

Integrated modelling of foraging behaviour, energy budget and memory properties

S. Esposito^{a,*}, G. Incerti^b, F. Giannino^c, D. Russo^a, S. Mazzoleni^a

^a Dipartimento Arboricoltura, Botanica, e Patologia Vegetale, Università degli Studi di Napoli Federico II, via Università 100, 80055 Portici, Napoli, Italy

^b Dipartimento di Scienze della Vita, Università degli Studi di Trieste via Giorgieri 10, 34127 Trieste, Italy

^c Dipartimento di Ingegneria Agraria e Agronomia del Territorio, Università degli Studi di Napoli Federico II, via Università 100, 80055 Portici, Napoli, Italy

ARTICLE INFO

Article history:

Received 5 August 2009

Received in revised form 12 January 2010

Accepted 23 January 2010

Available online 24 February 2010

Keywords:

Body mass

Food distribution

Individual-based model

Learning

Prey–predator interactions

ABSTRACT

A predator's foraging performance is related to its ability to acquire sufficient information on environmental profitability. This process can be affected by the patchy distribution and clustering of food resources and by the food intake process dynamics.

We simulated body mass growth and behaviour in a forager acting in a patchy environment with patchy distribution of both prey abundance and body mass by an individual-based model. In our model, food intake was a discrete and stochastic process and leaving decision was based on the estimate of net energy gain and searching time during their foraging activities. The study aimed to investigate the effects of learning processes and food resource exploitation on body mass and survival of foragers under different scenarios of intra-patch resource distribution.

The simulation output showed that different sources of resource variability between patches affected foraging efficiency differently. When prey abundance varied across patches, the predator stayed longer in poorest patches to obtain the information needed and its performance was affected by the cost of sampling and the resulting assessment of the environment proved unreliable. On the other hand, when prey body mass, but not abundance, varied among the patches the predator was quickly able to assess local profitability. Both body mass and survival of the predator were greatly affected by learning processes and patterns of food resource distribution.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

The energy budget of a forager depends on its ability to modify its behaviour in response to the spatial and temporal variability of food resources (Kramer, 2001). An efficient exploitation of food showing a heterogeneous spatial distribution (Wiens, 2000) requires foraging efforts to be concentrated within areas of higher resource profitability (Valone and Brown, 1989). Therefore, the time foragers spend in a given patch is a behavioural choice strongly influencing their energy intake (Pyke, 1984; Basset et al., 2002).

The theory of optimal foraging investigated the problem of how to exploit patchily distributed food in order to maximize long-term energy gain rates (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). According to the classical model of Charnov (1976), which represents energy intake as a continuous process, a forager's optimal behaviour should consist of quitting to forage in a patch and moving to the next when the actual energy intake in the former (local information) falls below the average intake rate

offered by the entire habitat (global information: Olsson and Brown, 2006).

In nature, assessing information at both local and global levels is inevitably associated with uncertainty. Moreover, foragers acquire knowledge of habitat profitability during their foraging activities (Mangel, 1990; Valone, 1991). In these cases, i.e. when information has to be actively sampled and used, foraging behaviour may often deviate from patterns predicted for “omniscient” foragers assumed to have unlimited access to information at both local and global scales (Bernstein et al., 1988, 1991; Rodríguez-Gironés and Vásquez, 1997; Eliassen et al., 2007).

Several models have studied how the information acquisition process can improve foraging efficiency. According to Dall et al. (2005) learning by foragers is a complex process integrating newly acquired information with old experience. Some foraging models focused on the trade-off between the cost of harvesting information and the benefit of using it (Valone, 1989; Mangel, 1990; Eliassen et al., 2007). The extent to which information acquisition enhances foraging efficiency depends on the state of the resources, in terms of spatial and temporal dynamics and stochasticity (McNamara and Houston, 1985; Valone, 1992; Hirvonen et al., 1999; Fortin, 2002). According to Nishimura (1994), the adequate memory capacity of a forager can be partially predicted on the basis

* Corresponding author. Tel.: +39 081 7754850; fax: +39 081 7760104.

E-mail address: sesposito@unina.it (S. Esposito).

of the stochastic patterns of between-patches and within-patch profitability.

Because the information on patch quality is often gained from acquisition of food, the way to represent information is influenced by the way foraging process is represented (Ward et al., 2000). Since work done by Charnov (1976), other foraging models (Bernstein et al., 1988, 1991; Grass and Roberts, 1992; Nishimura, 1994; Fortin, 2002; Nolet et al., 2006a,b) have considered food intake as a continuous deterministic process where foragers assess patch profitability by the instantaneous net energy intake rate or food intake rate. Such a representation of intake dynamics is inadequate to represent the real search–capture processes that, in most cases, are discrete and stochastic events (McNamara, 1982; Ward et al., 2000).

Environmental stochasticity has been indeed considered as an important factor in behavioural ecology (Caraco and Giraldeau, 1991; Yoshimura and Clark, 1991). Some models have featured resource intake implemented as a discrete stochastic process (Oaten, 1977; Brown, 1988; Iwasa et al., 1981; Valone, 1991; Olsson and Holmgren, 1999; McNamara et al., 2006; Olsson and Brown, 2006). In these studies, following the Bayes theorem, foragers assess the quantity of food contained in a patch on the bases of the time spent in the patch and the number of food items consumed there.

In all stochastic models reported in the literature, foragers assess environmental quality either as searching time or energy gain, whereas foraging costs are often neglected from a behavioural point of view. Traditionally, foraging models have been developed to assess the optimal foraging strategy to maximize energy intake and have been rarely linked with an energy metabolism model (Moen et al., 1997). On the other hand, energy metabolism models have been used to predict the energy survival requirements, with no explicit consideration of behavioural foraging mechanisms (Moen et al., 1997; Basset et al., 2002). However, integrating foraging and energy metabolism models would be essential to understand the long-term consequences of foraging decisions (Moen et al., 1997).

In this study we present a new individual-based foraging behaviour model integrated with an energy metabolism model. In our model predators operate in a patchy environment of heterogeneously distributed food resources where both the decision to leave the foraging patch and the learning process are based on the evaluation of both searching efforts and energy reward. The study aimed to investigate the effects of learning processes and food resource exploitation on body mass and survival of foragers under different scenarios of patchily distributed resources.

2. The model

The behaviour of a forager has been modelled by an individual-based (IBM) spatial implicit approach, i.e. with an implicit representation of spatial patterns and distance between patches.

The model simulates body mass growth and foraging dynamics in a patchy environment with different patterns of prey abundance and body mass.

The forager's energy budget arises from the balance between the energy costs of maintenance and foraging and the energy gain obtained by food intake. Foraging behaviour is implemented as a sequence of discrete processes: prey search, food processing (handling and digesting), commuting between foraging areas and resting. The switch between activities depends on decision rules based on the predator's internal state and food resources availability. A conceptual diagram of model structure is shown in Fig. 1a.

Prey capture is a stochastic event, occurring only as a consequence of prey search (a behaviour prompted by "internal" variables of predator such as the level of satiety). The probability of catching prey depends on prey abundance and search

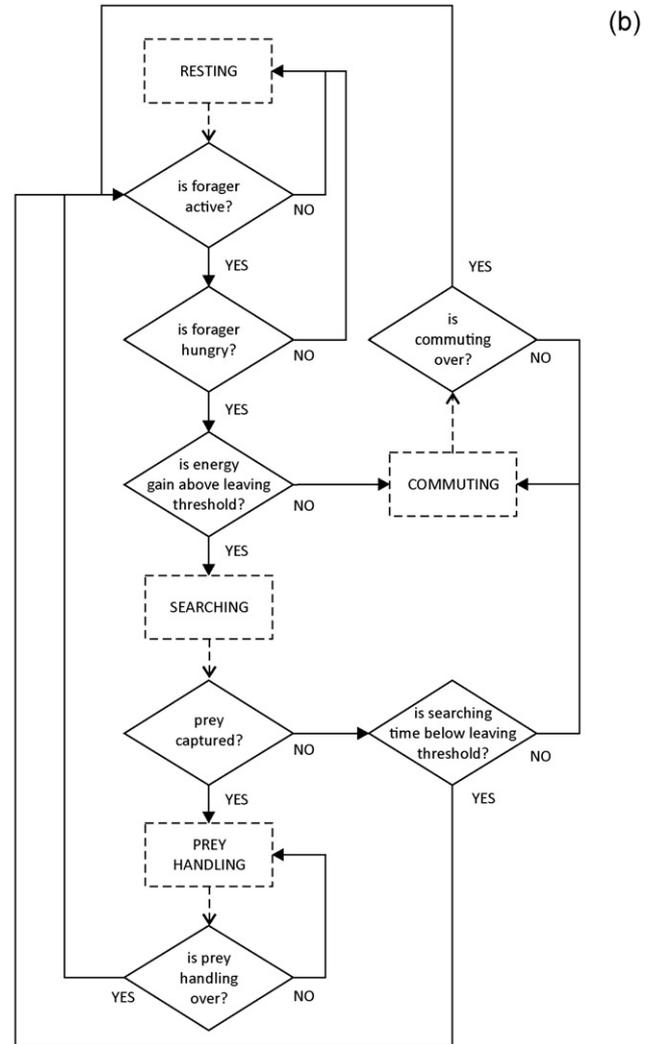
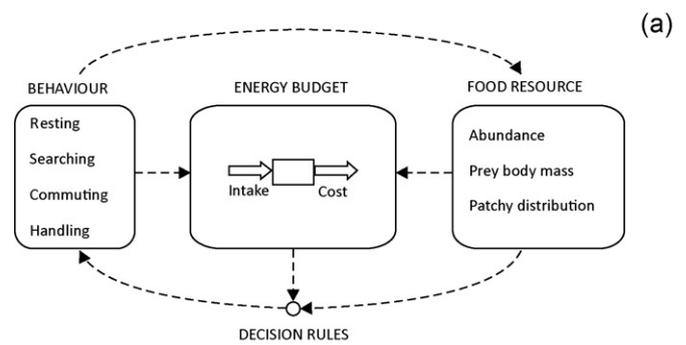


Fig. 1. (a) Conceptual diagram of model structure. The predator energy budget is affected by both behaviour and food resources. Behaviour is driven by decision rules based on both internal energy status and resources availability, the latter being affected by predator behaviour. (b) Schematic flow chart of decision rules.

efficiency, whereas energy costs associated to foraging processes are continuous over time, with rates depending on the occurring activity.

The predator's ability in exploiting food resources varies over time in terms of time spent in more and less profitable patches. This is implemented by means of a self-adapting leaving decision, based on rules relating local and global information about both net energy gain and capture frequency.

The model was implemented by the system dynamic software Simile (Muetzelfeldt and Massheder, 2003).

2.1. Energy budget

The variation of predator body mass (B) is defined by the difference between assimilated food and foraging costs:

$$\frac{dB}{dt} = \text{assimilated food rate} - \text{foraging costs} \quad (1)$$

The amount of food (F) contained in the predator's stomach at each time step is calculated according to the following equation:

$$\frac{dF}{dt} = \min[M, (F_{\max} - F)] \cdot k_h - F \cdot k_d \quad (2)$$

where t is time, M is the body mass of captured prey, F_{\max} the maximum capacity of predator's stomach, k_h the handling rate and k_d the digesting rate. In the equation the positive and negative terms are given, respectively, by the ingestion and digestion processes.

The F_{\max} value is calculated as an allometric function of the individual body mass, following Basset et al. (2002):

$$F_{\max} = \alpha_1 B^{\alpha_2} \quad (3)$$

where α_1 is an allometric constant independent of body mass and α_2 is an allometric scaling exponent.

The food assimilated is defined as a percentage (a : assimilation efficiency) of the digested food that becomes available for growth or physiological processes, the remainder being lost in the excretion processes or as heat (Begon et al., 1996).

The foraging costs in each time unit are allometrically calculated as a function of individual body mass (Peters, 1983). Resting (r), searching (s), food processing (f), and commuting (c) energy costs depend on their respective allometric coefficients ($\beta_{1,k}$ where $k \in \{r, s, f, c\}$) and the allometric scaling exponent (β_2), according to the following equation:

$$C_k = \beta_{1,k} \cdot B^{\beta_2} \quad (4)$$

For simplicity, the allometric coefficient $\beta_{1,k}$ was considered constant for all daily activities (searching, food processing, commuting) and halved for resting (Nagy et al., 1999; White and Seymour, 2005; Nagy, 2005; Voigt et al., 2006; Packard and Boardman, 2009).

Then the variation of predator body mass is calculated as:

$$\frac{dB}{dt} = \begin{cases} \{F \cdot k_d\} \cdot a - C_k & \text{if food processing is active } (k = f) \\ -C_k & \text{if food processing is not active } (k \in \{r, s, c\}) \end{cases} \quad (5)$$

2.2. Foraging behaviour

Searching, handling and commuting processes are mutually exclusive, so that only one activity may occur at a given time step, while digesting can take place simultaneously with other activities. A schematic representation of the flow chart of decision rules in the model is reported in Fig. 1b.

A circadian rhythm of activities is implemented in the model, in which resting is the baseline state, taking place either during the night (12-h) or when no other activity occurs.

Starting to search for prey is a stochastic event based on a searching decision rule depending on the level of satiety of the predator, defined as the ratio between the ingested food and the maximum stomach capacity of the individual ($\sigma = F/F_{\max}$).

Then, the probability of starting to search (P_s) is calculated through a logistic model in which the values of centre (0.5) and steepness (0.1) parameters are derived in such a way as to attribute maximum ($P_s \cong 1$), minimum ($P_s \cong 0$) and median values ($P_s = 0.5$)

to the corresponding satiety levels ($\sigma = 0$, $\sigma = 1$, and $\sigma = 0.5$, respectively):

$$P_s = 1 - \frac{1}{1 + e^{(0.5-\sigma)0.1^{-1}}} \quad (6)$$

Search activity can only start during daytime, whenever an automatically generated random value between 0 and 1 at each time step is lower than P_s . Searching stops when a prey item is captured or when a predator decides to move elsewhere. Capture is also a stochastic event, depending on both prey abundance in the current patch (A_p) and search efficiency of the predator (γ). The probability of capture (P_c) is thus calculated according to an exponential model (Eliassen et al., 2007) in which search efficiency ($\gamma = 0.03$) was adjusted to calibrate maximum ($P_c \cong 1$) and minimum ($P_c \cong 0$) values to the range of prey abundance ($1 \leq A_p \leq 100$) implemented in the model:

$$P_c = 1 - e^{-\gamma A_p} \quad (7)$$

After capturing a prey item, the forager starts immediately to handle it. Food processing lasts until prey is completely digested.

Commuting activity starts according to a leaving decision rule and lasts for a time period defined by the travel time parameter (T_p), indirectly indicating the distance between patches. T_p is assumed constant over time and across all environmental patches. When the foragers stops commuting, enters a new patch randomly selected within the environment.

The leaving decision, i.e. the interruption of prey search in a patch and the decision to move elsewhere, is taken according to two rules. The decision to leave a p th patch is taken either when the searching time ($t_{s,p}$) exceeds a threshold value of capture time (τ_p) or when the net intake rate after processing a prey item (e_p) is lower than a threshold value of net energy gain (ε_p).

The predator enters the first patch with initial values of expected capture time (τ_0) and net energy gain (ε_0) representing "a priori" estimates of environment profitability. These can be regarded as genetically inherited traits of the predator (Eliassen et al., 2007), which can be modified by individual learning.

When the predator leaves the p th patch, the average capture time ($\bar{t}_{s,p}$) and net energy gain rate (\bar{e}_p) experienced within that patch are both calculated according to the following equations:

$$\bar{t}_{s,p} = \frac{T_p + \sum_{i=1}^{n_p} t_i}{n_p} \quad (8)$$

where T_p is the commuting time to the p th patch, t_i is the searching time spent to capture prey item i , and n_p is the total number of captured prey items in the patch; and:

$$\bar{e}_p = \frac{\Delta B_p}{T_p + t_p} \quad (9)$$

ΔB_p is the variation of the individual net energy occurred in the p th patch including the commuting cost, and t_p is the total time spent there, including searching, food processing and resting time.

On this basis the predator updates the threshold values representing its expectations in terms of acceptable searching time and net energy gain (τ_{p+1} and ε_{p+1} , respectively). This is done following Eliassen et al. (2007) and Bernstein et al. (1988), respectively:

$$\tau_{p+1} = \bar{t}_{s,p} w_t + \tau_p (1 - w_t) \quad (10)$$

$$\varepsilon_{p+1} = \bar{e}_p w_e + \varepsilon_p (1 - w_e) \quad (11)$$

where w_t and w_e are the relative weights given to the last experiences.

With $w_t = 0$ and $w_e = 0$, $\tau_{p+1} = \tau_p = \dots = \tau_0$ and $\varepsilon_{p+1} = \varepsilon_p = \dots = \varepsilon_0$. This implies a totally fixed behaviour, regulated by initial values, i.e. the leaving decision is genetically predetermined and the behaviour does not change over time.

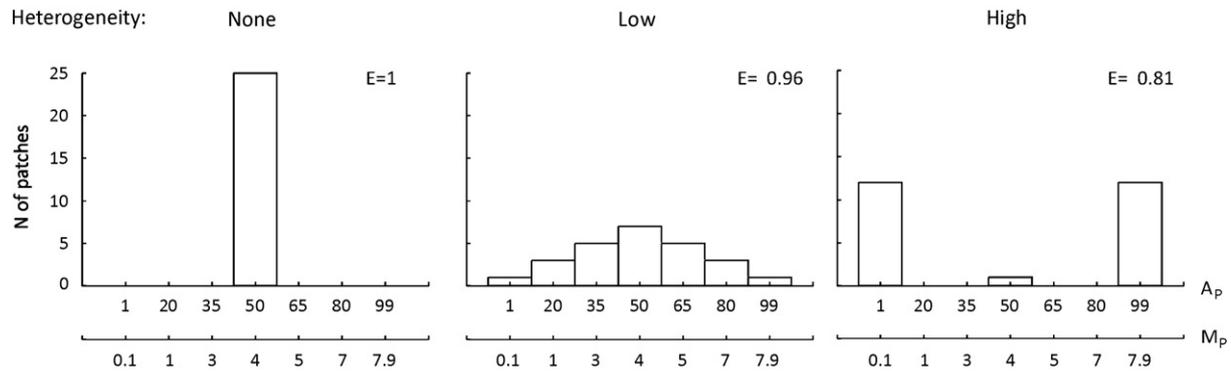


Fig. 2. Frequency distributions in patches of prey abundance (A_p) and individual mass (M_p) used in the simulation exercises. E values refer to Pielou's evenness index. The cases with high average prey abundance ($A = 50$) and body mass ($M = 4$) are reported as an example.

With $w_t = 1$ and $w_e = 1$, $\tau_{p+1} = \bar{\tau}_p$ and $\varepsilon_{p+1} = \bar{\varepsilon}_p$. This implies a totally flexible behaviour, i.e. the leaving decision is based only on the last experience with changing over time according to the capture dynamics in the previous searching patch.

With w_t and w_e ranging between 0 and 1 (extremes excluded) the predator behaviour depends on the environment profitability experienced over time. In these cases a shorter or longer memory does correspond to higher or lower values of w , respectively. Thus, we defined w_t as a capture-time memory factor, and w_e as capture-energy memory factor.

2.3. Food resources

Food resources are spread in 25 patches composing the foraging environment. Patch location is not explicitly implemented, but the distance between patches can be reflected by the travel time parameter (T_p).

The food resources of the modelled environment depend on both prey abundance and body mass in the different patches. The total resource abundance (R_{tot}) can be calculated as:

$$R_{tot} = \sum_{p=1}^n (A_p \cdot M_p) \tag{12}$$

where p is the patch index, n the total number of patches, A_p and M_p are abundance and individual mass of prey items in the p th patch, respectively.

Given a fixed value of overall food resources, different distributions among the patches of both prey body mass and abundance were considered (Fig. 2).

The heterogeneity of the distribution among the patches for both A_p and M_p was assessed by Pielou's evenness index (E_A and E_M , respectively) based on Shannon diversity index:

$$E_A = \frac{-\sum_{p=1}^n (A_p / (n \cdot A)) \cdot \ln(A_p / (n \cdot A))}{\ln(n)} \quad \text{and} \tag{13}$$

$$E_M = \frac{-\sum_{p=1}^n (M_p / (n \cdot M)) \cdot \ln(M_p / (n \cdot M))}{\ln(n)}$$

where A and M are the average prey abundance and body mass of the environment (mean of all patches), and n is the total number of patches (25).

The less prey abundance and body mass vary among the patches (the lower the heterogeneity of distributions), the higher are E_A and E_M , respectively.

When the predator enters a patch, prey depletion occurs over time according to the number of captures in the patch. We assumed, to simplify, an instantaneous recovery of prey abun-

dance to its initial state when the predator leaves the patch. In this way, resource stocks are affected by the foraging activity only at single-patch scale, whereas the overall environmental prey availability is maintained constant every time a predator enters a new patch.

3. Simulation design

Different simulation exercises were designed to test the model and observe the effects of resources and memory parameters on predator body mass and survival. The values assigned to the model parameters are reported in Table 1.

Multiple values were applied to the following parameters and different runs were done according to a factorial combination of their values: average prey abundance (A , three values: 5, 10 and 50), average prey body mass (M , five values ranging between 0.1 and 4 g), their distribution in patches (three values of both E_A and E_M), travel time (T_p , four values ranging between 10 and 300 min), capture-time (w_t) and capture-energy (w_e) memory factors (six values each), ranging from 0.005 to 1. Values of $w = 0$ were avoided because they would correspond to a fixed behaviour in terms of expected average capture time (τ_0) and expected average net energy gain (ε_0). At start of simulation, the initial values were set to $\tau_0 = 60$ min and to $\varepsilon_0 = 0$.

The factorial design for the simulations exercises included 19,440 initial states (three levels of $A \times 5$ of $M \times 3$ of $E_A \times 3$ of $E_M \times 4$ of $T_p \times 6$ of $w_t \times 6$ of w_e). For each of the 19440 states, 200 replicates were run for 525,600 time steps, corresponding to a 1-year timescale with time steps assumed as 1 min.

The model outputs were mean and standard deviations of predator body mass at long-term and total time spent in each patch during the simulations calculated for all the replicates.

To minimize oscillations over time of predator body mass due to the effect of food intake discreteness and stochasticity, output values were recorded at the first minute of each day (1440 time steps) and averaged over the last 30 days of simulation (from time step 482,400 to the run end).

We also carried out the following model applications:

- (1) Effects of prey abundance and body mass in patches and travel time on predator body mass in conditions of homogeneous distribution of resources.
- (2) Effects of the initial predator body mass on its value at long term for different environmental scenarios and memory properties.
- (3) Effects of the distributions in patches of prey abundance and body mass on the predator body mass in conditions of high total resource availability and low travel time.

Table 1
Model parameters with related symbols, units and values used in the simulations.

Symbol	Parameter	Unit	Assigned value
Energy			
B	Predator body mass	g	10, 100, 200, 300 (initial value)
F	Food contained in the stomach	g	–
F_{\max}	Maximum capacity of predator's stomach	g	–
k_h	Handling rate	min^{-1}	0.1
k_d	Digesting rate	min^{-1}	0.4
α_1	Allometric constant of maximum stomach capacity	–	0.125
α_2	Allometric exponent of maximum stomach capacity	–	0.75
r, s, f, c	Resting, searching, food processing and commuting	–	–
C_k	Energy costs where $k \in \{r, s, f, c\}$	g min^{-1}	–
$\beta_{1,k}$	Allometric coefficient of energy costs where $k \in \{r, s, f, c\}$	min^{-1}	$\beta_{1,r} = 0.0005\beta_{1,s} = \beta_{1,f} = \beta_{1,c} = 0.001$
β_2	Allometric exponent of energy costs	–	0.75
a	Assimilation efficiency	%	0.77
Behaviour			
σ	Satiety level	–	–
P_s	Probability of starting to search	–	[0, 1]
P_c	Probability of capture	–	[0, 1]
γ	Searching efficiency	–	0.03
p	p th patch (patch index)	–	–
$t_{s,p}$	Current searching time	min	–
e_p	Net energy gain rate after processing a prey item	g min^{-1}	–
τ_p	Threshold value of capture time	min	60 (initial value)
ε_p	Threshold value of net energy gain rate	g min^{-1}	0 (initial value)
$\bar{t}_{s,p}$	Average searching time	min	–
\bar{e}_p	Average net energy gain rate	g min^{-1}	–
n_p	Total number of captured prey	–	–
t_p	Time spent in p th patch	min	–
w_t	Capture-time memory factor	–	0.005, 0.05, 0.5, 0.75, 0.95, 1
w_e	Capture-energy memory factor	–	0.005, 0.05, 0.5, 0.75, 0.95, 1
Environment			
A	Average prey abundance in patches	–	5, 10, 50
M	Average prey body mass in patches	g	0.1, 1, 2, 3, 4
A_p	Initial prey abundance in p th patch	–	1, 20, 35, 50, 65, 80, 99 ^a
M_p	Prey body mass in p th patch	g	0.1, 1, 3, 4, 5, 7, 7.9 ^a
T_p	Travel time to p th patch	min	10, 100, 200, 300
R_{tot}	Total resource abundance	g	–
E_A	Evenness of prey abundance distribution	–	1, 0.96, 0.81
E_M	Evenness of prey mass distribution	–	1, 0.96, 0.81

^a Values of A_p and M_p depend on values of E_A and E_M , and on A and M , respectively. Values for simulation cases with $A = 50$, $E_A = 0.81$ and $M = 4$, $E_M = 0.81$ are shown (see also Fig. 2).

(4) Effect of memory properties on predator body mass in scenarios of high heterogeneous distribution of both prey abundance and body mass. Foragers with different behavioural strategies were also compared in terms of total time spent in each patch in relation to the patch profitability. Then, individual mortality was assessed by the number of cases with body mass equal to zero in each simulation condition.

4. Results

The individual body mass of foragers was significantly affected by the variation of simulated ecological conditions (Fig. 3). Predator body mass increased at greater values of both body mass and abundance of prey (Fig. 3a). Travel time had a negative effect on predator body mass and this was apparently more pronounced under low prey abundance as suggested in Fig. 3b.

The different values of initial predator body mass selected in the simulation all led to the same level of average sustainable body mass because the latter depended only on the available food resources (Fig. 4). In agreement with the pattern already described for Fig. 3, lower levels of prey abundance produced smaller values of the mean long-term individual biomass (see cases $A = 50$, 10 and 5, respectively, in Fig. 4). Increasing resource abundance heterogeneity affected body mass stability leading to larger stochastic fluctuations of this variable (Fig. 4). Under resource heterogeneity conditions, predator's memory properties determine the magni-

tude of body mass oscillations and ultimately mortality. When both heterogeneous resource abundance and short memory occurred, stochastic oscillations were so pronounced to expose the predator to a higher death risk, especially at low prey abundance (see bottom graphs in Fig. 4).

The average predator body mass at long term was influenced by distributional patterns of both prey abundance and prey body mass. A positive effect of increasing heterogeneity of prey body mass was always evident (Fig. 5), whereas a higher heterogeneity of prey abundance increased predator body mass only when prey body mass distribution was also heterogeneous. This trend disappeared when prey body mass was fully homogeneous within prey population, and a slight decrease was noticed at increasing levels of heterogeneity of prey abundance. Since in simulations we averaged predator body mass as obtained at different values of forager memory length (w_t and w_e in Table 1) and kept the energetic costs of foraging constant, neither the latter nor memory length affected the results. The variability of predator body mass at long term, depending only on memory length, increased with the heterogeneity of both prey abundance and mass distribution in patches.

To explore the influence of memory properties on foraging performance, we analyzed two opposite situations of heterogeneous distribution of prey body mass and abundance. In the former scenario, featured a high heterogeneity of prey abundance and full prey body mass homogeneity (Fig. 6a), the predator mass increased considerably in proportion to both time- and energy-memory lengths (Fig. 6a). These two factors showed a similar effect, since the mini-

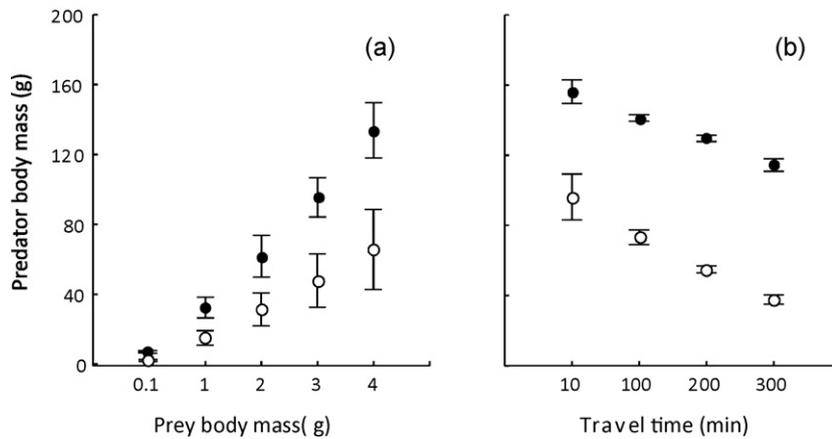


Fig. 3. Effects of prey body mass (a) and travel time (b) on predator body mass at long term in homogeneous distribution of resources at two different levels of average prey abundance ($A = 50$ and 10 , closed and open circles, respectively). Data points refer to averages and standard deviations of 144 (a) and 36 (b) simulation cases obtained by permutations of travel time (a), capture-time and capture-energy memory factor (a and b), each for 200 replicates (values in Table 1). Results in (b) refer to conditions of prey mass = 4 g. Duration of the simulations: 525,600 time steps (1 year).

mum individual body mass corresponded to the shortest memory of both. Long memory values of one type will compensate for short values of the other (Fig. 6a). Standard deviations, representing stochastic variability, increased as either memory lengths decreased.

In the latter scenario, i.e. at high and null heterogeneity degrees of prey body mass and abundance, respectively (Fig. 6b), the situation was very different, with overall much larger individual body masses of predators which were affected by the length of capture-energy memory but not by the capture-time memory. In general, a

shorter memory corresponded to an increased stochastic variability.

In both scenarios, the time spent in each patch depended more strictly on patch profitability (longer foraging time being spent in richer patches) for predators with a longer memory (Fig. 7a and b). Under a high heterogeneity of prey abundance and prey body mass homogeneity (Fig. 7a) the overall time spent in patches was longer than under opposite conditions (Fig. 7b).

When prey abundance was heterogeneous, mortality rates of predators increased compared to conditions of heterogeneous

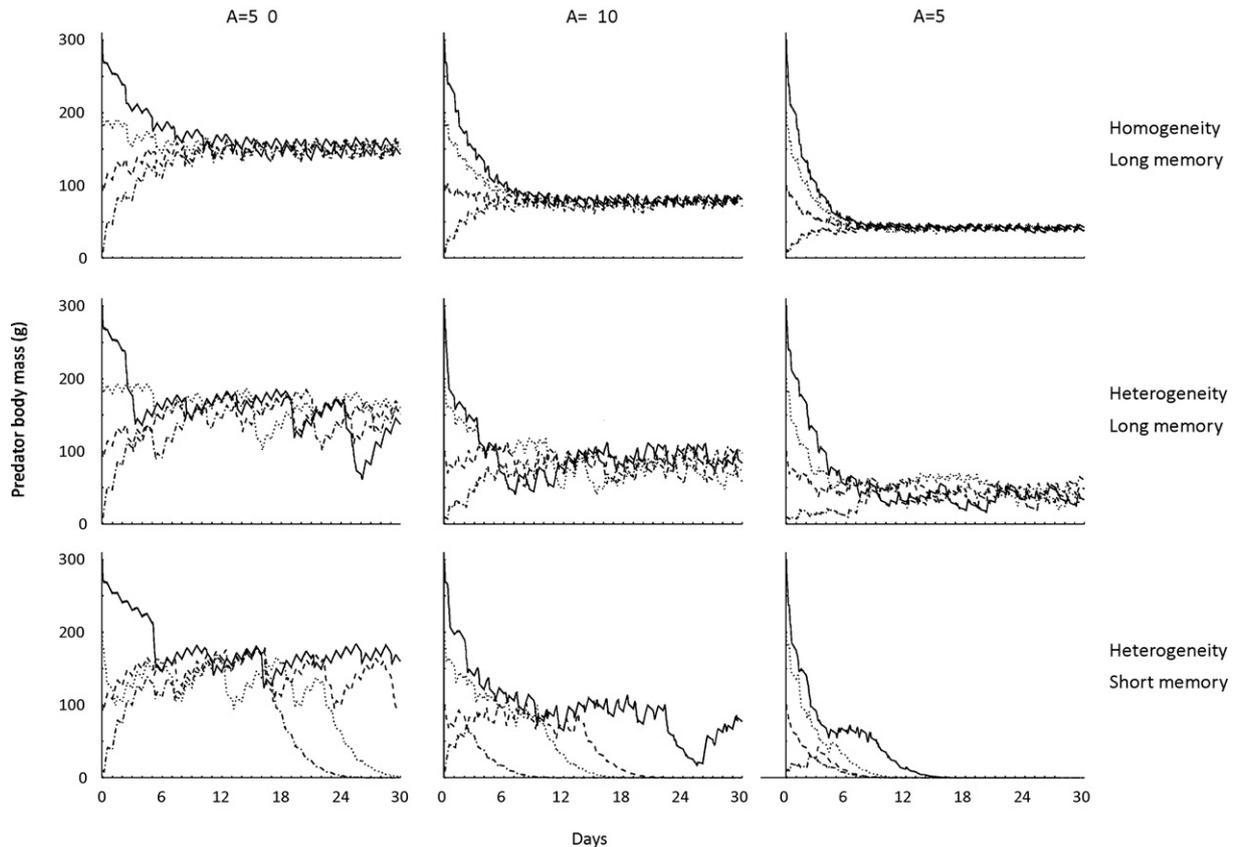


Fig. 4. Body mass time sequences of individuals with different initial body mass values and either long ($w_t = w_e = 0.005$) or short ($w_t = w_e = 0.95$) memory. Reported cases refer to three different levels of average prey abundance in patches (A) with either homogeneous ($E_A = 1$) or heterogeneous ($E_A = 0.81$) distribution, in condition of short travel time ($T_p = 10$ min) and prey body mass equal for all patches ($M = 4$ g and $E_M = 1$). Duration of simulations: 43,230 time steps (1 month).

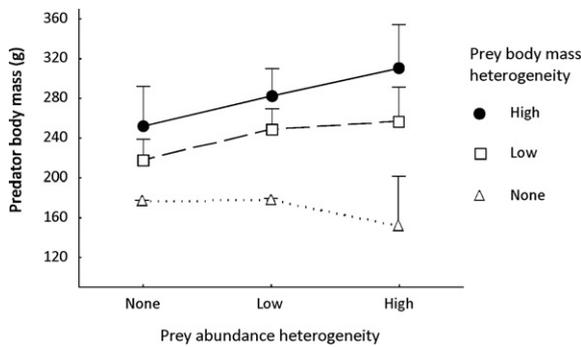


Fig. 5. Effects of heterogeneity of prey abundance and body mass distribution on predator body mass. Levels of heterogeneity correspond to evenness values as reported in Fig. 2. Data points refer to averages and standard deviations of 36 simulation cases obtained by multifactorial permutations of time- and energy- memory factors (six levels each, see Table 1), each for 200 replicates in condition of short travel time ($T_p = 10$ min) and high average prey abundance ($A = 50$) and body mass ($M = 4$ g) in patches. Duration of simulation: 525,600 time steps (1 year).

prey body mass which led to the survival of most predators (Table 2). A shorter individual memory (i.e. a memory assigning the greatest weight to the latest experience) increased predator mortality.

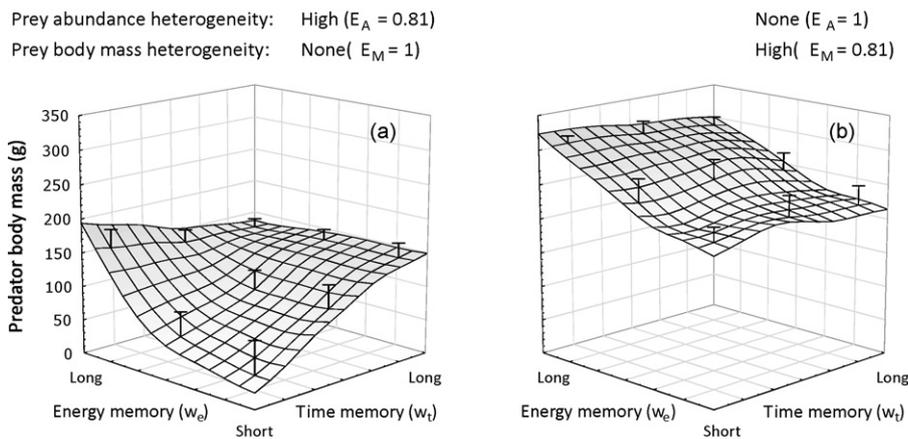


Fig. 6. Effects of energy- (w_e) and time- (w_t) memory length on predator body mass at long term (values of w_e and w_t in Table 1) under two scenarios (a and b) of distribution among patches of both prey abundance (E_A) and body mass (E_M). Data refer to averages (interpolated surface) and standard deviations (vertical bars) for 200 replicates in condition of short travel time ($T_p = 10$ min) and high average prey abundance ($A = 50$) and body mass ($M = 4$ g) in patches. Duration of simulation: 525,600 time steps (1 year).

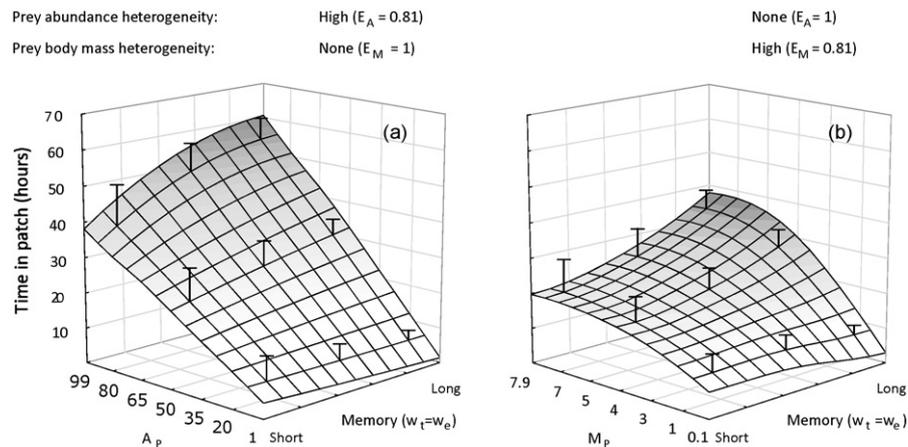


Fig. 7. Time spent (hours) by foragers in the p th patch as a function of either initial prey abundance (A_p) or body mass (M_p) in the patch, for different values of memory length (with $w_e = w_t$ value in Table 1) and under two scenarios (a and b) of distribution in patches of both prey abundance (E_A) and body mass (E_M). Data refer to averages (interpolated surface) and standard deviations (vertical bars) of 200 replicates in condition of short travel time ($T_p = 10$ min) and high average prey abundance ($A = 50$) and body mass ($M = 4$ g) in patches. Duration of simulation: 525,600 time steps (1 year).

5. Discussion

The model we propose proved effective in representing a forager’s behaviour based on a relatively simple set of intrinsic and food resource properties (food item abundance, energy content and distributional patterns of such variables). Specifically, it provided a rather realistic representation of the effects of food resource patterns, time invested in foraging patches and the interaction between such variables on the predator body mass, and ultimately on its survival.

In our modelling exercise, the forager’s body mass within a given resource scenario reaches a given level regardless of initial values, in accordance with many empirical studies showing that mean body mass are set by food availability and habitat quality (e.g. Dobson and Kjelgaard, 1985; Boutin, 1990; Prop and Deerenberg, 1991; Pettorelli et al., 2002; Russo, 2002).

Our simulations highlighted the influence of resource distribution among patches on patch exploitation (Wallis de Vries and Schippers, 1994) with clear consequences for predator body mass and survival. In fact, in order to effectively use heterogeneously distributed resources, a predator should be capable to assess environmental profitability and choose patches more profitable than the overall average (Valone and Brown, 1989; Vásquez et al., 2006; Laca, 2008).

Table 2
 Predator mortality in relation to both energy (w_e) and time (w_t) memory factor, under two different scenarios of distribution in patches of prey abundance (E_A) and body mass (E_M). Data refer to percent of individuals with body mass = 0 at the end of simulation runs. For simulation conditions see caption of Fig. 6.

Prey abundance heterogeneity: Prey body mass heterogeneity: w_e	High ($E_A = 0.81$) Null ($E_M = 1$) w_t						Null ($E_A = 1$) High ($E_M = 0.81$) w_t					
	0.005	0.05	0.5	0.75	0.9	1	0.005	0.05	0.5	0.75	0.9	1
0.005	0.4	2.1	7.9	7.5	10.0	10.8	0	0	0	0	0	0
0.05	1.7	1.3	12.9	17.9	20.0	25.0	0	0	0	0	0	6.7
0.5	0.8	0.8	17.9	25.4	32.9	37.1	0	0	0	0	0	3.3
0.75	3.3	1.7	16.7	26.3	37.1	40.4	0	0	0	0	0	0
0.9	1.3	1.7	19.2	31.3	40.4	43.3	0	0	0	0	0	0
1	0.8	2.1	17.9	25.8	40.4	43.3	0	0	0	0	0	6.7

One of the advances of our model was the discrete representation of energy intake during foraging, overall providing a more realistic representation of foraging than the models with a continuous energy intake and highlighting the different performances related to the kind of information processed by the forager. Our approach implies that the predator can decide to leave the patch either when the information on net energy gain of the patch is available after food capture and processing or, before the capture, when the current searching time exceeds estimated average environmental value.

When resource abundance is patchily distributed, both searching time and net energy gain become useful to assess patch profitability and prompt quitting the site. A logical consequence of the discreteness of energy intake was that in poor patches, where capture was rarer, the predator took longer to assess the local profitability than in rich patches where prey was frequently encountered, with consequent overuse of poor patches. This is in agreement with previous modelling work (Ward et al., 2000) showing that capture frequency affects learning rate. Because the forager expectation of patch profitability is influenced by the experience in the previously visited patches (Vásquez et al., 2006; Eliassen et al., 2007), the overuse of poor patches led to a low expectation of environmental profitability, with consequent overuse of all patches. When a predator overused a patch incurred in the so-called lost opportunity (LO) cost (Kohlmann and Risenhoover, 1998) by not moving to other undepleted patches. The energy cost of such inefficient forage led to marked oscillations in predator body mass and increased the death risk, mostly in scenarios with high heterogeneity of prey abundance, in agreement with Kohlmann and Risenhoover (1998) who note that the LO cost increases with the variance of environmental reward rate. In fact, when prey abundance is highly heterogeneous, the predator is likely to move from very poor to very rich patches and *vice versa* with inexact expectations of patch profitability and consequently this leads to their over- or underuse (Vásquez et al., 2006). Predictability of patch quality is a main decision factor for many terrestrial and marine predators (e.g. seabirds, Schneider, 1993; but see Weimerskirch et al., 2005; swans, Nolet et al., 2006a,b; seals, Sparling et al., 2007) and a negative effect of environmental heterogeneity on the ability to optimize patches exploitation is known from field studies (Valone and Brown, 1989; Laca, 2008).

A decrease of mean body mass and survival was evident in our model for scenarios of highly heterogeneous prey abundance mostly for predators with short memory properties. In fact, the predator's assessment of patch profitability was more sensitive to environmental variability and consequently it was not able to exploit the patches efficiently, as was demonstrated by the profitability-dependence of the time invested in patches. The predator ability to concentrate foraging efforts in more profitable patches increased with memory length. These results are consistent with previous studies (McNamara and Houston, 1985;

Valone, 1992; Nishimura, 1994; Hirvonen et al., 1999; Fortin, 2002), reporting that a higher consideration of old experience can be advantageous if patch profitability is stable over time, while a higher weight given to the experience of each food sampling event would make learning more sensitive to the natural variability and to sampling errors.

Unlike when prey abundance is heterogeneously spread, when prey body mass is heterogeneously distributed the predator body mass responded positively. In this case the time taken to assess the patch is the same for all patches because profitability assessment is carried out after food capture and processing, and prey abundance and handling rate were the same for all patches in the simulations. A quick evaluation of an unsatisfactory patch followed by the leaving decision on the one hand increased the commuting frequency with a subsequent higher energetic cost of exploration of different patches, on the other enabled the predator to exploit more profitable patches with an abatement of the LO costs. At high levels of heterogeneity of prey body mass, a better foraging performance arose from the trade-off between higher commuting efforts and lower LO costs. This is in agreement with Krakauer and Rodríguez-Gironés (1995) and Eliassen et al. (2007), reporting that the predator performance is related to the cost-benefit balance between exploring and exploiting the environment. In our case, a higher cost of commuting was compensated by a larger information sampling, providing on average an improved assessment of environmental profitability.

A realistic aspect of our approach was that it may represent how a predator can vary its foraging performance in environments with equal overall profitability but different patterns of prey body mass and abundance. Unlike single-rule based models (Bernstein et al., 1988; Eliassen et al., 2007), our modelling approach, by implementing two distinct behavioural rules based on both prey abundance and energy content, allowed us to fully investigate different conditions of environmental heterogeneity and their effects predator survival and fitness.

The models considering food intake as a continuous process (e.g. Bernstein et al., 1988, 1991; Grass and Roberts, 1992; Nishimura, 1994; Fortin, 2002; Nolet et al., 2006a,b) were unable to assess the dependence of foraging performance on different sources of intake variability.

In Bayesian forager models, resource intake is implemented as a discrete stochastic process, with foragers capable of instantaneous estimate of patch profitability (Rodríguez-Gironés and Vásquez, 1997; van Gils et al., 2003; Valone, 2006; McNamara et al., 2006). In this approach, decisions derived from Bayesian updating typically lead to higher fitness (Green, 1987; Valone, 2006) with modelled foragers exhibiting a positive density-dependence resource harvesting, and with the estimated environmental richness converging to the real values (Rodríguez-Gironés and Vásquez, 1997). In our model the reliability of the estimates of environmental profitability is affected by the stochasticity of the information acquisition process.

Further applications of the model are possible to improve the understanding of the interactions between forager behaviour, metabolism and resource pattern, as well as their effects on forager's fitness. The model could be, for example, a useful tool to achieve a better understanding of prey selection patterns in relation to predator body mass across different taxonomical groups or predator guilds.

References

- Basset, A., Fedele, M., DeAngelis, D.L., 2002. Optimal exploitation of spatially distributed trophic resources and population stability. *Ecol. Model.* 151, 245–260.
- Begon, M., Harper, J.L., Townsend, C.L., 1996. *Ecology: Individuals, Populations, Communities*, third ed. Blackwell Scientific Publications, Oxford, UK, pp. 733–734.
- Bernstein, C., Kacelnik, A., Krebs, J.R., 1988. Individual decision and the distribution of predators in a patchy environment. *J. Anim. Ecol.* 57, 1007–1026.
- Bernstein, C., Kacelnik, A., Krebs, J.R., 1991. Individual decision and the distribution of predators in a patchy environment. II. The influence of travel cost and structure of the environment. *J. Anim. Ecol.* 60, 205–225.
- Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates—patterns, problems, and the future. *Can. J. Zool.* 68, 203–220.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predator risk and competition. *Behav. Ecol. Sociobiol.* 22, 37–47.
- Caraco, T., Giraldeau, L.A., 1991. Social foraging: producing and scouring in a stochastic environment. *J. Theor. Biol.* 153, 559–583.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.
- Dall, S., Giraldeau, L.A., Olsson, O., McNamara, J.M., Stephens, D.W., 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* 20, 187–193.
- Dobson, F.S., Kjelgaard, J.D., 1985. The influence of food resources on life-history in Columbian ground squirrels. *Can. J. Zool.* 63, 2105–2109.
- Eliassen, S., Jørgensen, C., Mangel, M., Giske, J., 2007. Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. *Oikos* 116, 513–523.
- Fortin, D., 2002. Optimal searching behaviour: the value of sampling information. *Ecol. Model.* 153, 279–290.
- Grass, C.L., Roberts, W.M., 1992. The problem of temporal scale in optimization: three contrasting views of hummingbirds visit to flowers. *Am. Nat.* 140, 829–853.
- Green, R.F., 1987. Stochastic models of optimal foraging. In: Kamil, A.C., Krebs, J.R., Pulliam, H.R. (Eds.), *Foraging Behaviour*. Plenum Press, pp. 273–410.
- Hirvonen, H., Ranta, E., Rita, H., Peuhkuri, N., 1999. Significance of memory properties in prey choice decisions. *Ecol. Model.* 115, 177–189.
- Iwasa, Y., Higashi, M., Yamamura, N., 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.* 117, 710–723.
- Kohlmann, S.G., Risenhoover, K.L., 1998. Effects of resource distribution, patch spacing, and preharvest information on foraging decision of northern bobwhites. *Behav. Ecol.* 9 (2), 177–186.
- Krakauer, D.C., Rodríguez-Gironés, M.A., 1995. Searching and learning in a random environment. *J. Theor. Biol.* 177, 417–419.
- Kramer, D.L., 2001. Foraging behavior. In: Fox, C.W., Roff, D.A., Fairbairn, D.J. (Eds.), *Evolutionary Ecology: Concepts and Case Studies*. Oxford University Press, New York, pp. 232–246.
- Laca, E.A., 2008. Foraging in a heterogeneous environment. In: Prins, H.H.T., van Langevelde, F. (Eds.), *Resource Ecology: Spatial and Temporal Dynamics of Foraging*. Springer, pp. 81–100.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100, 603–609.
- Mangel, M., 1990. Dynamic information in uncertain and changing environment. *J. Theor. Biol.* 146, 317–332.
- McNamara, J.M., 1982. Optimal patch use in a stochastic environment. *Theor. Popul. Biol.* 21, 269–288.
- McNamara, J.M., Houston, A.I., 1985. Optimal foraging and learning. *J. Theor. Biol.* 117, 231–249.
- McNamara, J.M., Green, R.F., Olsson, O., 2006. Bayes' theorem and its application in animal behaviour. *Oikos* 112, 243–251.
- Moen, R., Pastor, J., Cohen, Y., 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78 (2), 505–521.
- Muetzelfeldt, R., Massheder, J., 2003. The Simile visual modelling environment. *Eur. J. Agron.* 18, 345–358.
- Nagy, K.A., 2005. Field metabolic rate and body size. *J. Exp. Biol.* 208, 1621–1625.
- Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. *Ann. Rev. Nutr.* 19, 247–277.
- Nishimura, K., 1994. Decision making of a sit-and-wait forager in an uncertain environment: learning and memory load. *Am. Nat.* 143, 656–676.
- Nolet, B.A., Fuld, V.N., van Rijswijk, E.C., 2006a. Foraging cost and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* 112, 353–362.
- Nolet, B.A., Klaassen, R.H.G., Mooij, W.M., 2006b. The use of a flexible patch leaving rule under exploitative competition: a field test with swans. *Oikos* 112, 342–352.
- Oaten, A., 1977. Optimal foraging in patches: a case for stochasticity. *Theor. Popul. Biol.* 12, 263–285.
- Olsson, O., Holmgren, N.M.A., 1999. Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. *Oikos* 87, 251–263.
- Olsson, O., Brown, J.S., 2006. The foraging benefits of information and the penalty of ignorance. *Oikos* 112, 260–273.
- Packard, G.C., Boardman, T.J., 2009. A comparison of methods for fitting allometric equations to field metabolic rates of animals. *J. Comp. Physiol. B* 179, 175–182.
- Peters, R.H., 1983. *Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Pettorelli, N., Gaillard, J.M., Duncan, P., Van Laere, G., Kjellander, P., Liberg, O., Delorme, D., Maillard, D., 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. *Proc. R. Soc. Lond. B.* 269, 747–753.
- Prop, J., Deerenberg, C., 1991. Spring staging in Brent geese *Branta bernicla*—feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87, 19–28.
- Pyke, G.H., 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15, 523–575.
- Rodríguez-Gironés, M.A., Vásquez, R.A., 1997. Density-dependent patch exploitation and acquisition of environmental information. *Theor. Popul. Biol.* 52, 32–42.
- Russo, D., 2002. Elevation affects the distribution of the two sexes in Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae) from Italy. *Mammalia* 66, 543–551.
- Schneider, D.C., 1993. Scale dependent spatial dynamics: marine birds in the Bering Sea. *Biol. Rev.* 68, 579–598.
- Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., Thomson, D., 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Anim. Behav.* 74, 207–218.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press.
- Valone, J.T., Brown, J.S., 1989. Measuring patch assessment abilities of desert granivores. *Ecology* 70, 1800–1810.
- Valone, T.J., 1989. Group foraging, public information and patch estimation. *Oikos* 56, 357–363.
- Valone, T.J., 1991. Bayesian and prescient assessment: foraging whit preharvest information. *Anim. Behav.* 42, 569–577.
- Valone, T.J., 1992. Information for patch assessment: a field investigation with black-chinned hummingbirds. *Behav. Ecol.* 3, 211–222.
- Valone, T.J., 2006. Are animals capable of Bayesian updating? An empirical review. *Oikos* 112, 252–259.
- van Gils, J.A., Schenk, I.W., Bos, O., Piersma, T., 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *Am. Nat.* 161, 777–793.
- Vásquez, R.A., Grossi, B., Márquez, I.N., 2006. On the value of information: studying changes in patch assessment abilities through learning. *Oikos* 112, 298–310.
- Voigt, C.C., Kelm, D.H., Visser, G.H., 2006. Field metabolic rates of phytophagous bats: do pollination strategies of plants make life of nectar-feeders spin faster? *J. Comp. Physiol. B* 176, 213–222.
- Wallis de Vries, M.F., Schippers, P., 1994. Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia* 100, 107–117.
- Ward, J.F., Austin, R.M., MacDonald, D.W., 2000. A simulation model of foraging behaviour and the effect of predation risk. *J. Anim. Ecol.* 69, 16–30.
- Weimerskirch, H., Gault, A., Cherel, Y., 2005. Prey distribution and patchiness: factors affecting the foraging success and efficiency of wandering albatrosses. *Ecology* 86, 2611–2622.
- White, C.R., Seymour, R.S., 2005. Allometric scaling of mammalian metabolism. *J. Exp. Biol.* 208, 1611–1619.
- Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science Ltd., Oxford, pp. 9–31.
- Yoshimura, J., Clark, C.W., 1991. Individual adaptations in stochastic environments. *Evol. Ecol.* 5, 173–192.