

How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake

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Animals often alternate between searching for food locally and moving over larger distances depending on the amount of food they find. This ability to switch between movement modes can have large implications on the fate of individuals and populations, and a mechanism that allows animals to find the optimal balance between alternative movement strategies is therefore selectively advantageous. Recent theory suggests that animals are capable of switching movement mode depending on heterogeneities in the landscape, and that different modes may predominate at different temporal scales. Here we develop a conceptual model that enables animals to use either an area-concentrated food search behavior or undirected random movements. The model builds on the animals' ability to remember the profitability and location of previously visited areas. In contrast to classical optimal foraging models, our model does not assume food to be distributed in large, well-defined patches, and our focus is on animal movement rather than on how animals choose between foraging patches with known locations and value. After parameterizing the fine-scale movements to resemble those of the harbor porpoise *Phocoena phocoena* we investigate whether the model is capable of producing emergent home ranges and use pattern-oriented modeling to evaluate whether it can reproduce the large-scale movement patterns observed for porpoises in nature. Finally we investigate whether the model enables animals to forage optimally. We found that the model was indeed able to produce either stable home ranges or movement patterns that resembled those of real porpoises. It enabled animals to maximize their food intake when fine-tuning the memory parameters that controlled the relative contribution of area concentrated and random movements.

What enables animals to respond optimally to the plethora of environmental conditions that they are exposed to during their lives? The answer to this question is partly linked to their selection of foraging strategies, which is one of the central topics in behavioral ecology (Schoener 1971, Krebs and Davies 1984). Recent studies suggest that animals are capable of switching among different canonical movement modes depending on their internal state, environmental factors and physiological constraints on their movement (Fryxell et al. 2008, Nathan et al. 2008). Different movement modes tend to characterize behavior at different spatial and temporal scales (Morales et al. 2004, Fryxell et al. 2008, Owen-Smith et al. 2010), but the mechanisms that control the behavioral shifts are poorly understood.

Much of the theory of animal movement is based on the premises that individuals attempt to optimize their foraging behavior by selecting among alternative resource patches (Bartumeus and Catalan 2009). Several studies have discussed how foraging is influenced by cognitive processes, and particularly how an individual's behavior reflects its ability to remember favorable patches from previous visits and to navigate back to them (Tan et al. 2002, Gautestad and Mysterud 2005, Van Moorter et al. 2009). The cost of

moving to different food patches has also been incorporated in numerous optimal foraging models (Griffiths 1980, Mitchell and Powell 2004, Matsumura et al. 2010). In addition it is increasingly recognized that landscape composition affects animal movement (Bowne and Bowers 2004, Hengeveld et al. 2009, McNamara and Houston 2009, Humphries et al. 2010). The present study extends existing theory of optimal foraging by shifting the focus from which patches animals should select in order to forage optimally. Instead we discuss how food intake can be increased through the choice of fine-scale movement mode for animals that continuously move through a landscape comprising a large number of small food patches. Which movement mode is optimal depends on the spatial distribution and amount of food found in the patches.

Animal movement has frequently been modeled using correlated random walk (CRW) models (Turchin 1998, Morales et al. 2004, Bartumeus et al. 2005, Getz and Saltz 2008) where turning angles are correlated. Such models have been used to faithfully reproduce the fine scale movements for a large number of species, particularly in homogeneous environments (Turchin 1998, Morales et al. 2004), and CRW behavior has sometimes been interpreted

as the by-product of locally scanning the environment for food (Bartumeus et al. 2005). One disadvantage of CRW models is that they result in animals that gradually move further away from their starting point, which renders them unsuitable for generating the home ranges found in many species (Solow 1990, Börger et al. 2008). Most often such home range behavior has been modeled by forcing animals to stay within particular resource patches or to be central place foragers (reviewed by Börger et al. 2008). This is inappropriate for species whose movements are not constrained to particular patches and that do not have to return to the same place repeatedly. An alternative is to introduce a spatial memory which can enable animals to remain within stable home ranges (Van Moorter et al. 2009). Here we build on this approach by allowing individuals to use a combination of undirected food search (CRW) and a memory-based tendency to return to places they have been before. By letting the relative contribution of the two types of behavior depend on how profitable animals expect them to be the model permits them to adjust their behavior according to local variations in food availability.

In order to demonstrate how this novel conceptual framework can be used to generate realistic movement tracks, we parameterized the model for harbor porpoises *Phocoena phocoena* using data collected in the inner Danish waters. Porpoises often have well-defined home ranges that last for several weeks or months, although they sometimes switch behavior and move to new areas (Nabe-Nielsen et al. unpubl.). Porpoises feed on a wide range of fish species (Börjesson et al. 2003) and although the spatial distribution of their prey is largely unknown in the study area, it is presumably related to patchy environmental features such as reefs, eelgrass beds and upwelling zones (Schneider et al. 2008, Laidig et al. 2009, Reese et al. 2011). This suggests that a foraging model based on movement between small food patches may be realistic for porpoises. The model we present here incorporates all available data on animal movements in order to produce realistic movement patterns for the harbor porpoise, yet it is sufficiently simple and general to be applicable for a wide range of species. We investigate whether the model allows stable home ranges to emerge and if it can reproduce the large-scale movement patterns of real porpoises based on a combination of undirected CRW behavior and spatial memory behavior. We conclude the paper by evaluating whether animals can maximize their food intake by adjusting the balance between the two alternative movement modes in the model. As this is the case the model supports the idea that it can be evolutionarily advantageous even for animals in complex environments to base their foraging behavior on a few, simple mechanisms.

Methods

Model overview

Movement results from two different mechanisms in our model: an intrinsic exploratory behavior and an ability to move towards previously visited food patches. We model the intrinsic behavior as a correlated random walk (CRW)

and let the ability to return to previously visited patches be controlled by a spatial memory. Here the relative importance of the two movement modes is controlled by the animal's expected benefit of using each of them.

The direction of the move \mathbf{s}_t from time t to time $t + 1$ is calculated from the sum of two vectors corresponding to the two terms in the equation

$$\mathbf{s}_t^* = \mathbf{x}_t(k + E_t) + \sum_c R[c]_t \mathbf{i}[c]_t \quad (1)$$

where the first term represents a weighed CRW and the second represents a spatial memory move. The animal's tendency to move according to the CRW depends on a short-term memory of how much food it has eaten in the recent past, that is, how satiated it is, and a constant k . Here k can be interpreted as the animal's tendency to keep moving following its intrinsic behavior irrespective of the amount of food acquired. The unweighed correlated random walk move is described by the vector \mathbf{x}_t .

The animal's tendency to move towards previously visited food patches depends on how profitable it expects it to be to return to each of them, $R[c]_t$. The $\mathbf{i}[c]_t$ are unity vectors pointing towards each of the locations the animal has visited in the past. The sum of the individual attraction vectors is a vector that points towards the area that the animal expects to be most rewarding based on previous experiences. Equation 1 can be normalized as

$$\mathbf{s}_t = \frac{\|\mathbf{x}_t\|}{\|\mathbf{s}_t^*\|} \times \mathbf{s}_t^* \quad (2)$$

in order to ensure that the length of \mathbf{s}_t and movement speed are unaffected by the animal's past foraging success. Here $\|$ denotes the Euclidean norm.

Resource dynamics and landscape representation

The landscape we used for the simulations included small food patches that animals usually passed through in a single time step, but no other sources of environmental variation. The landscape was infinite, but composed of identical blocks that all covered 1000×1000 grid cells. Each block contained 1000 randomly distributed, diamond-shaped food patches, each covering 13 cells (the effect of patch size on foraging behavior was explored in the Supplementary material Appendix 1).

Initially all cells in the food patches had the same value, or utility ($U = U_{\max}$), but when an animal entered a cell it consumed all the food found there. In this study the maximum cell value U_{\max} was set to 1 for all patches. After the animal moved out, the value of the cell increased logistically until food was replenished:

$$U[c]_{t+1} = U[c]_t + r_U \times U[c]_t \left(1 - \frac{U[c]_t}{U[c]_{\max}} \right) \quad (3)$$

For a resource growth rate $r_U = 0.2$ food was replenished after approximately two days (Supplementary material Appendix 1 Fig. A1). The logistic growth function assumes that the prey populations gradually recover until reaching carrying capacity. It is often suitable for describing recovery

in both biological and physical systems (Garrett 2012). Cells outside the food patches had $U=0$.

Assessing the benefit of returning to previously visited food patches

An animal's expectation of how profitable it would be to return to a place where it has been before, $R[c]_t$, is modeled to depend on its ability to remember the place, $M_R[c]_t$, but also on how much food it found there, $U[c]$, and how costly it would be to return to it. We use the same approach as Mitchell and Powell (2004) and Van Moorter et al. (2009) and let this cost increase linearly with distance $D[c]$,

$$R[c]_t = \frac{M_R[c]_t \times U[c]}{D[c]_t} \quad (4)$$

where $D[c] > 1$. Both $U[c]$ and $D[c]$ could be measured in terms of the amount of energy used or obtained, and $M_R[c]$ is unitless. The animal's ability to remember places is modeled using a spatial memory, or reference memory, M_R . We let M_R decrease logistically with time, following Van Moorter et al. (2009),

$$M_R[c]_{t+1} = M_R[c]_t - r_R \times M_R[c]_t \times (1 - M_R[c]_t) \quad (5)$$

where the shape of the logistic curve is determined by the reference memory decay rate, r_R .

Assessing the benefit of using an undirected search for food

Theoretical work indicates that random walks (in particular Lévy walks) may increase an animal's likelihood of encountering food in sparse environments with randomly distributed food patches (Viswanathan et al. 2008). A CRW introduces a directional persistence (Bartumeus et al. 2005) that may be beneficial to animals that would otherwise risk returning to patches where they have eaten all the food. This movement mode could therefore be the default choice for animals living in landscapes with small, randomly distributed food patches, although their tendency to keep following this behavior should decrease if it does not allow them to find food for some time. In our model we let the animals' memory of the food they have found in the recent past be determined by the short-term satiation memory, M_S . We let M_S decay following the same logistic equation as M_R (Eq. 5), but let its shape be controlled by the satiation memory decay rate, r_S , where $r_S \geq r_R$. The animal's expectation of how profitable it is to move at random can then be described as

$$E_t = \sum_c M_S[c]_t \times U[c] \quad (6)$$

Correlated random walk model

An animal that exclusively follows its intrinsic behavior moves the step \mathbf{x}_t during the period t to $t+1$. Here all time steps have the same length. We let the distance moved

during this time step, δ_t , correlate positively with the distance moved in the previous time step,

$$\delta_t = R_1 + a\delta_{t-1} \quad (7)$$

Further, we let the turning angle ψ_t at time t be negatively correlated with the previous turning angle and with distance moved when $\delta_{t-1} < m$,

$$\psi_t = \begin{cases} R_2 - b\psi_{t-1} + R_3 \left(1 - \frac{\delta_{t-1}}{m}\right) & \text{if } \delta_{t-1} < m; \\ R_2 - b\psi_{t-1} & \text{if } \delta_{t-1} \geq m. \end{cases} \quad (8)$$

When animals move $\geq m$ per time step the turning angle becomes small and relatively constant, which we observed to be the case for porpoises (Supplementary material Appendix 2 Fig. A6). Here δ_{t-1} indicates the distance moved just before the turn ψ_t , a , b and m are positive constants, $R_1 - R_3$ are stochastic variables and t is time. This model is more complex than standard CRW models, which permits it to be employed even for animals that tend to turn less steeply when moving faster. We explore the implications of using a standard CRW in Supplementary material Appendix 2 Table A2.

Parameterization of harbor porpoise movement in simulation model

In order to test whether our model was capable of producing realistic movement patterns, we conducted a simulation study based on data for harbor porpoises in the inner Danish waters. First we parameterized the CRW model using information about the fine-scale movements of a single porpoise individual collected using dead-reckoning instruments (Wilson et al. 2007). The animal was equipped with a speed sensor, pressure sensors and a 3D-compass. Output from these instruments were recorded every 6 s over a 17.5-h period where the animal was swimming on water depths of 1–20 m in Great Belt, Denmark. Subsequently a detailed movement track was produced by path integration.

We analyzed the autocorrelation structure of δ (\log_{10} of distance moved per 30-min) and ψ (turning angle) in the dead-reckoning dataset (Supplementary material Appendix 2 Fig. A4) as well as the relationship between δ and ψ (Supplementary material Appendix 2 Fig. A5). Although the choice of using a 30-min time step was arbitrary, it was guided by the observation that real animals must adjust their swimming direction at least every 30-min in order to avoid land (Nabe-Nielsen unpubl.).

The parameters a , b , m and $R_1 - R_3$ (Eq. 7–8) were obtained by iteratively fitting a version of the simulation model that included only the CRW component until it was able to reproduce the autocorrelation structure observed in the dead-reckoning data (Supplementary material Appendix 2 Fig. A6) when letting each cell in the landscape represent 100×100 m in a natural landscape. The fitting of the CRW model to the dead-reckoning data assumes that the tagged animal was not actively moving towards previously visited foraging grounds (see details in Supplementary material Appendix 2). A visual inspection of its movement track suggested that this was indeed the case. Only values $R_1 < 1.18$ were accepted in the simulations, which ensured

that the model animals never moved further per 30-min interval than the tracked animal. Although the fine-scale movement patterns are likely to vary among porpoise individuals the importance of such variations on the simulated large-scale movement patterns was not explored here.

Both the pure CRW model and the model that also included r_R and r_S were implemented in NetLogo 4.1.2 (Wilensky 1999). The distance moved per 30-min step, the turning angles after each step and the animals' x and y coordinates were continuous variables.

Evaluating the model fit using pattern-oriented modeling

In order to evaluate whether different memory decay rates allowed home ranges to emerge and if they resulted in realistic tracks we ran simulations using a wide range of r_R and r_S combinations for three different values of r_U (Table 1). Each parameter combination was used for producing one simulation, and the simulated tracks were compared with those of satellite-tracked porpoises. Each simulation ran for 15 000 time steps, resulting in 313 daily positions (with one position for every 48 time steps).

The analyses of both simulated tracks and those of satellite-tracked animals were based on three different statistics; residence times, net displacement distances and kernel density home range estimates. Residence time is the average amount of time an animal spends within circles of a given radius drawn around each position in a track. It characterizes shifts between localized behavior and more directed movements (Barraquand and Benhamou 2008). In this study the residence times were calculated on basis of circles with a radius of 5 km. This radius was the smallest possible that yielded estimates without abrupt peaks (Nabe-Nielsen unpubl.). The net displacement distances were the total distance moved since the start of the track, measured in a straight line (Dray et al. 2010). The size of the home ranges was estimated using the least squares cross validation method as recommended by Seaman et al. (1999).

Calculations were done using the adehabitat package (Calenge 2006) in R (R Development Core Team) for the 50% isopleth, which yields robust estimates even with relatively low sample sizes (Börger et al. 2006). Tracks were characterized as producing stable home ranges if they resulted in displacement distances that reached an asymptotic value.

In order to evaluate whether a given combination of r_R and r_S resulted in realistic tracks we adopted the pattern-oriented modeling approach (Wiegand et al. 2003, Grimm et al. 2005, Grimm and Railsback 2012). This approach can be used for parameterizing simulation models by comparing a set of system-level patterns emerging from a model to the corresponding real-world patterns (Kramer-Schadt et al. 2007). We used the following patterns for comparing real and simulated tracks: mean residence times, maximum net displacement distances within the first 80 days of each track and home range sizes calculated for the first 80 days of each track. As the model did not include land, the simulated tracks were compared to those of real animals that were on the average > 6 km from land. Approximate 95% confidence intervals were calculated for each pattern as the mean ± 2 SE based on tracks of real animals. Before calculating the confidence intervals the mean residence times and home range sizes were \log_{10} transformed to achieve normality. Simulated tracks were characterized as reproducing a pattern from the satellite-tracks when the mean value for the simulation fell within the confidence interval calculated from the satellite-tracks.

Data on the movement of real porpoises

Movement tracks were obtained for real porpoises that had been tracked in Kattegat, the Belt Sea and the western Baltic Sea (the inner Danish waters) using Argos satellite transmitters. Data was available for 44 animals from April 1997–May 2009 (Sveegaard et al. 2011), but only 34 individuals with data for ≥ 30 days and with $\geq 80\%$ of the positions separated by < 3 days were used here. The precision of the

Table 1. List of parameters in the simulation model and their biological interpretation. $N(x, y)$ signifies a normally distributed stochastic variable with mean x and standard deviation y . Source indicates whether parameter estimates were fixed, obtained using pattern oriented modeling (POM) or estimated from dead-reckoning data (DR; Supplementary material Appendix 2). The effects of changing the parameters r_U and p were explored in Fig. 4 (r_U), Fig. 5 (p) and in the Supplementary material Appendix 1.

Parameter	Source	Value range	Description
r_S	POM	0.05, 0.06, 0.07, ..., 0.12	Satiation memory decay rate; determines how fast the animals get hungry after eating.
r_R	POM	0.05, 0.10, 0.15, 0.20, 0.25, 0.50	Reference memory decay rate; determines how fast the animals forget the location of previously visited food patches.
r_U	Fixed	0.002, 0.02, 0.2	Resource growth rate; the rate that food recovers with after being eaten.
U_{\max}	Fixed	1	Maximum patch utility; highest possible value of a cell.
k	Fixed	0.001	Inertia constant; the animal's tendency to keep moving using CRW irrespective of foraging success.
p	Fixed	1, 5, 9 or 13 cells	Number of grid cells per patch.
a	DR	0.94	Autocorrelation constant for $\log_{10}(d/100)$ where d is distance moved [m] per 30 min.
b	DR	0.26	Autocorrelation constant for turning angles.
m	DR	0.74	Limit for when turning angles stop decreasing with speed.
R_1	DR	$N(0.42, 0.48)$	\log_{10} distance moved per time step (mean ± 1 SD).
R_2	DR	$N(0, 38)$	Turning angles between steps (mean ± 1 SD).
R_3	DR	$N(96, 28)$	Parameter controlling relationship between turning angles and step length (Eq. 8).

recorded satellite positions was highly variable due to variations in the number of received satellite uplinks and signal quality. We therefore used the SAS Argos-Filter ver. 7.03 (D. Douglas, USGS, Alaska Science Center, Alaska, USA) to eliminate the most deviant positions from the tracks before calculating residence times.

Testing for optimal foraging behavior

We tested whether an adjustment of the balance between undirected random movements and area-concentrated food search behavior allowed the simulated animals to maximize their food intake. If the food intake is highest for intermediate values of B in the equation

$$\mathbf{s}_t^* = \mathbf{x}_t(k + E_t) + B \sum R[c_t] \mathbf{i}[c_t] \quad (9)$$

it indicates that animals can optimize their foraging behavior by finding the right balance between the two movement types.

We tested whether this was the case by running 96 simulations for each landscape (with 1, 5, 9 and 13 cell food patches), with values of B ranging from 5–160. In this analysis we used a combination of memory decay rates that could reproduce the patterns observed in nature and where the satiation memory at the same time decayed faster than the reference memory ($r_R = 0.10$ and $r_S = 0.15$; Table 2, A1). Here r_U was set to 0.2, which permitted resources to replenish in a patch before the animals forgot its location

Table 2. Patterns corresponding to tracks simulated with different r_S and r_R values and $r_U = 0.2$. The patterns were Res t: Mean \log_{10} residence time; Disp: Maximum displacement distance within the first 80 days; HR: \log_{10} kernel home range size. The satellite-track mean $\pm 2 \times \text{SE}$ is provided. Patterns were accepted if the simulated values fell within this range (indicated with T). Count indicates the number of patterns that were accepted. Count values are underlined where the short-term satiation memory diminished as fast or faster than the long-term spatial memory.

Parameters			Simulated values			From satellite tracks			Acceptable			
r_S	r_R	$r_S \geq r_R$	Res t	Disp	HR	Res t	Disp	HR	Res t	Disp	HR	Count
0.05	0.05	T	0.461	119.5	3.41	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T		T	<u>2</u>
0.05	0.06		0.469	152.3	3.35	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T	T	T	3
0.05	0.07		0.468	196.2	3.54	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T	T	T	3
0.05	0.08		0.535	172.5	3.39	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45		T	T	2
0.05	0.09		0.539	105.2	3.33	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45			T	1
0.05	0.10		0.511	154.0	3.31	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T	T	T	3
0.05	0.11		0.533	85.5	3.15	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.05	0.12		0.458	150.3	3.22	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T	T	T	3
0.10	0.05	T	0.557	65.8	3.16	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.10	0.06	T	0.528	61.8	3.18	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.10	0.07	T	0.592	73.8	3.08	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.10	0.08	T	0.420	110.5	3.33	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T		T	<u>2</u>
0.10	0.09	T	0.634	222.5	3.63	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45		T	T	<u>2</u>
0.10	0.10	T	0.471	171.8	3.46	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T	T	T	<u>3</u>
0.10	0.11		0.450	53.8	3.13	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T			1
0.10	0.12		0.597	156.1	3.51	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45		T	T	2
0.15	0.05	T	0.696	54.4	2.87	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.06	T	0.547	98.6	3.19	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.07	T	0.670	83.8	3.04	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.08	T	0.724	113.0	3.05	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.09	T	0.521	95.3	3.18	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.10	T	0.500	89.1	3.27	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45	T		T	<u>2</u>
0.15	0.11	T	0.559	82.2	3.19	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.15	0.12	T	0.583	140.6	3.38	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45		T	T	<u>2</u>
0.20	0.05	T	0.776	51.8	2.79	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.06	T	0.710	86.8	2.86	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.07	T	0.633	111.8	3.10	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.08	T	0.756	72.2	2.83	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.09	T	0.594	125.7	3.18	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.10	T	0.632	75.2	2.76	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.11	T	0.551	63.9	2.90	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.20	0.12	T	0.534	99.1	3.30	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45			T	1
0.25	0.05	T	0.853	68.1	2.62	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.06	T	0.987	57.5	2.65	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.07	T	0.796	85.7	2.88	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.08	T	0.680	60.8	2.73	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.09	T	0.667	66.6	2.96	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.10	T	0.648	40.3	2.78	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.11	T	0.671	90.9	3.03	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				
0.25	0.12	T	0.597	86.7	3.03	0.38 ± 0.14	195.9 ± 69.2	3.66 ± 0.45				

(Supplementary material Appendix 1 Fig. A1). All simulations ran for 15 000 time steps.

Results

Effects of variations in memory decay rates on home range emergence

The simulated animals displayed behaviors ranging from area concentrated movements to gradual movements away from their starting point depending on their ability to remember previously visited food patches. The area concentrated movements (*sensu* Benhamou 1992) occurred when animals increased their search effort in a particular area by biasing their moves towards patches where they previously found food. The most area-concentrated movements, and hence the most stable home ranges, were observed when animals rapidly lost memory of the food they had recently encountered (i.e. high r_S) while remembering positions of patches where they found food some time ago (i.e. low r_R) (Fig. 1, Supplementary material Appendix 1 Table A1). This caused their displacement distances to reach asymptotic values after approximately 150 days (Fig. 1; $r_S = 0.5$). These animals moved only 40–80 km from their starting point and had residence times in the range 13–26 days, indicating that they kept returning to a small number of patches for a long time.

The persistence of the home ranges was affected by the resource growth rate and by the size of the food patches. Residence times were generally long in landscapes where food replenished rapidly (with high r_U ; Supplementary material Appendix 1 Table A1) and where animals would therefore keep finding food when returning to the same patch repeatedly. In landscapes with smaller patches (but with the same number of patches) animals found less food during each visit to a particular patch. Here the residence times were relatively short, indicating that animals were less likely to return to a patch they had recently visited.

Memory decay rates producing realistic movement patterns

The model was capable of producing displacement patterns similar to those observed for porpoises in nature (Fig. 1, 2) and to simultaneously reproduce the three quantitative patterns that were calculated for the satellite-tracked animals (Table 2). The simulation model reproduced the residence times observed for real animals far from land (Fig. 3) when using low values of r_S combined with a wide range of r_R values in landscapes where food replenished after approximately two days ($r_U = 0.2$; Fig. 4). Tracks produced using these parameters were nearly indistinguishable from real porpoise tracks (Supplementary material Appendix 1 Fig. A2, A3). The model produced realistic residence times for a wider range of parameter combinations if food

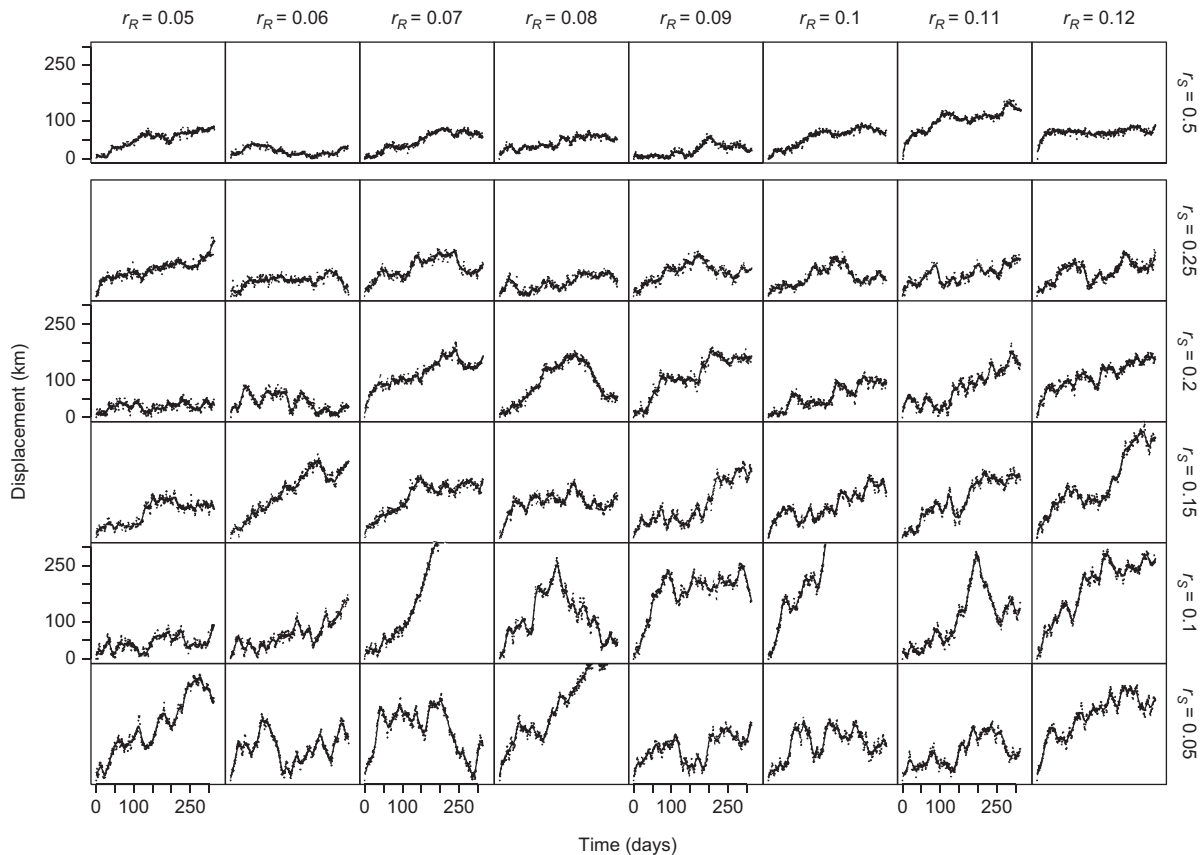


Figure 1. Displacement distances in tracks simulated using different combinations of r_R and r_S . One position is shown per day. Based on landscape with 13 cell patches and $r_U = 0.2$.

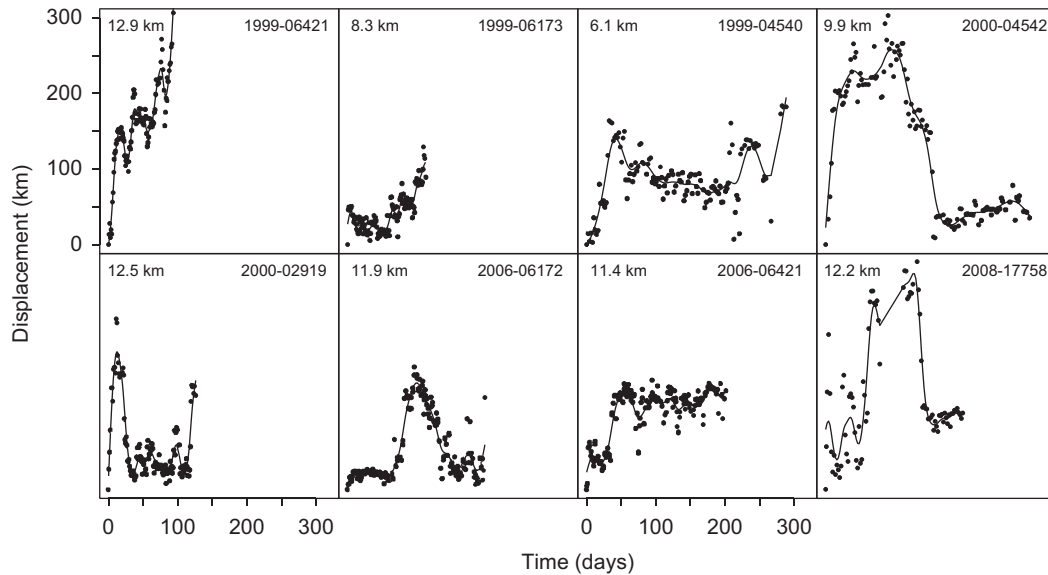


Figure 2. Displacement distances for the eight satellite-tracked porpoises with ≥ 80 daily positions that were observed at average distances > 6 km from the coast. The year of tagging, tag number and average distance to land is shown in top of each panel.

replenished after ~ 100 days ($r_U = 0.002$) than when food replenished more rapidly.

Realistic maximum displacement distances and home range sizes could be generated for a range of r_S and r_R values (Table 2). Realistic displacement distances were only found for $r_S \leq 0.10$ whereas realistic home ranges could be produced for a wide range of parameter combinations. Nearly all the satellite-tracked animals displaced 100–300 km during a period of six months, and most of them occasionally moved back towards the place they came from (Fig. 2). Similar patterns were found for animals simulated using $r_S \leq 0.10$.

Due to the stochastic nature of the simulations none of parameter combinations could ensure that realistic values were always produced for the three emergent patterns investigated in this study. All three patterns were often matched simultaneously when $r_S = 0.05$ for a wide range of r_R -values. The simulated tracks occasionally reproduced more than one of the patterns observed for real animals when $r_S \leq 0.15$ and $r_R \geq 0.1$ (Table 2).

Parameters characterizing intrinsic behavior in harbor porpoises

After calibrating the correlated random walk behavior in the model it was able to reproduce the fine-scale movements observed in nature. The autocorrelation structure for distance moved per time step and for turning angles resembled those observed in the dead-reckoning data (Supplementary material Appendix 2 Fig. A4, A5). At the same time the model produced the relationship between turning angle and movement speed observed in nature (Supplementary material Appendix 2 Fig. A6). The parameters controlling autocorrelation in the distance moved per time step (a and R_1) and in turning angles (b , m , R_2 and R_3) are presented in Table 1. The value of m indicates that turning angles stop decreasing with distance moved when animals move > 0.55 km per half-hour step.

Optimizing foraging behavior

The food intake was highest when the simulated animals used a combination of correlated random walk behavior and memory-based behavior (Fig. 5). The model therefore enables animals to optimize their foraging behavior. For $r_U = 0.2$ the highest food intake was attained for $B \sim 40$ in landscapes with food patches covering 1–13 cells. Tracks produced with this B -value were highly area-concentrated, as animals repeatedly returned to the same few patches (the mean residence time was 19.6 days when patches covered 5 cells and 15.6 days when they covered 13 cells). A similar movement track could be obtained for a B -value of 1 using a combination of high r_S and low r_R values.

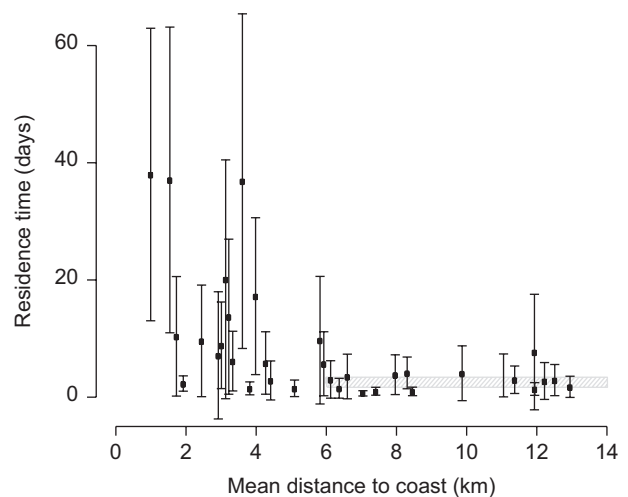


Figure 3. Residence time ± 1 SD vs mean distance to coast for satellite-tracked porpoises. Each point is based on 26–242 daily positions for a single animal. Porpoises that were on the average > 6 km from land had mean residence times = 2.9 days. The hatched area corresponds to the confidence interval calculated for \log_{10} residence time.

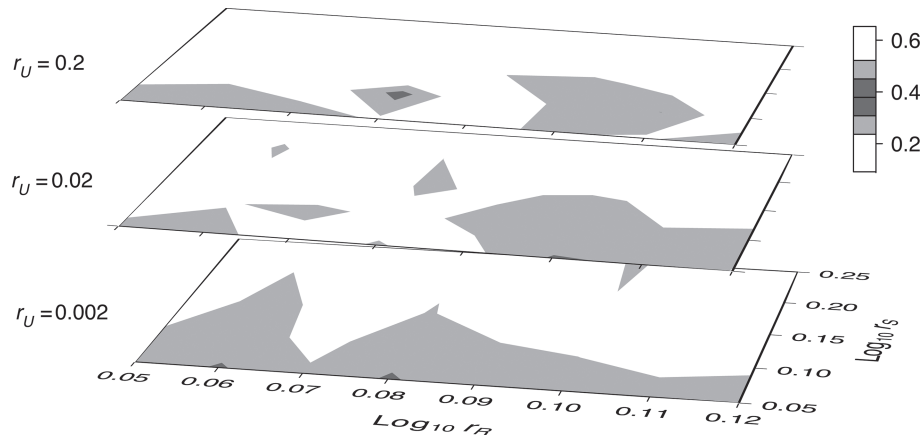


Figure 4. Mean residence time for simulated porpoises with different reference and satiation memory decay rates (r_R and r_S). Light grey cells correspond to values falling within the confidence interval calculated for satellite-tracked animals and dark grey cells to those falling within the mean ± 1 SE. The data used for creating the figure are provided in Supplementary material Appendix 1 Table A1.

Discussion

There is a growing awareness that animal movement may result from different mechanisms acting on different spatial and temporal scales (Fryxell et al. 2008, Nathan et al. 2008). The model we present here incorporates a mechanism that operates at fine spatial and temporal scales (intrinsic behavior, modeled with a correlated random walk, CRW) as well as a cognitive process ($\sum R \times i$ in Eq. 1). This cognitive process enables animals to cope with variations in food densities at coarser scales and to return to areas they remember to possess food when they are incapable of finding food by walking at random. In nature such an ability to switch between alternative feeding strategies is likely to be prevalent. The black-tailed deer *Odocoileus hemionus*, for example, has been observed to switch between local foraging for scattered food items and more extended movements in search for new feeding grounds (Gillingham et al. 1997), and sable antelopes *Hippotragus niger*

(Owen-Smith et al. 2010) are forced to relocate frequently during winter when local food resources rapidly deplete. Similarly, Nakamura (1985) demonstrated how ladybird beetles search for food within a relatively limited area for some time after encountering high-quality prey.

Our model is capable of generating emergent home ranges, which is evident from the low and relatively constant displacement distances that are attained after approximately 150 days for high r_S values (Fig. 1) as well as from the high residence times for these tracks. Such home ranges cannot be achieved with simple random walk models (Börger et al. 2008), and nearly all other models with an ability to produce home ranges have introduced reflecting patch boundaries or central place foraging in order to do so (Stamps and Krishnan 1999, Moorcroft and Lewis 2006). The home ranges generated in our model are most stable when animals rapidly lose the memory of the food they have recently found (high values of r_S). This causes them to avoid using the intrinsic exploratory behavior, which, as far as they can remember, has not enabled them to find food recently. Instead their movements are governed by their attraction to previously visited food patches, and in particular to the ones nearby. In landscapes with small food patches or where food replenished slowly, the animals found less food in each patch. This caused them to be less attracted to previously visited patches and to have less stable home ranges, as evidenced by the shorter residence times. These results demonstrate that very simple mechanisms are sufficient to enable animals to stay within a home range, even in landscapes with a large number of minute food patches that they continuously have to move between. As the dynamics of animal populations are often intricately linked to the individuals' ability to stay in profitable areas (Armsworth and Roughgarden 2005, Bowler and Benton 2005, Nabe-Nielsen et al. 2010), the model may also improve our ability to simulate population dynamics based on realistic behavioral mechanisms.

The realism of the model presented here is underlined by its ability to produce movement tracks that closely resemble those of satellite-tracked harbor porpoises. A pattern-oriented modeling approach revealed that the model was

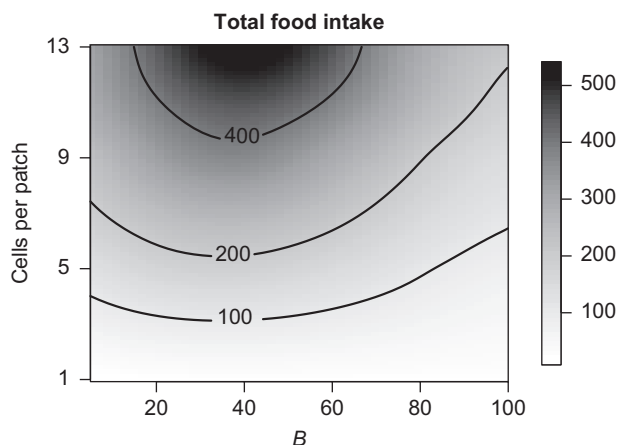


Figure 5. Maximizing food intake by shifting the balance between CRW and spatial memory behavior (see Eq. 9 for a definition of B) for landscapes with patches of different sizes. The difference in shading indicates total food consumed over 15000 steps and with $r_U = 0.2$.

capable of simultaneously reproducing the residence times, displacement distances and home range sizes observed for real animals, while using a CRW to faithfully reproduce the animals' fine-scale movements. There were, however, aspects of porpoise movement that the model could not reproduce. The satellite-tracked animals with the lowest residence times (< 1.5 days), for example, had highly directional movements that could not be generated by our model without modifying the underlying CRW behavior. Similarly, the model did not produce as large variation in residence times as observed for real animals. These presumably responded to local variation in food availability, disturbances, oxygen depletion or other physical parameters that were not included in the model. Some of the differences between the simulated and real animals may also result from the limitations associated with using a two-dimensional model for describing the movements of a species that lives in a three-dimensional environment. The large variation in the residence times of real porpoises may, for example, be related to limits to how far an animal can move horizontally when diving deep, something that is not considered in the model. One way to modify the model to make it more suitable for diving mammals might be to include the cost of diving explicitly in Eq. 4 by adding it to D_r . Such a model could result in a more realistic representation of the movements, but only when including realistic variations in bathymetry. When more data becomes available the simulated behavior could be made more realistic by letting the fine-scale movements differ among animals and with bathymetry in the same way as in nature. Currently the robustness of the fine-scale movement model is not known.

The spatial memory, which enables animals to remain within a limited area, has been incorporated in several other models (Folse et al. 1989, Mitchell and Powell 2004, Van Moorter et al. 2009). The model by Van Moorter et al. (2009) was movement-based and able to generate home ranges, and can therefore be compared directly to the one we present here. Both models include a spatial reference memory that allows animals to return to previously visited areas. The models differ in that the animals' tendency to be random walkers is constant in their model, whereas we let it depend on the amount of resources they have been able to acquire by walking at random (through E_r). Instead of E_r , Van Moorter et al. introduce a logistically decreasing 'working memory' (M_w) that serves to delay the animals' tendency to return to places where they previously found food (by multiplying a term equivalent to $R[c]$, in our model with $1 - M_w$). Further, Van Moorter et al. rescale the patch values to sum to one. In the hypothetical example where an animal has previously only visited one patch with food, this rescaling would cause it to be attracted to that patch with the same strength no matter how far away it is. We consider this unrealistic, but it is likely that the rescaling is needed in their model in order to enable it to generate home ranges. The model we present here differs from the one presented by Van Moorter et al. (2009) in building upon clearly separated and easily interpretable mechanisms (hunger and spatial memory) and in its ability to produce movement tracks that closely resemble those of real animals.

The model presented here allows animals to maximize their food intake by shifting the balance between walking at random and using a spatial memory when foraging. It differs from classical optimal foraging models in that animals choose between alternative movement strategies rather than between alternative patches. In the classical models animals decide to leave a patch based on knowledge of the alternative patches: They leave when the food acquisition rate becomes lower than the one they expect to get elsewhere (Charnov 1976, Krebs and Kacelnik 1991, Mitchell and Powell 2004, Bartumeus and Catalan 2009). In our model the animals repeatedly leave the highly profitable, but small, patches they encounter. The model is likely to be suitable for animals that behave like cows that walk at their own pace as long as they find food here and there, but that turn towards other foraging grounds if they start getting hungry. In contrast to the classical optimal foraging models our model provides animals with a mechanism that enables them to leave a food patch without having any explicit knowledge about the food levels elsewhere in the landscape.

Our study demonstrates that a simple model where animal movement results from a combination of two different biologically realistic foraging strategies is sufficient to produce movement patterns that strikingly resemble the ones we observe in nature, even for a complex organism like the harbor porpoise. McNamara and Houston (2009) suggested that many species are exposed to such a variety of environmental conditions that they are unlikely to have evolved different behavioral responses for every one of them. Instead their movement may reflect simple mechanisms that allow them to adapt to changing environmental conditions. The model we present here illustrates that very simple mechanisms are, indeed, all that is needed to produce realistic movement tracks and allow animals to optimize their foraging behavior.

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Supplementary material (available online as Appendix oik-00069 at <www.oikosoffice.lu.se/appendix>). Appendix 1 and 2.