefficient; LPD: -0.019 , HPD: -0.049). We first tested the data for goodness of fit against a Lévy distribution and subsequently calculated the Lévy index (μ) with a linear regression of the double logarithmic frequency distribution of flight lengths, where the regression coefficient is equivalent to $-\mu$ (Viswanathan et al. 1999). The slope μ was then tested for differences between the plots.

Simulation of pseudopaths

We simulated movement paths that are statistically equivalent to the observed movement paths and compared their performance with that of the observed paths. They were generated using the bootstrap procedure as described by Turchin (1998), in which each step consists of a random draw from the observed step length and turn angle distributions for that plot. Pseudopaths were generated for both the step lengths and turn angles (SL) and for the flight lengths and accompanying turn angles (LW). As was the case for the observed paths, we let the pseudopaths begin at a random point within one of the release areas of a plot. The performance of a path was defined as the amount of available browse encountered within a distance x from the path divided by the area of the movement path with radius x (Figure 2). The performance was calculated for all observed movement paths and simulated pseudopaths for $x = 0.5$ m. On average, the browse availability per square meter was 7% in plot LPD and 12% in plot HPD. Per plot, the performance of the observed movements was compared with the plot average using a t -test and with both types of simulated pseudopaths using ANOVA followed by Dunnett’s post hoc test for comparison to a control.

Analyzing foraging efficiency

To analyze the foraging efficiency of the observed goats, the efficiency of their foraging behavior was defined by means of their sampling and browsing efficiency. The sampling efficiency was calculated as the number of visited patches per observation divided by the total distance traversed. The

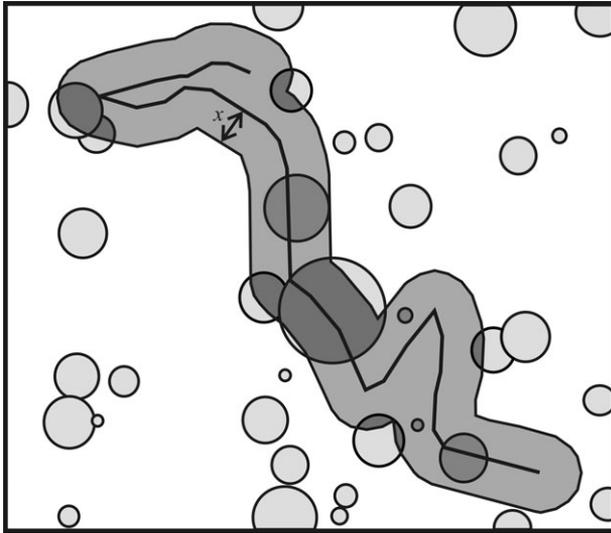


Figure 2

Calculating the performance of the observed and simulated movement paths: available browse encountered (dark) divided by the area of the movement paths with width x (0.5 m). The surface area of the dark circles represents the amount of browse available to the goats. Hence, the performance of the movement paths is represented by the percentage of the searched area that contains forage.

browsing efficiency was calculated as the time spent browsing divided by the time spent walking. The sampling and browsing efficiencies were subsequently tested for differences between the plots.

To quantify the influence of behavior on the difference in foraging efficiency between the plots, we disentangle the effect of the increase in patch density and changes in behavior on the foraging efficiency. First, we compare the experienced patch encounter rates when moving in both plots with the same movement strategy. We do this by generating pseudopaths using the above mentioned approach based on the step length and turn angle distributions of the observed movement paths in plot LPD. Using the method as explained above (Figure 2), we calculated the performance of the simulated movement paths. The ratio of the path performance in HPD to the path performance in LPD is used as a proxy for the change in foraging efficiency that is due solely to the increase in patch density. Second, we calculate the same ratio in performance of the observed paths in both plots, resulting in a difference in patch encounter rate that is caused by the increase in patch density plus a possible change in movement behavior. The difference in sampling efficiency between the plots includes possible additional effects of the use of visual environmental cues in movement decision making. Finally, the ratio in browsing efficiency between plot HPD and plot LPD will show the total difference in foraging efficiency between the 2 plots as a result of the difference in patch density, the adjustment of movement behavior, and changes in time allocation.

RESULTS

Analyses of discretized movement paths

The distributions of the step lengths of both plots differed significantly (Mann–Whitney, $U_{2938,2939} = 3190954.0$, $P < 0.001$), with shorter steps in plot HPD than in plot LPD: median 2.00 m in plot HPD and 2.24 m in plot LPD (see Table 1 and Figure 3). The distributions of turn angles of both plots deviated significantly from a uniform circular distribution

Table 1
Summary of results

Plot	LPD	HPD	HPD/ LPD
Patch density (patches/ha)	178	294	1.65
Median step length (m)	2.24	2.00	
Mean turn angle ($^{\circ}$)	0	0	
r (length of the mean resultant vector)	0.75	0.6	
Trend of r over time (day^{-1})	+0.015	-0.014	
Average length of movement path (m)	63.0	53.6	
Net displacement per observation (m)	30.7	24.6	
Speed during locomotion (m/s)	1.4	1.1	
Area:length ratio	1.3	1.0	
μ (slope flight length distribution)	2.1	2.9	
Sampling efficiency (patches/m)	0.020	0.040	2.00
Browsing efficiency	0.7	2.6	3.71
Performance of SL pseudopaths based on LPD movement characteristics	6.79	10.71	1.58
Performance of observed paths	7.06	12.44	1.76
Average time per patch (s)	28.7	52.06	1.81

(plot LPD: Rayleigh's Uniformity test, $z = 1565.686$, degrees of freedom [df] = 2826, $P < 0.001$; plot HPD: Rayleigh's Uniformity test, $z = 1019.276$, df = 2827, $P < 0.001$) and from each other (chi-square test, $\chi^2 = 273.025$, df = 71, $P < 0.001$) (Figure 4). The angular mean of the turn angle distributions of both plots was 0° (t -test, $t = -1.435$, df = 2826, $P = 0.151$ for LPD and t -test, $t = 0.30$, df = 2827, $P = 0.976$ for HPD), and the distributions were symmetrical around the angular mean (plot LPD: Mann–Whitney, $U_{1469,1358} = 993130.0$, $P = 0.842$; plot HPD: Mann–Whitney, $U_{1395,1433} = 974302.0$, $P = 0.245$). The length of the mean resultant vector (r), as measure of the strength of directionality, was significantly lower in plot HPD (ANOVA, $F_{1,28} = 58.673$, $P < 0.001$): 0.60 compared with 0.75 in plot LPD. We also found a significant decrease of r over time (i.e., observation days) in plot HPD, but there was a significant increase over time in plot LPD (ANOVA, $F_{0,20} = 9.203$, $P < 0.001$) (Figure 5).

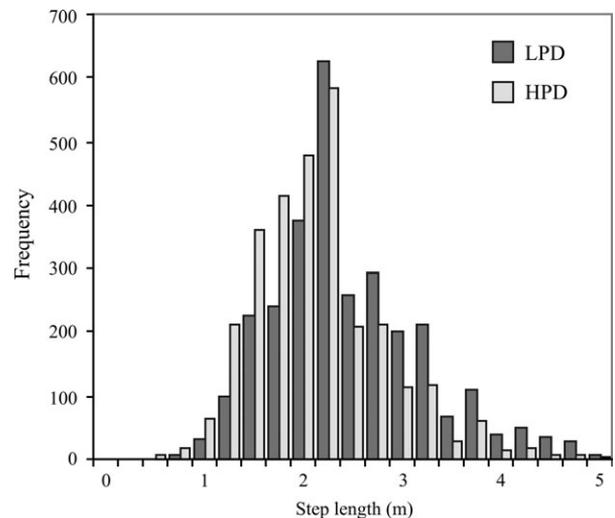


Figure 3

Frequency distributions of step lengths for both plots ($n = 2938$ in LPD and $n = 2939$ in HPD) using all recorded positions. Because the sampling intervals for the steps are equal (5 s), the frequency distributions also represent the frequency distributions of speeds in each plot.

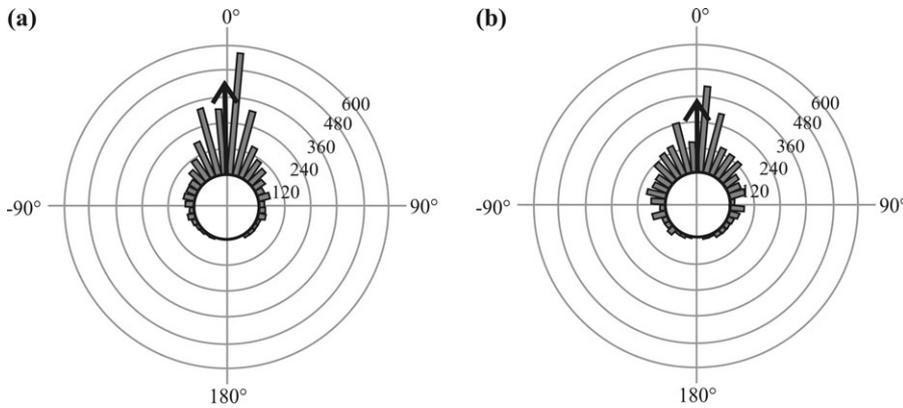


Figure 4
Circular frequency distributions of turn angles in (a) plot LPD ($n = 2827$) and (b) plot HPD ($n = 2828$). The concentric circles represent frequency increments of 120, and the numbers at the outer circle represent degrees. The direction of the arrows represents the mean turn angle (0° for both plots) and their lengths represent the strength of directionality ($r = 0.75$ for plot LPD and 0.60 for plot HPD, with $r = 1$ at the outer circle). See text for statistics.

The movement paths in plot HPD were significantly shorter than in plot LPD (Mann-Whitney, $U_{111,111} = 4849.5$, $P = 0.006$), as was the net displacement (ANOVA, $F_{1,220} = 8.405$, $P = 0.004$). The goats had a lower speed in plot HPD compared with LPD (Mann-Whitney, $U_{111,111} = 4739.5$, $P = 0.003$). No significant difference in time spent walking was found between the plots. Analyses of the searching intensity index showed that the goats foraging in plot LPD had a higher area:length ratio than while foraging in plot HPD (Mann-Whitney, $U_{111,111} = 4759.0$, $P = 0.003$): 1.3 in plot LPD compared with 1.0 in plot HPD.

Flight lengths

The distributions of flight lengths could be well described with Lévy distributions: a power-law relationship fits the data with $R^2 = 0.90$. The goats moved with $\mu = 2.1$ in plot LPD compared with $\mu = 2.9$ in plot HPD (Figure 6), with μ being significantly higher in plot HPD than in plot LPD (ANOVA, $F_{1,28} = 11.168$, $P = 0.002$). The data fitted an exponential distribution with $R^2 = 0.87$, whereas a linear regression on the untransformed data yielded $R^2 = 0.72$.

Simulated pseudopaths

In both plots, the performance of the observed movement paths was not different from the plot average. In plot LPD, the performance of the observed movement paths was not

different from the performance of the random sequences of either the steps or the flights and corresponding turn angles (ANOVA, $F_{2,330} = 1.72$, $P = 0.181$). In plot HPD, the observed movement paths had a significantly higher performance than the pseudopaths of flight lengths and tended toward a higher performance than the pseudopaths of step lengths (ANOVA, $F_{2,330} = 3.219$, $P = 0.041$; Dunnett's test observed SL: $P = 0.066$; observed LW: $P = 0.043$) (Figure 7).

Foraging efficiency

The goats foraging in plot HPD had a significantly higher sampling efficiency (Mann-Whitney, $U_{111,111} = 3701.5$, $P < 0.001$) and browsing efficiency (Mann-Whitney, $U_{111,111} = 3095.5$, $P < 0.001$). They visited more patches per movement path (Mann-Whitney, $U_{111,111} = 4010.0$, $P < 0.001$) and spent more time browsing per observation (ANOVA, $F_{1,158} = 34.881$, $P < 0.001$). Both indices of foraging efficiency showed a larger difference between the plots than the difference in patch density would indicate (Table 1).

To quantify the effect of different causes on this disproportional increase in foraging efficiency, we partition the effects of the different factors studied. Based on the path characteristics observed in the plot LPD, we find that the performance of the pseudopaths is 1.58 times higher in plot HPD than in plot LPD (Table 1). Because the movement strategy of these pseudopaths is the same in both plots, this difference is only due to an increase in patch density.

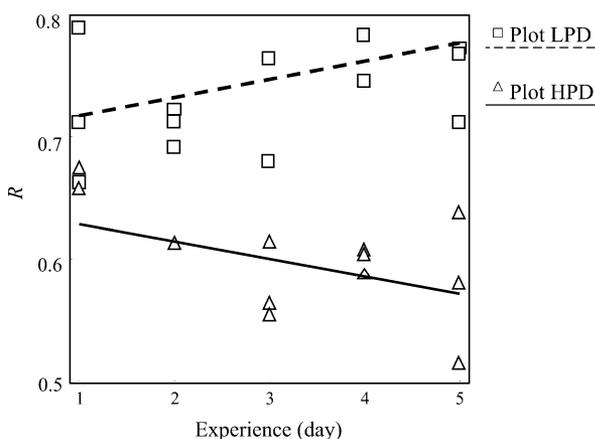


Figure 5
The strength of directionality (r) of the turn angle distributions in relation to increasing experience with the plots, here the number of days of exposure to the plots.

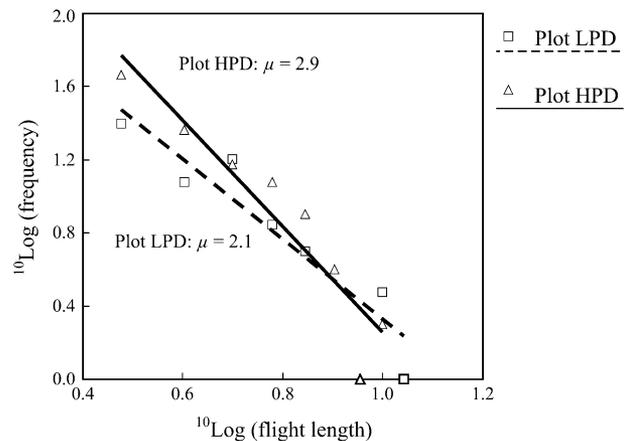


Figure 6
Frequency distribution of flight lengths for both plots, with μ from the Lévy distribution $P(l) \sim l^{-\mu}$ of flight lengths (l) being the regression coefficient of a linear regression between $^{10}\log(\text{frequency})$ and $^{10}\log(\text{flight length})$.

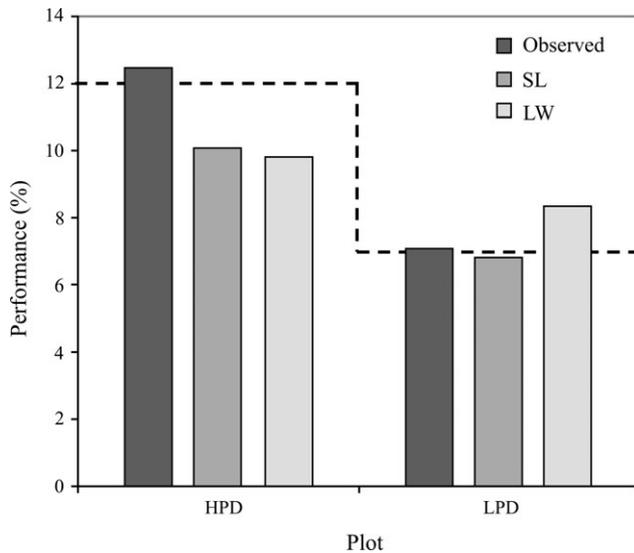


Figure 7

Performance of the observed and simulated movement paths in both plots, for $x = 0.5$ m. The movement paths are simulated for both the step lengths and corresponding turning angles (SL), as well as for the flight lengths (LW) and angles. The performance is expressed as the percentage of the searched area that contains available forage, see also Figure 2. The dotted line represents the plot average (plot LPD: 7% and plot HPD: 12%). Within plot LPD, there were no significant differences in the performance between the observed paths and both simulated pseudopaths, whereas in plot HPD both simulated pseudopaths had a lower performance than the observed paths, see text for statistics.

Additionally, because we showed that the movement strategies differ between the plots, we calculated the same ratio in performance of the observed paths in both plots, revealing a 1.76-fold increase (Table 1) that is caused by an increase in patch density plus a change in movement strategy. If we now look at the differences in observed sampling and browsing efficiencies between the plots, we see that in HPD, the goats visit twice the number of patches per distance unit and have a browsing efficiency that is 3.71 times higher. Because the time spent walking did not differ between the plots, this increase in browsing efficiency originates from an increased number of patches being visited combined with a longer residence time per patch (Table 1).

DISCUSSION

In this paper, we experimentally analyzed several key aspects of animal movement and foraging behavior in relation to the density of resource patches. Our main focus is the shape of the movement paths as a fundamental determinant of the efficiency of movement strategies. Our first hypothesis that the movement paths become more tortuous resulting in shorter steps and larger turning angles when patch density increases was supported by the data. The steps were significantly shorter in plot HPD, whereas the level of directionality in turn angles was lower. Hence, more large turns occurred in the movement paths of the goats in plot HPD. The goats did not exhibit a preference for either right or left turning, which corresponds with research on Angora goats (Ganskopp 1995), goldenrod beetle (Goodwin and Fahrig 2002), and reindeer (Mårell et al. 2002). However, they showed a higher tendency to maintain a similar heading from one time step to the next in plot LPD. These results agree with predictions about deviations from a random walk

(Kareiva and Shigesada 1983; Bovet and Benhamou 1988; Turchin 1991; Crist et al. 1992; Johnson et al. 1992; Ward and Saltz 1994; Bergman et al. 2000). Also our other measures for the tortuosity of the movement paths (e.g., net displacement and searching intensity index) confirmed our hypothesis that the tortuosity of the paths increased with increasing patch density. In plot HPD, the goats thus exhibited highly tortuous movement paths, resulting in a lower net displacement. In plot LPD, however, the goats exhibited straighter movements, resulting in a higher net displacement. Straight paths increase the chance of finding areas with high food density (Crist et al. 1992; McIntyre and Wiens 1999; Viswanathan et al. 1999; With et al. 1999; Zollner and Lima 1999; Bartumeus et al. 2005). Combining this with a lower speed and distance traversed in plot HPD results in intensive foraging on a small area in an HPD environment but extensive foraging on a larger area in a LPD environment. These findings support the concept of area-restricted search (e.g., Kareiva and Odell 1987; Haskell 1997; Mårell et al. 2002), stating that foragers increase the frequency or magnitude of turning and decrease the speed of locomotion after encounters with food resources.

Our second hypothesis that the goats moved with $\mu \approx 2$ of the Lévy distribution of flight lengths in plot LPD but with $\mu \approx 3$ in plot HPD was also supported by the data. As in other studies (Levandowsky et al. 1988; Cole 1995; Schuster and Levandowsky 1996; Viswanathan et al. 1996; Viswanathan et al. 1999; Atkinson et al. 2002; Mårell et al. 2002; Bartumeus et al. 2003; Ramos-Fernández et al. 2004), the observed flight length distributions could be well explained by Lévy distributions. The goats followed movements with a Lévy distribution of flight lengths with $\mu = 2.1$ in plot LPD, but with $\mu = 2.9$ in plot HPD. These results correspond with findings of authors studying the movement of other species (Focardi et al. 1996; Viswanathan et al. 1996, 1999; Atkinson et al. 2002; Mårell et al. 2002; Bartumeus et al. 2003; Ramos-Fernández et al. 2004). These results provide empirical evidence for theoretical expectations that LW with $\mu \approx 2$ are optimal when resources are scarce but that the principal advantage of a flight length distribution with $\mu \approx 2$ becomes negligible when there are ample patches because then a Brownian strategy (i.e., $\mu \geq 3$) becomes an optimal solution (e.g., Viswanathan et al. 1999; Bartumeus et al. 2003, 2005). In plot LPD, the goats approached this predicted optimal strategy with $\mu = 2.1$, whereas in plot HPD the goats indeed tended to move according to Brownian motion by moving with $\mu = 2.9$. Hence, we agree with the conclusions from Bartumeus et al. (2003) that Brownian motion should not be considered as a null model, but rather as another movement strategy that is optimal under high resource levels, and to expect a switching behavior between Lévy and Brownian strategies as optimal solutions when resource levels increase.

In addition to the findings that patch density influences the statistical characteristics of the movement paths, we compared the performance of the observed movement paths with statistically equivalent pseudopaths, both for the step lengths and turn angles and for the flights and turns, to test whether these statistical properties of the discretized movement paths do reliably predict the efficiency of the movement strategies. In plot LPD, the observed paths did not perform significantly better than the pseudopaths. In plot HPD, however, the performance of the observed paths was significantly higher than the pseudopaths generated from the flights and tended to be higher than the pseudopaths generated from the steps and turns. Hence, the sequence of steps and turns did not significantly matter in a LPD environment, whereas it did matter in the HPD plot. Consequently, the statistical distributions of step/flight lengths and turn angles are sufficient to characterize

the efficiency of movement behavior in a LPD environment, whereas these properties are insufficient when patches are more abundant. Because animals use visual information cues from the surrounding environment to increase the efficiency of their foraging process (Kohler 1984; Gross et al. 1995; Bailey et al. 1996; Laca 1998) and these cues are more abundant when resource density increases, these cues are probably at the basis of the higher observed performance in the HPD plot. Hence, the statistical properties of the movement paths become relatively less important when resource levels increase and the sequence of steps and turns becomes important due to the use of these cues. On the other hand, in low patch abundance, the relative importance of information cues and thus the sequence of steps and turns becomes negligible and the statistical distributions of step lengths and turn angles can be used to predict the performance of movement strategies. This might explain why we could not find a significant difference in performance between the observed and simulated movement paths in the LPD plot.

To test our fourth and last hypothesis, namely, that due to adaptations in their movement strategy to the density of patches, the goats are able to increase their foraging efficiency disproportional to an increase in patch density, we analyzed the sampling and browsing efficiencies of the goats. Both indices for foraging efficiency showed a significant increase with increasing patch density. The sampling and browsing efficiencies even showed a larger difference between the plots than would be expected from the difference in patch densities between both plots (see Table 1). This increase in foraging efficiency agrees with studies on other animals (Crist et al. 1992; Viswanathan et al. 1996; Stapp and Van Horne 1997; Gillis and Nams 1998; Schultz 1998; Schultz and Crone 2001; Fortin 2002; Nolet and Mooij 2002). Our attempt to differentiate between the different causes underlying this disproportional increase in foraging efficiency with increasing patch density shows that the observed increase in foraging efficiency is caused by 3 factors. First, an increase in patch density results in an increase in foraging return, even when employing the same movement strategy. Second, behavioral adaptations of the movement strategy to the density of patches encountered increase the patch encounter rate. Subsequent use of available environmental cues increases the number of patches that can be visited even further, thereby enabling higher foraging reward. Third, the goats spent more time per patch in plot HPD. Combining this with the increased number of patches visited, the goats spent more time browsing in the plot HPD. Thus, an increase in patch density increases the patch encounter rate. Changes in movement behavior and the use of visual cues result in an additional increase in patch encounter rate. By combining this with a change in the time allocated to foraging, the goats obtained a disproportional increase of their foraging success.

The goats used in this research had no previous experience with the plots and therefore did not have prior knowledge regarding the distribution of the food patches. With more experience in the plots, they would be presumed to increase their expectation of the patch density in the plots (Bailey et al. 1996). The observed decrease in time of the strength of directionality in plot HPD and its increase in time in plot LPD could indicate that the goats used this experience to adjust their movement paths to the experienced density. It is possible that the goats, when first confronted with the plots, moved after a naive distribution of turn angles but adjusted this distribution in response to the experienced resource density. No other differences due to experience were found (μ , sampling efficiency, and browsing efficiency remained constant), which contradict the results of Gillingham and Bunnell (1989), Johnson (1991), Noda et al. (1994), and Laca (1998), who

showed that foragers increase their foraging efficiency with increasing experience.

In this paper, we show a positive correlation between patch density, movement path sinuosity, and foraging efficiency of a large mammalian herbivore. It provides further evidence that foragers often adjust their decision making in relation to the density of food resources and by doing so are able to increase the efficiency of their foraging behavior. The novelty of our analysis is that we are able to relate statistical properties of discretized movement paths with empirical measures of foraging activity and efficiency. Furthermore, we provide empirical evidence for several theoretical predictions on movement and foraging behavior in relation to the density of food patches. We show that many characteristic properties of animal movement and foraging behavior are influenced by the patch density of the environment. These characteristic properties include the shape of the step length and turn angle distributions; the exponent μ of the Lévy distribution of flight lengths; the length, speed, and net displacement of the movement paths; and indices regarding foraging efficiency. The data show a switch from Lévy motion with $\mu \approx 2$ in a low resource density environment to a tortuous movement strategy with $\mu = 2.9$ at high resource abundance, thereby tending toward Brownian motion. Moreover, the sequence of steps and turns becomes important when resources are abundant, and we argue that this originates from an increased amount of information cues available to the foragers to include in their decision making. With a change in movement behavior with increasing patch density, the goats were able to raise the efficiency of their foraging behavior more than proportional to the increase in resource abundance. These findings provide further experimental evidence for theoretical expectations, and we hope this will contribute to the development of theory on foraging animals by investigating mechanisms behind foraging behavior.

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