



Do Ungulates Exhibit a Food Density Threshold? A Field Study of Optimal Foraging and Movement Patterns

S. Focardi; P. Marcellini; P. Montanaro

The Journal of Animal Ecology, Vol. 65, No. 5. (Sep., 1996), pp. 606-620.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28199609%2965%3A5%3C606%3ADUEAFD%3E2.0.CO%3B2-D>

The Journal of Animal Ecology is currently published by British Ecological Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns

S. FOCARDI*, P. MARCELLINI§ and P. MONTANARO*

*Istituto Nazionale per la Fauna Selvatica, Via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia, Italy; and
§Dipartimento di Matematica "U. Dini", Università di Firenze, Viale Morgagni 67/A, 50134 Firenze, Italy

Summary

1. The behaviour of ungulates foraging in non-patchy habitats is studied with the help of a new model of optimal foraging based on a time minimization utility function. The model predicts that an animal uses a foraging station only if the biomass exceeds a prescribed threshold level. Moreover, the forager does not consume all the available food but it gives up the station when food density reaches the threshold level.

2. The assumptions of the model were tested using 36 foraging paths of adult female fallow deer (*Dama dama* L.) in two different study areas (one wild and one fenced) and seasons (summer and autumn, respectively). Despite the ecological differences between the two sites, the deer exhibited the same pattern of search behaviour which can be described as a first-order biased random walk. Neither herd seemed able to detect and exploit food patches.

3. Partial consumption of food was regularly observed in both study areas. There is strong evidence that the fenced-in animals behaved in agreement with the model's prediction, abandoning the foraging stations when the biomass density fell below 10 g m⁻² of dry matter. On the other hand, the deer living in the wild exhibited a more variable foraging behaviour.

4. The theoretical analysis shows that in comparison to the fenced-in deer those in the wild require more information to correctly evaluate the threshold level of their more heterogeneous environment.

5. It is argued that the foraging behaviour of fallow deer consists of two basic components: a random search for food coupled with a threshold in the selection of foraging stations.

Key-words: fallow deer, food search, mathematical model, optimal foraging behaviour.

Journal of Animal Ecology (1996), **65**, 606–620

Introduction

The predictions of optimal foraging models are often characterized by the existence of thresholds, i.e. by discontinuities in the behaviour of the animals determined by non-linear responses to resources. In his pivotal paper on the diet selection of herbivores, Westoby (1974) noted that diet optimization, based on linear programming models 'generates a non-linear relation between the content of an individual nutrient in a food and animal preference for the food'. Another instance of strong discontinuity in foraging behaviour is given by the zero-one rule predicted by standard diet choice models (Stephens & Krebs 1986): a prey type is either always included in the diet or always rejected dependent upon its profitability, partial pref-

erence is forbidden. Thresholds arise also in the analysis of optimal patch-residence time based on the marginal value theorem (MVT) (Charnov 1976): the threshold is determined by the long-term average rate of foraging. Arditi & Dacorogna (1988) generalized Charnov's (1976) predictions and showed that a threshold, at which foraging is given up, should exist whatever the food distribution is. This prediction is valid for every strictly increasing functional response, even if it is linear.

On the contrary, alternative theoretical approaches, e.g. satisficing (Myers 1983; Ward 1992) or hedypagia (see Provenza & Balph 1990 for a recent review), predict more gradual changes in foraging behaviour. Even anatomo-physiological constraints are unlikely to predict thresholds. If diet choice in

ruminants depends on body size (Demment & Van Soest 1985) or on the structure of the digestive system (Hofmann 1989) we expect to observe a smooth gradient of feeding styles rather than abrupt discontinuities.

Actual behaviour, however, often does not fit the predictions of optimal foraging models. For instance, partial preference in diet choice seem to be more the rule than the exception (Illius & Gordon 1990, 1993). McNamara & Houston (1987) discuss possible explanations for partial preferences which may, or may not, be compatible with an optimality approach.

When applied to ungulates, contingency models have exhibited poor predictive powers (Owen-Smith & Novellie 1982; Belovsky 1984; Owen-Smith 1993). In contrast, Belovsky (1978, 1984) claimed a high predictive success for linear programming models. His conclusions have been contested by Hobbs (1990) and Owen-Smith (1993), who suggest that the success of linear programming models is serendipitous, i.e. that under certain circumstances wrong assumptions may yield good predictions. Serendipity may be detected from the data. For instance, Owen-Smith (1993) showed that a linear programming model may predict the average diet of the kudu but not variations within a short time scale (days or meals). Moreover, Huggard (1994) questioned the validity of statistics used in Belovsky's model validation. Such criticism has been rejected by Belovsky (1994).

There are some studies (Åström, Lundberg & Banell 1990; Jiang & Hudson 1993) that successfully explain patch exploitation by ungulates on the basis of the MVT. However, Focardi & Marcellini (1995) noted that the assumption of a patchy food distribution is generally not realistic for ungulates, which exploit common and often poor-quality food sources. Arditi & Dacorogna (1988 and related papers) have successfully modelled optimal foraging in the case of arbitrary food distribution. Focardi & Marcellini (1995) studied the foraging ecology of ungulates using a model based on the minimization of total foraging time and excursion length and adopting more realistic constraints. The main assumptions of this model are that: (i) animals have some general knowledge of food distribution in their habitat but no specific knowledge of the position of favourable foraging stations; (ii) search and foraging are intermingled activities; and (iii) the search process is on a small spatial scale, i.e. there is no long-range detection of food items. The model predicts the existence of a critical biomass value (the threshold λ) which separates selected and refused foraging stations. More precisely, if $\rho(x)$ is the food density at point x , an animal will forage at x if and only if $\rho(x) > \lambda$, otherwise it will ignore the station if $\rho(x) \leq \lambda$. Foraging should stop when λ units of food remain in the foraging station. The threshold depends on the animal's functional response, its speed during displacement between foraging stations, maximal rumen content and length of the foraging path.

The importance of using biologically valid assump-

tions in modelling foraging processes is a general plea. Illius & Gordon (1990) wrote that 'the sordid details of the real world cannot be ignored, even by theoreticians'. In general, optimal foraging models are based on the assumption of independent Poisson encounters with prey (Stephens & Krebs 1986) but search mechanisms may be more complex and such complexity may strongly modify foraging behaviour (McNair 1979; McNamara & Houston 1987). Spalinger & Hobbs (1992) have shown that, on a small spatial scale, the interplay between searching, handling and food density strongly influences the feeding rate of ungulates. Focardi & Marcellini (1995) accounted for such constraints in their model by adopting the formula proposed by Real (1979). On the other hand, long-range search mechanisms could be used by animals to exploit environmental heterogeneities. For instance, foraging rate might increase if the animal is able to detect biomass gradients in the environment, locate distant but more profitable food sources, or detect areas with a higher than average food biomass ('fuzzy patches'). Such searching strategies have to be based on suitable mechanisms of orientation. Bovet & Benhamou (1988, 1990) have developed a general framework upon which to model search behaviour. Basically, animal paths are represented by discrete steps of fixed length, whereas the orientation of a step with respect to the previous one (angular turn) is a stochastic variable. In many cases animals exhibit a biased random walk, i.e. the distribution of angular turns is unimodal and bell-shaped, with mean 0° . These models allow us to study complex search mechanisms such as kinesis or taxis (see Fraenkel & Gunn (1961) for a classical treatment and Tranquillo & Alt (1990) for an updated review). Several observations suggest (Pyke 1978, 1983) that animals increase the amount of turning following encounters with prey (*area-restricted search*). Klino- and ortho-kinesis might account for such behaviour: a scalar stimulus (e.g. food density) might influence the turning rate (positively) or the speed (negatively), respectively. A suitable statistical description of the amount of turning in a path is made possible by the definition of its sinuosity (Bovet & Benhamou 1988):

$$S = \sigma/\bar{d}^{0.5}, \quad \text{eqn 1}$$

where σ is the angular standard deviation of turning angles and \bar{d} the mean step length. Animals can modulate path sinuosity in order to improve the efficiency of food search (Bovet & Benhamou 1991).

We studied the foraging behaviour of female fallow deer in two different areas in order to obtain information which was less dependent on the local situation. The structure of the habitats where the animals foraged is comparable in both sites (open pastures mainly composed of graminoids), an environment where a food patch is unlikely to occur (Illius & Gor-

don 1993). The main difference between the two study areas is that one is a wild habitat with a very heterogeneous food distribution while the other is a fenced-in zone with a much more even and 'artificial' food distribution pattern.

The aims of this study on female fallow deer are to: (i) give a detailed description of the foraging paths; (ii) verify whether or not these deer exhibited area-restricted search behaviour; (iii) see if their foraging behaviour is characterized by partial food consumption; (iv) discern to what extent search and foraging behaviour are comparable in the two herds; and (v) verify whether or not our data are consistent with the existence of a food-biomass threshold.

The analysis of foraging paths seemed particularly interesting as it has seldom been attempted with ungulates (Underwood 1983; Gillingham & Bunnell 1989) despite its being a possible source of important information. Moreover, the results of Focardi & Marcellini (1995) are strictly consistent only if animals move randomly. The assessment of whether or not food consumption is partial was deemed important because it has been described in other species (Illius & Gordon 1990, 1993).

Methods

STUDY AREAS

The study was carried out in two sites in Italy: on the Castelporziano Preserve near Rome, and on the Montepaldi Estate, near Florence. Castelporziano, one of the most important relict Mediterranean forests in Italy, has a surface area of 40 km². Montepaldi, a fenced-in property, has a surface area of 0.52 km².

At Castelporziano observations were made from 14 May 1992 to 29 September 1992 in a large open pasture with abundant graminoids (*Lolium perenne* L., *Phleum pratense* L., *Anthoxanthum odoratum* L., *Avena barbata* Potter, *Lamarckia aurea* Moenck and *Stipa capensis* Thunb.) exploited by about 60–80 fallow deer.

At Montepaldi observations were made from 10 October 1993 to 3 November 1993 in a meadow where the most important graminoids are *Avena* spp., *Brachypodium pinnatum* Beauv., *Bromus mollis* (= *hordeaceous*) L., *Bromus sterilis* L., *Cynodon dactylon* L. and *Dactylis glomerata* L. with a population of 90 deer.

The two herds consisted mainly of does, fawns and yearlings. Only females older than one year were considered: these are easily distinguished from the smaller fawns both in summer and autumn.

In both areas the observer and the tracking device were concealed in a 5-m high seat. At Castelporziano two high seats (No. 3 and No. 4) were used to observe an area of pasture of 300 × 700 m; at Montepaldi one high seat was available to observe an area of 200 × 150 m.

The tracking device consisted of an electronic compass, a telemeter with a precision of 1 m at 150 m and a videotape recorder camera (Focardi *et al.* 1994), which allowed a precise estimate of animal's position within a 150 m radius around the highseat. Within this range the position of the deer was recorded by measuring its distance from the observer and its azimuth; the activity was videotaped and the amount of time devoted to different behaviours (foraging, moving, etc.) was measured at the next second from the films, using a stop watch. Animals used the pastures mostly to forage at twilight, while for other activities (e.g. ruminating) they preferred to shelter in the wood. We use the foraging time within each foraging station as a proxy for the amount of harvested food. Foraging time is given by the time necessary for cropping and processing food (Spalinger & Hobbs 1992); these authors have shown that (under conditions of high density of food) the intake rate becomes constant and the mass of ingested food is directly proportional to the foraging time as defined above.

The position of all accepted foraging stations (AS) and of most of the refused foraging stations (RS) was established with the help of coordinates, field tracks and external reference cues pinpointed by the videotape. A foraging station was considered refused when the animals, keeping their head down, looked at, but did not eat, the vegetation. This posture clearly differs from that when they are either on the alert, harassed by flies or scanning the surroundings. There was some uncertainty in determining the occurrence of refused stations; however, these were not crucial to test our model as only data regarding the accepted stations were used.

The model's predictions are based not on the harvested biomass but on that left in the foraging station after the passage of the animal. The biomass of graminoids at each station was estimated by the point intercept method (Jonasson 1988; Focardi, Montanaro & Tinelli 1994) at Castelporziano and by mowing at Montepaldi. The point-intercept method is an efficient, non-destructive, method for estimating vegetation biomass but, to obtain more precise data, in the second part of the study the residual biomass was mown, oven-dried and weighed. In both methods 1 m² was sampled giving a yield of dry mass per m². Because the size of the foraging station is arbitrary and reflects our inability to detect animals movements smaller than 1 m, at Montepaldi we tested whether the size of the station might have influenced the results by comparing the biomass density at the centre of the square—0.25 m² (0.5 × 0.5 m)—with the rest of the sample (0.75 m²): no significant differences were found (Wilcoxon test $z = -0.5$, $P > 0.05$).

Because the probability of recording foraging paths at Castelporziano was relatively low, the observations lasted for about 4–5 months. The summer period is characterized by an almost complete absence of rain-

fall and not much change in the ecological situation. The number of animals is small enough to avoid important interference effects (at Castelporziano the probability of two paths intersecting once was 0.09). However, the first two paths recorded in May—a month characterized by a higher density and better quality of food (Poli, Focardi & Tinelli, in press)—were excluded from all analyses of the biomass values.

During the observation period 1-m² samples were also collected in order to estimate the distribution of forage biomass in the two study areas; 50 samples at Castelporziano, 25 at Montepaldi.

STATISTICAL ANALYSIS

The foraging path of deer may be represented mathematically as the time course of a two-dimensional vector $V(t)$. Deer movement is recorded by discrete positions with coordinates x_t, y_t ($t = 0, \dots, N$, where N is the number of points). The elements of the vector are displacement, d_t , i.e. the distance between two consecutive positions, and the angular change, or turning angle, α_t . Let β_t and β_{t-1} be the absolute orientation of $V(t)$ and $V(t-1)$, respectively; then $\alpha_t = \beta_t - \beta_{t-1}$. In our study, path segmentation is not arbitrary as in most other studies (Scharstein & Alt 1990) because animal positions represent both accepted and refused foraging stations: when a fallow deer moves between two foraging stations its trajectory is usually very linear and too fast to be followed by our tracking device. Turning occurs mainly when the animal leaves the foraging station. The few instances of abrupt turning outside the foraging stations were also recorded.

Search behaviour may be based on different mechanisms. In random search (Brownian motion) the distribution of α_t is uniform. Uniformity may be assessed using the Rayleigh test (Batschelet 1981). Bovet & Benhamou (1988, 1990) showed that many search patterns may be modelled as first-order biased random walks: α_t distribution is not uniform but clustered around 0° so that the animal tends to maintain its previous orientation. The amount of clustering around the mean direction, $\bar{\alpha}$, is given by the length of the resultant vector, r . If $r = 1$ all elements of $V(t)$ are parallel and the path is a straight line. The parameter r also represents the correlation between the turning angle (α_t) of each foraging path. The circular standard deviation, σ , can be derived from r (Batschelet 1981). The V -test was used to assess whether or not the turning angles are clustered around a preferred direction.

The autocorrelation function (ACF) of the vector $V(t)$ (over 4 steps, $t-1, \dots, t-4$) is used to analyse the searching pattern (Alt 1990). Several search mechanisms may yield similar ACF values, but random movement implies ACF values around zero, while systematic search patterns are characterized by more complex (e.g. oscillatory) ACF functions. The statis-

tical tools for discriminating between differential klinokinesis and taxis (cf. Benhamou & Bovet 1992) are not suited for this study because we have no idea about the position of one animal's target; however, these authors suggest that taxis, but not kinesis, should be characterized by a negative ACF of α_t .

The presence of area-restricted search based on klino- or ortho-kinesis was tested by computing the cross-correlation function (CCF) between α_t, d_t and foraging time over 5 steps ($t, t-1, \dots, t-4$). Area-restricted search should result in positive CCF between foraging time and turning angle and a negative CCF with displacement.

For the study of circular-circular and circular-linear correlation coefficients we adopted the non-parametric methods described in Batschelet (1981). For linear-linear correlation we used the Spearman-rank correlation test. Depending on the context, the symbol r is used to indicate the length of the resultant vector, the correlation coefficient, or the auto- and cross-correlation coefficients.

Because we have repeated measures for each animal, it is important, for a better evaluation of results, to discriminate between intra- and inter-individual sources of variability. By convention, the global distributions are plotted with open histograms, while the distributions relative to individual mean values (i.e. first-order means, *sensu* Batschelet 1981) with dots; because individual data are independent (different animals were observed at different times), the distribution of individual means (second-order distribution) represents the actual population variability. In the intra-individual tests (for directional orientation, correlation, etc.) significant results ($P < 0.05$), are indicated by black dots, non-significant results with open dots.

The differences between median values were compared by non-parametric statistical tests (Wilcoxon two-sample test and Kruskal-Wallis ANOVA); the difference between distribution variability with Fisher's variance ratio. Where parametric tests had to be used, non-normal distributions were transformed using Blom's scores.

All data manipulations and analyses were made using the SAS statistical package (SAS Institute Inc.).

Mathematical model

To introduce the mathematical model, let us consider a curve (physically described by the animal) in a two-dimensional domain, parametrized by a variable $x \in [0, l]$, with $x = 0$ and $x = l$ corresponding respectively to the initial and final points of the curve.

The *density* of food at a generic point $x \in [0, l]$ is denoted by $\rho(x)$. Food density is not necessarily continuous and, in the application, usually has discontinuities in the form of jumps in the interior of $[0, l]$.

To find out how long an animal remains feeding at

a point x , the dynamics of food consumption were evaluated in terms of the animal's *functional response* Φ , i.e. its *velocity* of food acquisition. Let τ be the foraging time that the animal spends at a point x to acquire food and δ the density of food eaten at x ; then the velocity of food acquisition at x is the derivative $d\delta/d\tau$ of δ with respect to τ ; therefore we have

$$\frac{d\delta}{d\tau} = \Phi(\rho - \delta), \quad \text{eqn 2}$$

where $\rho - \delta$ is the density of remaining food.

As a principal example we consider the *functional response* proposed by Real (1979), and given by

$$\Phi(\xi) = k \cdot \frac{\xi}{b + \xi}, \quad \text{eqn 3}$$

for some positive constants k and b , where $\xi = \rho - \delta$. Equation 3 is a special case of Real's functional response, the general case having been considered in Focardi & Marcellini (1995).

We can solve the ordinary differential equation 2 together with the (initial) condition that, if the animal does not eat at the point x (i.e. $\delta = 0$), then at x it does not spend time acquiring food ($\tau = 0$). Moreover, the time used by the animal to move and to search for food must also be taken into account; we assume that it moves with constant velocity V_0 . With some computations, the *total time to search and gather food* is given by

$$T = \frac{l}{V_0} + \int_0^l \left\{ \frac{1}{k} \delta + \frac{b}{k} \log \frac{\rho}{\rho - \delta} \right\} dx. \quad \text{eqn 4}$$

Denoting by $v(x)$ the amount of food gathered by the animal up to point x , we have $v(0) = 0$ and $v(l) = A$, where A is the rumen content, i.e. the maximum amount of food which can be eaten by the animal during a meal. Thus, v is related to δ (density of consumed food) by the condition

$$v'(x) = \frac{dv}{dx} = \delta. \quad \text{eqn 5}$$

The mathematical model is based on the minimization of the total time used by the animal to search for and gather food. By equations 4 and 5 the *total time to acquire food and moving* is

$$T(v, l) = \frac{l}{V_0} + \frac{1}{k} \cdot A + \frac{b}{k} \int_0^l \log \frac{\rho}{\rho - v} dx, \quad \text{eqn 6}$$

to be minimized with respect to the variables v and l . Since $0 \leq \delta \leq \rho$ and $\delta = v'$, the constraints to satisfy are

$$\{v: v(0) = 0, \quad v(l) = A, \quad 0 \leq v'(x) \leq \rho(x), \forall x \in [0, l]\}, \quad \text{eqn 7}$$

$$\int_0^l \rho(x) dx > A, \quad \text{eqn 8}$$

the second one being imposed by the assumption that during the excursion the animal finds all the food it need.

Focardi & Marcellini (1995) proved that there is a threshold λ , i.e. a positive number with the properties that, at every point x of the foraging path, where food density is less than or equal to the threshold value, i.e. $\rho(x) \leq \lambda$, the animal does not eat [$v'(x) = 0$]; conversely, if food density is greater than the threshold, i.e. $\rho(x) > \lambda$, then the animal forages at x and eats exactly $\rho(x) - \lambda$ units of food [i.e. $v'(x) = \rho(x) - \lambda$]. Note that the existence of a fixed threshold is a general feature of the optimization process and *does not depend* on the specific functional response $\Phi(\xi)$.

Results

FORAGING PATHS

Qualitative aspects

A total of 21 and 15 foraging paths were collected at Castelporziano and Montepaldi, respectively. A selection of eight out of the 36 recorded paths is shown in Figs 1a–d. The display of the qualitative features of the foraging paths of deer may be useful to better understand the subsequent quantitative analysis. At first glance the paths from the same habitat seem quite different, despite the deer being of the same age and sex, but closer inspection reveals several similarities. Most of the paths are characterized by a large number of foraging stations, where the animals remain for a short period of time; only once did the deer appear to forage on a large food patch (Fig. 1a). Both linear displacements (Fig. 1b) and sinuous paths (Fig. 1c) have been recorded; the deer seldom loop (Fig. 1d).

The mean sinuosity for all paths (eqn 1) was 0.8 rad $m^{-0.5}$ at Montepaldi, 0.6 and 0.4 for high seats No. 3 and No. 4 at Castelporziano, respectively. Sinuosity was significantly larger at Montepaldi than at Castelporziano (Wilcoxon test $z = 2.8$, $P < 0.01$) but if we compare Montepaldi with area No. 3 this difference vanishes (Wilcoxon test $z = -1.8$, $P < 0.05$) and there is no significant difference between high seats No. 3 and No. 4 at Castelporziano (Wilcoxon test $z = -1.8$, $P > 0.05$).

Orientation of the foraging excursions

The global distribution of the angular turns is showed in Fig. 2a,b. The frequency distribution of turns is non-uniform (Rayleigh test: Castelporziano, $z = 33.0$, $P < 0.001$; Montepaldi, $z = 7.0$, $P < 0.001$) and their resultant vector is significantly oriented at 0° (V-test: Castelporziano, $U = 8.1$, $P < 0.0001$; Montepaldi,

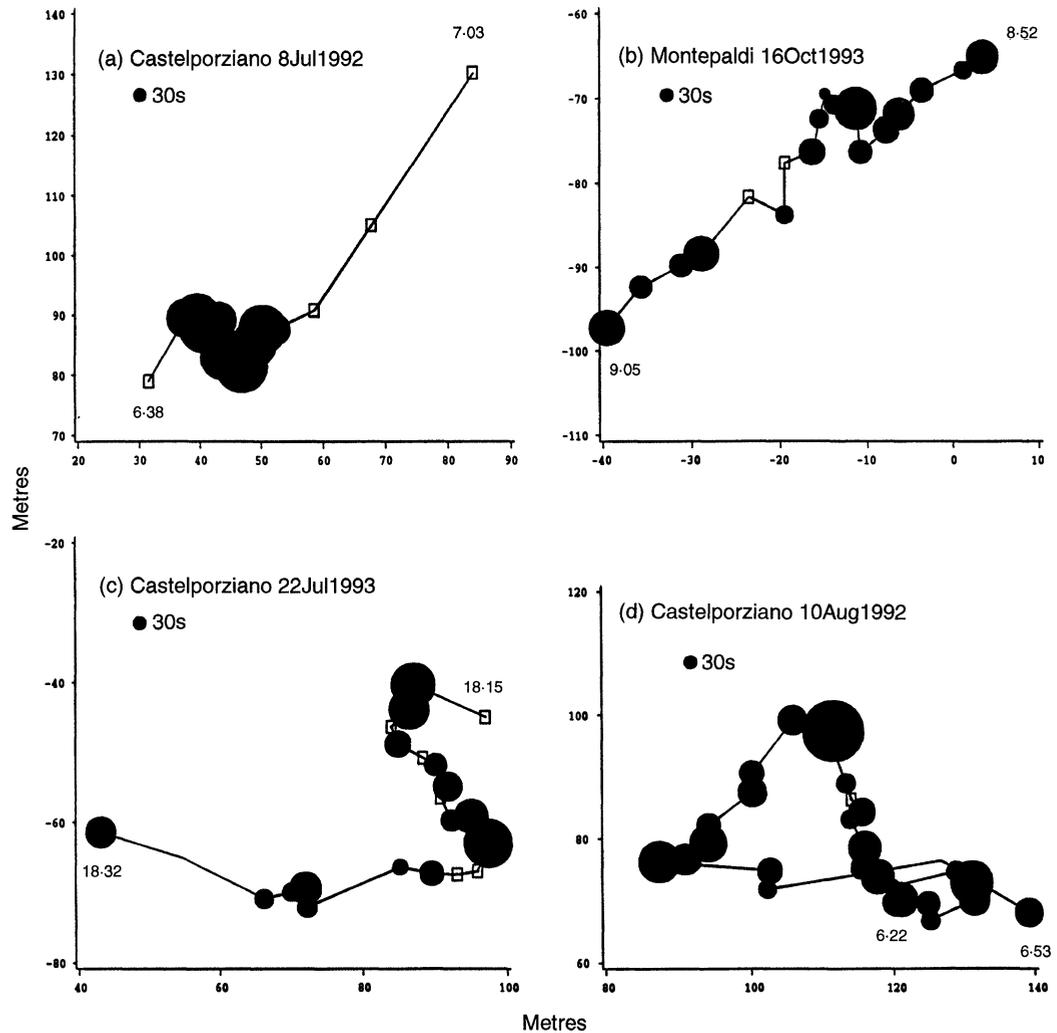


Fig. 1. Foraging paths of fallow deer. The surface area of the black circles is proportional to the foraging time at each selected station. Open squares represent refused foraging stations, where the deer search for food but do not forage. Coordinates are in meters. The high seat represents the origin of the coordinates and the positive x axis the direction of magnetic north. Initial and final time of observation are displayed.

$U = 3.7$, $P < 0.001$). The second order distribution is non-uniform at Castelporziano and uniform at Montepaldi (Rayleigh test: $z = 4.5$, $P < 0.01$ and $z = 1.1$, $P > 0.05$, respectively); the former distribution is also significantly oriented at 0° (V -test, $U = 3.0$, $P < 0.05$). The intra-individual scattering of turns is wide and only a few deer exhibit significantly oriented angular distributions (at 0°). There are no significant differences between the two study areas, either for global ($\chi^2_{12} = 18.8$, $P > 0.05$) or second-order distributions (Watson U^2 test: $U^2 = 0.07$, $P > 0.05$).

Foraging time

The distributions of foraging time are reported in Fig. 3a,b. The medians of the two global distributions are not significantly different (Wilcoxon test $z = -1.8$, $P > 0.05$). The same holds for the distributions of the individual means ($z = -0.25$, $P > 0.05$).

A comparison of global and second-order distributions within each area suggests that the latter distributions are less variable than the former at both Castelporziano ($F_{19}^{167} = 3.6$, $P < 0.01$) and Montepaldi ($F_{15}^{57} = 7.43$, $P < 0.001$). If we compare the two study areas we find the same variability for global distributions ($F_{15}^{67} = 1.7$, $P > 0.05$) while the second order distribution at Castelporziano is more dispersed ($F_{15}^9 = 3.5$, $P < 0.01$).

Searching behaviour

Because the autocorrelation function (ACF) coefficients for turns (Kruskal-Wallis ANOVA $\chi^2 = 0.05$, $P > 0.05$) and displacements (Kruskal-Wallis ANOVA $\chi^2 = 0.22$, $P > 0.05$) and their cross-correlation function (CCF) (Kruskal-Wallis ANOVA $\chi^2 = 1.6$, $P > 0.05$) are identical in the two study areas, the data for the following analysis were pooled.

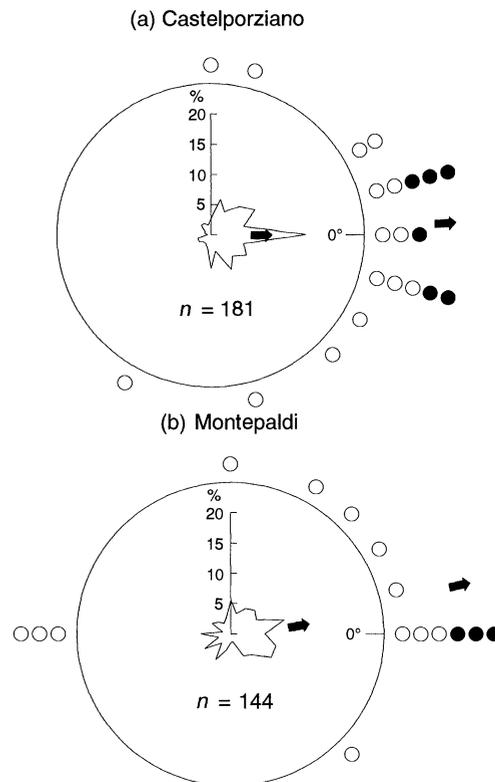


Fig. 2. Angular distribution of turns. Dots represent the resultant angle of each individual's path. Black dots represent individual distributions which are significantly oriented at 0° . Open dots refers to randomly oriented individual distributions. Inner and outer arrows are the resultant direction for global and second-order distributions, respectively. See text for details.

The plots of the ACF coefficients of vector $V(t)$ (Fig. 4a,b) show that (i) there is no significant correlation for turns or distance in most of the deer; (ii) there is no variation in the second-order mean r values as a function of the step; and (iii) the correlation coefficient for each step is zero (note that zero is included within two standard error limits).

However the CCF of turns with displacements is significantly positive for several deer (Fig. 4c), i.e. long displacements are correlated with large turns (around 180°): a deer tends to come back if, in some previous step, its movement was characterized by a long displacement; this mechanism reduces the probability of leaving the habitat. During foraging long displacements may occur if, for instance, the animal has been disturbed.

Area-restricted search

Deer exhibiting area-restricted search should move in such a way as to increase the probability of remaining within an area where they have encountered a high density of food. To remain within a patch an animal should increase the sinuosity of its path according to the attraction of the patch itself. Thus, negative cross-correlation coefficients should appear between time and displacement and positive ones between time and turns (Fig. 5a,b). Only one individual exhibited a significant correlation of time with turns. There is a small bias in the observed r values and the second-order estimation is significantly larger than zero. There is a large dispersion of the individual correlation

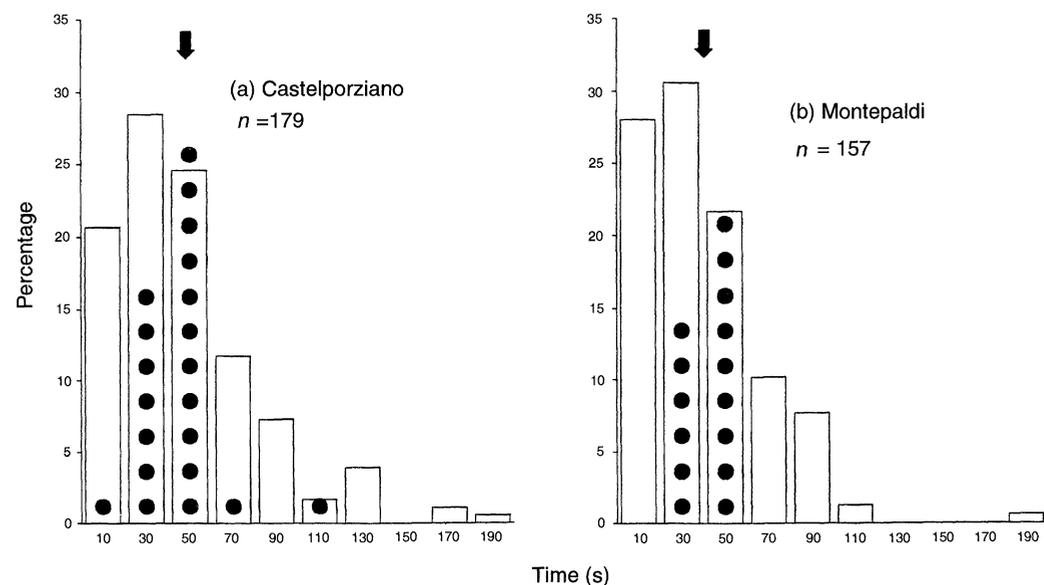


Fig. 3. Distribution of foraging times. Open histograms are global distributions, black dots represent first-order means and the arrow displays the value of the second-order mean.

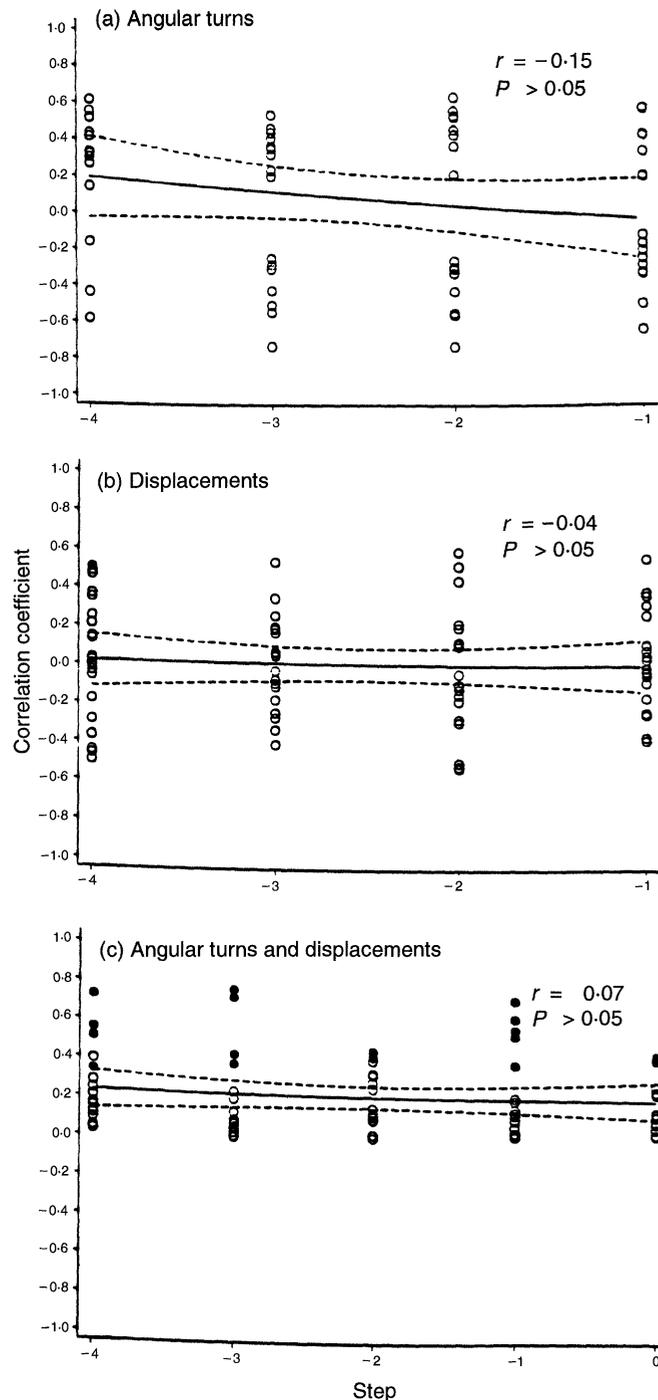


Fig. 4. Autocorrelation function (ACF) of turns. The continuous black line represents the regression of individual correlation coefficients with step (refer to statistics in figure). Dashed lines are the upper and lower two standard errors of the regression line. (b) ACF of displacements. (c) Cross-correlation function of turns and displacements. Dots represent the individual (first-order) correlation coefficients: black dots indicate a significant correlation ($P < 0.05$), open dots a non-significant one.

coefficients for displacement and the second-order r mean is not significantly different from zero.

FOOD DISTRIBUTION AND DENSITY

Spatial distribution of foraging stations

The pattern of food distribution in both areas was obtained by computing the orientated vector connecting each selected foraging station with the pre-

vious one (thus without taking into account the actual path followed by the animal). The bivariate distribution is reported in Fig. 6. The centres of the two ellipses are not significantly different (Hotelling T^2 test: $T^2_{2,300} = 4.8$, $P > 0.05$); however, the distribution at Castelporziano is clearly more dispersed than the one at Montepaldi so that the mean distance between foraging stations is larger in the former area (global mean: 6.1 m and 3.8 m, respectively). Both global

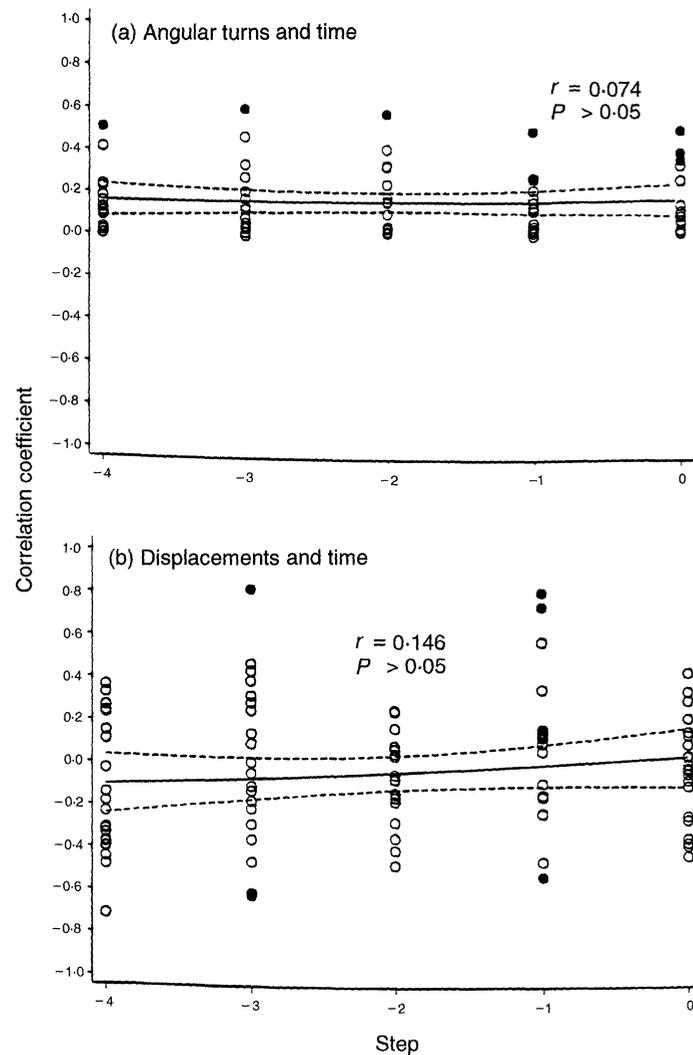


Fig. 5. Cross-correlation functions of (a) turns and (b) displacements with foraging time. Other symbols as in Fig. 4.

($\chi^2 = 14.5$, $P < 0.01$) and second-order (Wilcoxon test: $z = -2.02$, $P < 0.05$) distributions are different in the two study areas.

Biomass

A comparison (Fig. 7) of the dry matter distribution in refused, selected and control foraging stations shows (i) a greater variability of the control stations at Castelporziano than at Montepaldi, and (ii) that the distribution of the selected foraging stations at Castelporziano is characterized by a large number of upper outliers (i.e. of biomass values which exceed the median of, at least, two interquartile ranges). The biomass appears to be more evenly distributed at Montepaldi than the Castelporziano.

All the biomass distributions (except the R one at Montepaldi) are non-normal ($P < 0.01$). After data transformation, a two-way nested ANOVA showed that both area ($F_{482} = 538$, $P < 0.001$) and station type ($F_{499} = 29.4$, $P < 0.001$) are highly significant. All three groups differ at Montepaldi while at Castelporziano the control group differs from the other

two, while the R and S samples do not differ (Schiffé test, $P < 0.05$). A certain amount of vegetal biomass is always present, i.e. the R and S distributions both differ significantly from zero (no vegetation) even at the poorest R stations at Montepaldi ($t = 12.5$, $P < 0.0001$).

The differences between the mean values of C and S distributions can be used to estimate the average yield of a selected foraging station (11.3 g DM m^{-2} at Castelporziano and 7.5 g DM m^{-2} at Montepaldi). With respect to these values the amount of food remaining in the AS is larger (20.8 g DM m^{-2} at Castelporziano and 10.3 g DM m^{-2} at Montepaldi).

Do deer respond to biomass threshold?

Our model predicts that each deer should ignore a foraging station when the available biomass is equal or lower than a threshold λ and that the residual biomass should be identical at each station. Of course, under natural conditions it is impossible to observe if residual biomasses are perfectly equal: for instance, both the process of food handling (bites are discrete)

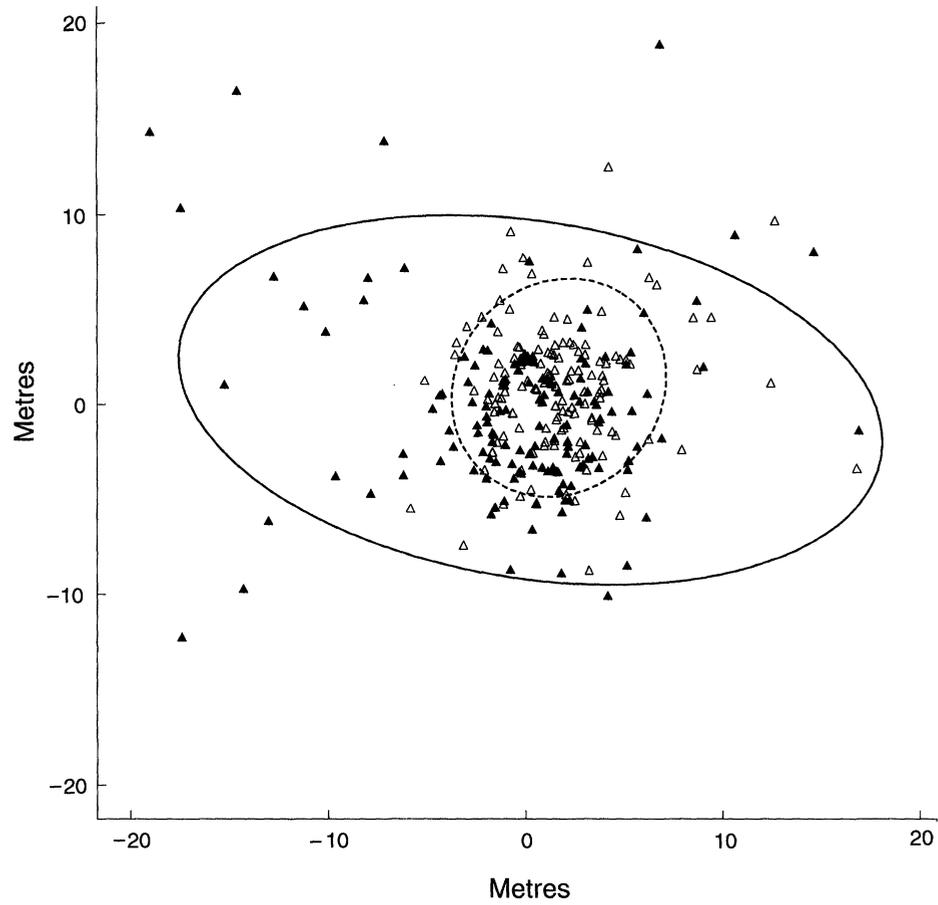


Fig. 6. Fiducial ellipses (99%) representing the bivariate distribution of coordinates of each selected foraging station with respect to the previous one, for Castelporziano (continuous line, black triangles) and Montepaldi (dashed line, open triangles). The oriented vector joining the origin of the axes to each point represents the polar coordinates of a foraging station with respect to the previous one.

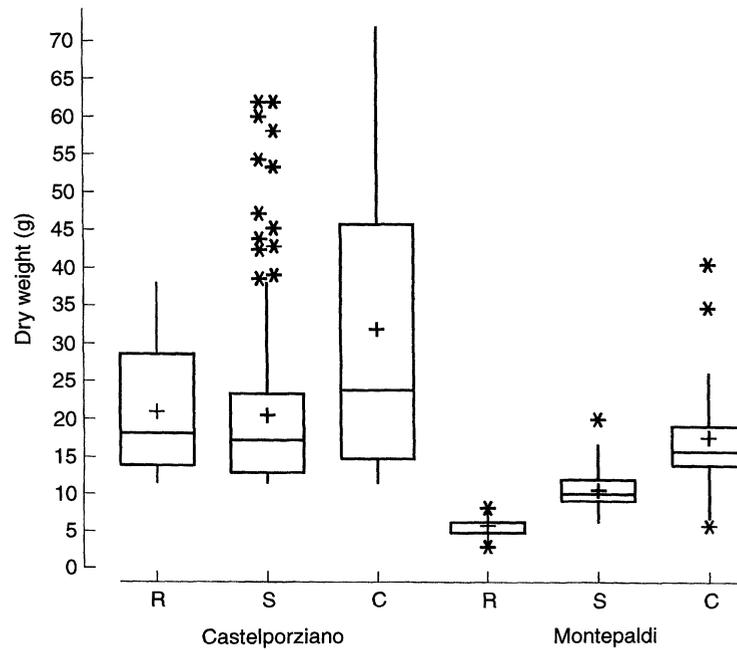


Fig. 7. Box-and-whisker plots of biomass value for refused foraging stations (R), selected foraging stations (S) and control stations (C). Crosses indicate the mean values and horizontal bars the median values of the distribution. The size of the box is two interquartile ranges. Stars represent the value of distribution outliers.

and the methods used to estimate the biomass introduce errors in the measurement. However, if the S distributions (cf. Fig. 7) are considered without outliers (Fig. 8a,c) the range of variation—especially of the first-order means—is very small. At Montepaldi the distribution is heavily concentrated around the average into two classes of 5 g DM m⁻²; at Castelporziano the situation is similar but both the global and the second-order distributions are much more variable than at Montepaldi ($F_{170}^{170} = 1.9$, $P < 0.001$; $F_{14}^{18} = 57.5$, $P < 0.001$, respectively). A comparison of the variances of global and second-order distributions shows that individual distributions are the least variable in both areas (Castelporziano: $F_{18}^{170} = 3.5$, $P < 0.01$; Montepaldi: $F_{14}^{170} = 12.1$, $P < 0.001$). An interesting feature of both S distributions is that they are sharply interrupted on their left tail.

In order to explain the greater variability observed at Castelporziano we checked the sources of variation (spotting seat, month and herd size) which were not present at Montepaldi. The high seats yielded no sig-

nificant effect (ANOVA, $F_{165} = 1.44$, $P > 0.05$) while herd size and month proved to have a significant influence on the animals' behaviour (ANOVA, $F_{165}^4 = 2.8$, $P < 0.05$; $F_{165}^3 = 5.2$, $P < 0.01$). However, most of the variance (18.4%) is explained by differences among individuals which are independent of the high seat, herd size and month (ANOVA, $F_{165}^{10} = 4.5$, $P < 0.001$). Despite these significant effects, the global model explains only 30.5% of the global variance; this probably means that other undetected factors influences the selection of food by fallow deer. On the contrary, at Montepaldi the biomass of the selected stations is the same for all individuals (Kruskal-Wallis ANOVA $\chi_{14}^2 = 11.3$, $P > 0.05$).

To remove the inter-individual variability, the average residual biomass, \bar{q} , was computed and for each AS of biomass $q(x)$, we computed the variable $z = q(x) - \bar{q}$. For a fixed biomass threshold, the z values are expected to be zero. At Montepaldi (Fig. 8d) 85% of the values are equal to zero (± 2.5 g DM m⁻²); at Castelporziano (Fig. 8b) the distribution is

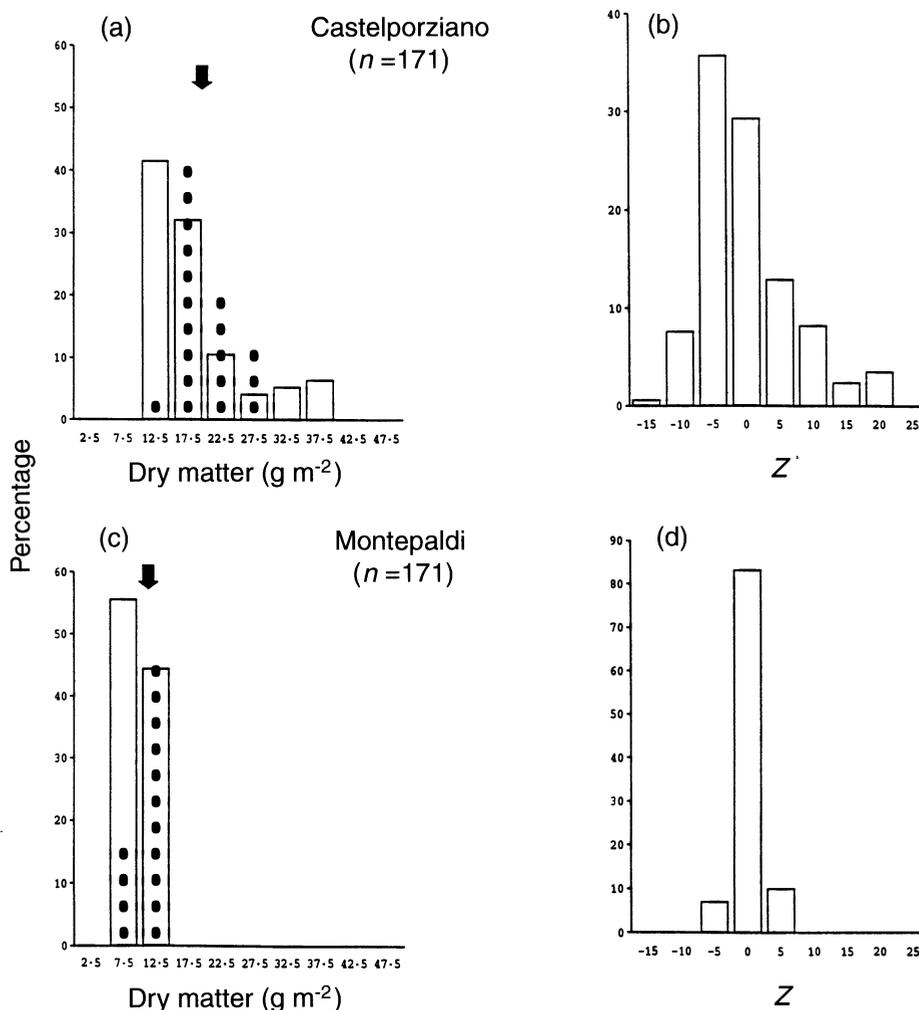


Fig. 8. Biomass distribution in selected foraging stations (without outliers) at (a) Castelporziano and (c) Montepaldi. The biomass values normalized with respect to the individual mean are given for (b) Castelporziano and (d) Montepaldi. Open histograms are global distributions, black dots represent first-order means and the arrow displays the value of the second-order mean.

more dispersed, but about 85% of the values lie in the range of ± 7.5 g DM m^{-2} around 0.

Can deer estimate the biomass threshold?

The amount of information necessary for an animal to estimate the optimal policy clearly depends on the complexity and variability of the foraging environment. The 'true' optimal threshold was computed using the actual distribution of food (i.e. the C distributions of Fig. 7) observed in our study areas (*Look-up Tables*, LUT). It was compared with the approximate solutions obtained using (i) mean value of distributions (M), and (ii) mean values and standard deviations (MSD). The other parameters of the model, A and V_0 , were experimentally estimated; the mean body weight is the same in both areas (46.8 and 46.6 kg at Castelporziano and Montepaldi corresponding to a rumen content of about 1500 and 1350 g of dry matter, respectively (Focardi, Poli & Tinelli 1995). Even V_0 is identical in the two areas (2 and 1.9 $m s^{-1}$ at Castelporziano and Montepaldi, respectively, Kruskal–Wallis ANOVA $\chi^2 = 2.4$, $P > 0.05$). Because the functional response of fallow deer is unknown, we assume $b = k = 1$. At Castelporziano the LUT value is 15.9 g DM m^{-2} versus a M value of 13.5 g DM m^{-2} and a MSD value of 16 g DM m^{-2} . At Montepaldi the three values were 7.5, 8 and 7.5 g DM m^{-2} , respectively. Clearly the amount of information necessary for deer to forage optimally is lower at Montepaldi than at Castelporziano, where the M estimate yields only a poor approximation of the actual value.

Discussion

The methodology used for this study of ungulate foraging behaviour includes several innovations. The analysis of field data is embedded in the framework of a new model of optimal foraging (Focardi & Marcellini 1995), which shifts the focus of analysis from the long-term processes characterizing most previous studies on diet choice in ungulates to the short-term assessment of individual behaviour. Several studies of this kind are present in the literature but have been usually performed on tame animals under controlled conditions (e.g. Gillingham & Bunnell 1989; Ginnett & Demment 1995), whereas our method of data collection allowed us to monitor animals living under natural conditions, provided that the food distribution in the environment is assessed.

Search behaviour

The predictions of optimal foraging models depend critically upon the assumed search strategy; the model presented here is consistent with a random movement pattern. Statistical analysis based on the auto- and cross-correlation functions (Alt 1990 and references

therein) have seldom been applied and, if so, usually to unicellular organisms or invertebrates.

Despite the differences in both the history of the two populations and their environment, as well as in the management practices and seasons when the study was performed in each area, the search and foraging behaviour of the deer appear to be very similar and stereotyped.

The movement of the deer can be described as a biased random walk without complex search mechanisms. Such a movement pattern is probably the simplest to be expected in such an animal. However, its simplicity is justified by the fact that the exploited food is very common and of relatively poor nutritive value, so that the adoption of more complex search mechanisms is probably unnecessary. According to Poli *et al.* (in press) the mean yield of a foraging station at Castelporziano, in terms of metabolizable energy, is 17.6 Kcal, i.e. about 1/200 of the per-day consumption (3500 Kcal) of a fallow deer (Hartfiel 1990). It would be interesting to apply a similar analysis to more selective foragers, specializing on less common food items of higher quality.

Effect of the study area

The comparison of deer behaviour in the two study areas has also shown that marked differences in ecology and management have a limited effect on the foraging behaviour of female fallow deer. The larger path sinuosity at Montepaldi might depend on the smaller size of this estate, however, the difference is relatively small. Even the physiological parameters are quite similar in the two study areas. The greatest differences between Castelporziano and Montepaldi concern the pattern of food density and distribution. The wilder habitat of Castelporziano results in a larger variability of food distribution than at Montepaldi. The Montepaldi environment is more predictable than that at Castelporziano and, in fact, the variability of the biomass threshold estimate is larger at Castelporziano than at Montepaldi. Probably the smallness of the Montepaldi estimate enables the deer to acquire a better knowledge of food availability than at Castelporziano where they range over a much larger surface area and, consequently, may have less detailed knowledge of the available habitats.

Probably fallow deer may increase or decrease the sinuosity of their paths in order, respectively, to remain in the selected habitat long enough to forage, or reduce the probability of returning to previously exploited foraging stations.

Test of model predictions

This study has shown that female fallow deer do not perceive patches, so that the assumption of a patchy food distribution is unrealistic. Thus, the use of Focardi & Marcellini's (1995) modelling approach is

more pertinent than the one based on the Marginal Value Theorem (Charnov 1976). Our model differs in that the animal evaluates the threshold on a very small scale and need not be aware of any patch; clearly if food is clumped the observer may have the impression that the forager 'invents' the patch (Kacelnik & Bernstein 1988).

In both areas the deer clearly and systematically left some food in the selected foraging stations, as predicted by our model. Various other factors could explain such pattern; for instance, the existence of qualitative differences among plants within a foraging station or the necessity of sampling food to track environmental variations. However, such factors are probably not important in our study areas since the food consumed by the deer is relatively homogeneous and it is not easy to discriminate among grass leaves within the same foraging location, even if a certain amount of clumping of the different species of forage can also occur. On the other hand, the many outliers characterizing the distribution of the selected foraging stations at Castelporziano (cf. Fig. 7) could represent situations where graminoids are especially unpleasant to deer. Unfortunately, we are unable to test this hypothesis as the food which remained at the selected foraging stations was not analysed for chemical composition. It is worth noting that at Montepaldi, where the conditions of the meadow are much more regular, very few outliers were found. A clear demonstration of partial food consumption in moose was given by Åström *et al.* (1990).

While the existence of partial food consumption may be explained in different ways, the existence of a fixed biomass threshold may only be explained by a model of optimal foraging. Our results suggest that all selected foraging stations have a very similar level of residual biomass at least at Montepaldi, while the evidence for Castelporziano is less clear. In the former study area the definition of the threshold appears to be almost a deterministic process. The presence of a sharp threshold which determines abandonment of the foraging station was clearly shown by Jiang & Hudson's (1993) study on wapiti.

Our study shows that, in both areas, knowledge of the average and standard deviation of the food distribution allows an animal to correctly estimate the biomass threshold. It is well known that many foragers are sensitive to both the mean and the variance of food distribution (Stephens & Krebs 1986). However, it is not clear how well ungulates are able to estimate such parameters. Gillingham & Bunnell (1989) showed that black-tailed deer can memorize a training food distribution, Vivås & Saether (1987) showed that moose can estimate food density and Langvatn & Hanley (1993) found that red deer can discriminate among patches on the basis of quality and quantity of food. The between-area qualitative differences observed in the threshold behaviour of fallow deer might be explained by the fact that in order

to evaluate the correct threshold value more information is necessary at Castelporziano than at Montepaldi.

In short, this study suggests that the spatial and temporal dynamics of foraging are determined by a combination of a stereotyped search pattern and the adoption of an optimal threshold.

Further studies

This analysis is clearly not final proof that fallow deer forage optimally. Stronger support would be given by a quantitative prediction of the threshold value. To do so it would be necessary to estimate the functional response of fallow deer. Information on the functional response of ungulates is scarce; however, the theoretical studies of Spalinger & Hobbs (1992) and Focardi & Marcellini (1995) show that the functional response is of fundamental importance in analysing the foraging behaviour of these animals. Moreover, the same animals should be tested under different environmental conditions (for instance in different seasons or habitats).

Focardi & Marcellini's (1995) model addresses only the allocation of foraging effort in space and time, but not the diet choice of the animals (cf. Hughes 1993). We purposely avoided such a complication by observing deer grazing on one category of food, but clearly a model including both aspects could be very important for interpreting the foraging behaviour of wild ruminants. Owen-Smith (1993) suggested that dynamic optimization (Lucan & Schmid-Hempel 1988) may cope with such a problem. We are trying to extend the theoretical approach used in the present paper to investigate diet choice.

Acknowledgements

We are grateful to Prof. Roger H. Hughes for his help in improving a first version of the manuscript and to an anonymous referee for his invaluable criticism of a latter version of this paper. We thank the director of Castelporziano and Prof. B.M. Poli (at Montepaldi) for their help.

References

- Alt, W. (1990) Correlation analysis of two-dimensional locomotion paths. *Biological motion* (W. Alt & G. Hoffmann eds.), pp. 254–268. Springer-Verlag, Berlin.
- Arditi, R. & Dacorogna, B. (1988) Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist*, **131**, 837–846.
- Åström, M., Lundberg, P. & Danell, K. (1990) Partial prey consumption by browsers: trees as patches. *Journal of Animal Ecology*, **59**, 287–300.
- Batschelet, E. (1981) *Circular Statistics in Biology*, Academic Press, London.
- Belovsky, G.E. (1978) Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology*, **14**, 105–134.

- Belovsky, G.E. (1984) Herbivore optimal foraging: a comparative test of three models *American Naturalist*, **124**, 97–115.
- Belovsky, G.E. (1994) How good must models and data be in ecology? *Oecologia*, **100**, 475–480.
- Benhamou, S. & Bovet, P. (1992) Distinguishing between elementary orientation mechanisms by means of path analysis. *Animal Behaviour*, **43**, 371–377.
- Bovet, P. & Benhamou, S. (1988) Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology*, **131**, 419–433.
- Bovet, P. & Benhamou, S. (1990) Adaptation and orientation in animals' movements: random walk, kinesis, taxis and path integration. *Biological Motion* (W. Alt & G. Hoffmann eds.), pp. 297–304 Springer-Verlag, Berlin.
- Bovet, P. & Benhamou, S. (1991) Optimal sinuosity in central place foraging movements. *Animal Behaviour*, **42**, 57–62.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.
- Demment, M.W. & Van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *American Naturalist*, **125**, 641–672.
- Focardi, S., Toso, S., Marcellini, P. & Montanaro, P. (1994) The grazing pattern of female fallow deer living in a coastal Mediterranean forest. *Proceedings of the XXIth IUGB Congress, Halifax, 15–20 August 1993*, pp.319–326.
- Focardi, S., Montanaro, P. & Tinelli, A. (1994) A non-destructive method for the estimate of vegetal biomass. *Proceeding of the XXIth IUGB Congress, Halifax 15–20 August 1993*, pp. 374–379.
- Focardi, S. & Marcellini, P. (1995) A mathematical framework for optimal foraging of herbivores. *Journal of Mathematical Biology*, **33**, 365–387.
- Focardi, S., Poli, B.M. & Tinelli, A. (1995) The nutritional carrying capacity of four Mediterranean habitats for fallow deer (*Dama dama*). *Revue d'Ecologie*, **50**, 97–107.
- Fraenkel, G.S. & Gunn, D.L. (1961) *The Orientation of Animals: Kinesis, Taxis and Compass reactions*, Dover, New York.
- Gillingham, M.P. & Bunnell, F.L. (1989) Effects of learning on food selection and searching behaviour of deer. *Canadian Journal of Zoology*, **67**, 24–32.
- Ginnett, T.F. & Demment, M.W. (1995) The functional response of herbivores: analysis and test of a simple mechanistic model. *Functional Ecology*, **9**, 376–384.
- Hartfiel, T.A. (1990) Nutrition and feeding. *Deer farming. A Practical Guide to German Techniques* (eds G. Rincken, W. Hartfiel & E. Korner), pp. 117–159. Farmer Press Books, Ipswich, UK.
- Hobbs, N.T. (1990) Diet selection by generalist herbivores: a test of the linear programming model. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 395–413. Nato ASI Series G20. Springer-Verlag, Berlin.
- Hofmann, R.R. (1989) Evolutionary steps of eco-physiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, **78**, 443–457.
- Huggard, D.J. (1994) A linear programming model of herbivore foraging: imprecise, yet successful? *Oecologia*, **100**, 470–474.
- Hughes, R.N. (1993) Diet Selection. An Interdisciplinary Approach to Foraging Behaviour, Blackwell Scientific Publications, Oxford.
- Illius, A.W. & Gordon, I.J. (1990) Constraints on diet selection and foraging behaviour in mammalian herbivores. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 369–392. Nato ASI Series G20. Springer-Verlag, Berlin.
- Illius, A.W. & Gordon, I.J. (1993) Diet selection in mammalian herbivores: constraints and tactics. *Diet Selection. An Interdisciplinary Approach to foraging Behaviour* (ed. R.N. Hughes), pp. 157–181. Blackwell Scientific Publications, Oxford.
- Jiang, Z. & Hudson, R.J. (1993) Optimal grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules. *Evolutionary Ecology*, **7**, 488–498.
- Jonasson, S. (1988) Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **52**, 101–106.
- Kacelnik, A. & Bernstein, C. (1988) Optimal foraging and arbitrary food distribution: patch models gain a lease of life. *Trends in Ecology & Evolution*, **3**, 251–253.
- Langvatn, R. & Hanley, T.A. (1993) Feeding-patch choice by red deer in relation to foraging efficiency. An experiment. *Oecologia*, **95**, 164–170.
- Lucas, J. & Schmid-Hempel, P. (1988) Diet choice in patches: time constraint and state-space solutions. *Journal of Theoretical Biology*, **131**, 307–332.
- McNair, J.N. (1979) A generalised model of optimal diets. *Theoretical Population Biology*, **15**, 159–170.
- McNamara, J.M. & Houston, A.I. (1987) Partial preferences and foraging. *Animal Behaviour*, **35**, 1084–1099.
- Myers, J.P. (1983) Perspectives in optimal foraging. *Commentary Perspectives in Ornithology* (eds A.H. Brush & G.A. Clark), pp. 216–221. Cambridge University Press, Cambridge.
- Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat? *American Naturalist*, **119**, 151–178.
- Owen-Smith, N. (1993) Assessing the constraints for optimal diet models. *Evolutionary Ecology*, **7**, 530–531.
- Poli, B.M., Focardi, S. & Tinelli, A. (in press) Composition and metabolizable energy of feed used by fallow deer (*Dama dama*) in a coastal Mediterranean ecosystem. *Small Ruminant Research*.
- Provenza, F.D. & Balph, D.F. (1990) Applicability of five diet selection models to various foraging challenges ruminants encounter. *Behavioural Mechanism of Food Selection* (ed. R.N. Hughes), pp. 423–459. Nato ASI Series G20. Springer Verlag, Berlin.
- Pyke, G.H. (1978) Are animals efficient harvesters? *Animal Behaviour*, **26**, 241–250.
- Pyke, G.H. (1983) Animal movement: an optimal foraging approach. *The ecology of Animal Movement* (eds I.R. Swingland & P.J. Greenwood), pp. 7–31. Clarendon Press, Oxford.
- Real, L.A. (1979) Ecological determinants of functional response. *Ecology*, **60**, 481–485.
- Scharstein, H. & Alt, W. (1990) The influence of discrete position measurements on the correlation analysis of 2-dimensional tracks. *Biological Motion* (W. Alt & G. Hoffmann eds.), pp. 278–280. Springer-Verlag, Berlin.
- Spalinger, D.E. & Hobbs, N.T. (1992) Mechanism of foraging in mammalian herbivores: a new model of functional response. *American Naturalist*, **140**, 325–348.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*, Princeton University Press, Princeton, NJ.
- Tranquillo, R.T. & Alt, W. (1990) Glossary of terms concerning oriented movements *Biological Motion* (eds W. Alt & G. Hoffman), pp. 510–517. Springer-Verlag, Berlin.
- Underwood, R. (1983) The feeding behaviour of grazing African ungulates. *Behaviour*, **84**, 195–243.
- Vivås, H.J. & Saether, B.E. (1987) Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology*, **56**, 509–520.
- Ward, D. (1992) The role of satisficing in foraging theory. *Oikos*, **63**, 312–317.
- Westoby, M. (1974) An analysis of diet selection by large generalist herbivores. *American Naturalist*, **108**, 290–304.

Appendix

Mathematical notations

Variable	Definition	Dimensions
λ	Threshold in the acquisition of food, i.e. the critical density of food	mass length ⁻¹
x	Position of a generic point in the excursion	length
$\rho = \rho(x)$	Food density at a generic point x	mass length ⁻¹
S	Path sinuosity	angle length ^{-1/2}
σ	Angular standard deviation	angle
\bar{d}	Mean step length	length
t	Time	time
x_i, y_i	Cartesian coordinates of animal position	length
$V(t)$	Displacement vector with elements (x_i, d_i)	angle, length
$\bar{\alpha}$	Mean turning angle	angle
r	Length of resultant vector or correlation coefficient	adimensional
l	Position of the final excursion point and length of the excursion path	length
τ	Foraging time per unit length, i.e. time spent at x to acquire food	time length ⁻¹
δ	Density of acquisition of food at x	mass length ⁻¹
$\xi = \rho - \delta$	Density of remaining food	mass length ⁻¹
$\Phi(\xi)$	Functional response, equal to the velocity of food acquisition	mass time ⁻¹
k	Parameter	mass time ⁻¹
b	Parameter	mass length ⁻¹
V_0	Velocity of the animal at x	length time ⁻¹
$T = T(v, l)$	Total time to acquire food and to move	time
$v = v(x)$	Amount of food gathered up to the point x	mass
A	Total amount of food gathered, i.e. maximum gut content	mass
$q(x)$	Residual biomass at AS	mass length ⁻²
\bar{q}	Mean residual biomass	mass length ⁻²