From randomness to traplining: a framework for the study of routine movement behavior

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INTRODUCTION

The eco-evolutionary interface between memory and movement has recently received much theoretical attention (van Moorter et al. 2009; Schlägel and Lewis 2014; Riotte-Lambert et al. 2015, see also Fagan et al. 2013). Despite conceptual advances and the opportunities offered by the improvement of tracking technologies, ecologists willing to address this topic are limited by the small analytical toolbox available to them. Currently, only a few statistical models allow gaining insights on the importance of memory in driving animal’s space use behavior (Merkle et al. 2014; Avgar et al. 2015).

As movement recursions, that is, repeated visits to specific places, are likely to be the manifestation of some use of spatial memory (Fagan et al. 2013), their study should make it possible to infer how spatial memory may drive movement behavior. Indeed, as environments are often spatially heterogeneous but partly predictable spatially and temporally, it should be advantageous for an individual to remember the locations of the most profitable resource patches and their temporal dynamics, so as it should then come back repeatedly at the most suitable times. Memory can thus be used to reduce the time spent searching for resources and to adjust the timing of recursions to resource renewal rates (Janson 1998; Ohashi et al. 2008; Bar-David et al. 2009; English et al. 2014; Riotte-Lambert et al. 2015). This may also help to defend resources by preemption (e.g., Ohashi et al. 2008; Noser and Byrne 2010; Janmaat et al. 2014). Food patches are not the only sites whose locations could be advantageously remembered, however. For example, it could be the case for water holes, shelters, nesting sites, or any place where the animal can find a limiting resource that is reusable. Thus, as expected, movement recursions are commonly observed (e.g., Watts 1998; Bar-David et al. 2009; Noser and Byrne 2010; Mueller et al. 2011; English et al. 2014). They usually lead animals to self-restrict their movements within a delimited area called a home range (HR, Börger et al. 2008). This form of site fidelity may affect various ecological processes, such as demography (Morales et al. 2010), habitat selection (Benhamou and Riotte-Lambert 2012), sociality (Galanti et al. 2006), and epidemiology (Kenkre et al. 2007).
Movement recursions to individual sites may result in patterns of repeated, ordered sequences of visits to different sites. We term these patterns “routine movement behavior.” Although this expression has sometimes been used to refer to small-scale daily movements in opposition to dispersal or migration (e.g., Van Dyck and Baguette 2005; Delattre et al. 2010; Volpe et al. 2014), we use it here more literally as the repeated use of routes connecting several sites in ordered sequences. Routine movement behavior may emerge from a balance between resource patch exploitation and renewal (Riotte-Lambert and Byrne 2010). It may also emerge from nutritional requirements, for example, if several resource types have to be acquired in a specific order and/or if a specific resource type (e.g., water) has to be acquired at specific time schedules (Raubenheimer et al. 2009). In any case, it may reflect the use of some level of large-scale spatial representations built-up in terms of networks of routes (Di Fiore and Suarez 2007; Benhamou 2010; Nosé and Byrne 2010), which may be used to efficiently revisit multiple known sites (i.e., travel route optimization).

One can suspect that the level of routine movement behavior performed by individuals may vary over ecological time scales with individual-level (e.g., age/experience and personality) and environmental-level factors (e.g., resource predictability and frequency of perturbations), as well as over evolutionary time scales (e.g., through the adaptation to new resource types and/or environments). However, given the paucity of information on this topic, this remains speculative and needs to be investigated.

Currently, tools available to study movement recursions can be used to identify where recursions occur in space (Benhamou and Riotte-Lambert 2012; Lyons et al. 2013) or time (Bar-David et al. 2009) and to test for periodic patterns in recursions (Riotte-Lambert et al. 2013). Thus, they noticeably focus either on recursions to a single site at a time or to several sites considered independently, as if they were disconnected and cannot be used to address questions relative to the sequence of the sites visited. Relatively simple approaches have been used to analyze a stereotyped kind of routine movement behavior, called traplining, which is performed by some nectarivores that repeatedly visit several flowers in virtually always the same order, following a single, well-defined circuit (Thomson et al. 1997; Lihoreau et al. 2012). This behavior has been mostly demonstrated in central place foragers under experimental settings and using a small number of resource patches (Lihoreau et al. 2012; Tello-Ramos et al. 2015). The use of efficient routes by noncentral place foragers and in more complex environments is likely to lead to noncyclic, less stable, repetitions of several sequences of visits at important sites. Events of all kinds (e.g., encounter with predators and bad weather) are also likely to introduce some additional randomness in the movement of individuals. Most studies that attempted to touch on the question of the repetition of movement sequences other than those performed by trapliners were limited to the visual inspection of movement data (Janson 1998; Di Fiore and Suarez 2007; Nosé and Byrne 2010; Jacoby et al. 2012). Recently, Ayers et al. (2015) proposed to quantify movement routine by computing the proportion of recursions occurring within repeated subsequences larger than a length threshold, but results can be very sensitive to this arbitrary parameter choice. Therefore, robust and flexible methods based on a sound conceptual framework to study routine movement behavior are currently lacking.

In this paper, we designed a new and comprehensive framework in order to 1) quantify the level of routine movement behavior based on the concept of conditional entropy, which has already been used in other fields to quantify the repetitiveness of sequences (e.g., in physiology: Porta et al. 1998; in linguistic: Rao et al. 2009; and in brain and cognitive sciences: Desrochers et al. 2010) and 2) detect repeated movement sequences in an automated and standardized way, by building on the principle of a procedure used for automatic music segmentation (Goto 2003). This framework can be applied to data from any animal displaying recursive movement (i.e., non-nomadic), irrespective of whether it uses a central place or not. We illustrate it with simulated movements for which the underlying processes are fully controlled and with actual movements of black-tailed deer (Odocoileus hemionus) introduced in a novel environment.

**METHODS**

Let us consider an individual’s large-scale movement modeled as a sequence of visits to specific sites (thus ignoring intra-site movements and the details of inter-sites movements, which both correspond to smaller scale movements; Benhamou 2014). One first needs to define the sites of interest, ideally on a biological basis. For example, sites can be determined a priori using habitat features that are likely to be important, given our knowledge of the animal’s biology (e.g., water holes and profitable habitat patches). When such knowledge is unavailable, they can be defined as the areas that elicit a particular behavior (e.g., area-concentrated searching) or that are intensively used or revisited most often (Benhamou and Riotte-Lambert 2012). Then, the sequence of the sites visited is used to compute a quantitative measure of routine movement behavior and to detect the specific subsequences that are repeated.

**Computing a quantitative measure of routine**

Routine movement behavior involves a degree of determinism (or regularity) in the movement sequence pattern, which can be defined as the opposite of uncertainty. In the information theory framework (Cover and Thomas 1991), the irreducible uncertainty of a sequence can be quantified by the minimum value of the conditional entropy, which is an extension of Shannon (1948)’s entropy. Shannon’s entropy is defined as:

\[
H_S = -\sum_{s \in \mathcal{S}} P(s) \log[P(s)]
\]

(1)

It is a global measure of the mean degree of uncertainty in a sequence of symbols \(s\), taken from a set of \(n\) symbols (in this study, the set of visited sites), based on their relative frequencies of occurrence \(P(s)\), without taking into account the history of preceding symbols. Note that we use here the number of different symbols \(n\) instead of 2 (used in the original formulation of entropy) for the base of the logarithm function so as to get \(H_S\) values that are normalized between 0 (no uncertainty) and 1 (when all symbols occur equiprobably: \(P(s) = 1/n\) for any \(s\)). As an extension of the entropy concept, the \(p\)th order conditional entropy, \(H_p\), quantifies the average uncertainty about the next symbol, knowing the string \(S_p = s_{p-1}...s_1s\) of the \(p \geq 1\) previously occurring ones, corresponding to visited sites in the present context, ranked from the oldest to the current one:

\[
H_p = -\sum_{s \in \mathcal{S}} P(s) \sum_{s \in \mathcal{S}} P(s_{p} | s) \log[P(s_{p} | s)]
\]

(2)
where $\sum$ represents the summation for all possible strings of $p$ sites successively visited. Note that for $p = 0$, the conditional entropy $H_p$ is equivalent to Shannon’s entropy $H_0$ as expressed in Equation 1. A general property of the conditional entropy is $H_{p+1} \leq H_p$ (e.g., Peng et al. 2014). Consequently, $H_1$ takes its maximum value at order $p = 0$ and progressively decreases as $p$ increases down to a minimal threshold value $H_{\text{min}}$, which corresponds to the irreducible part of the uncertainty of the whole sequence of visits; no additional knowledge about older visits can improve the prediction of the next visited site (Figure 1, red line). We propose to use $R = 1 - H_{\text{min}}$ as a quantitative measure of routine movement behavior. Furthermore, we propose to look at the lowest value of the order of dependency $p$ leading to $H_p \geq H_{\text{min}}$. This value, called $O$, corresponds to the most relevant order of dependency: lower orders involve a loss of information, whereas larger orders mean a more complex formulation without involving any information gain. For example, for a perfect trapper, the movement sequence corresponds to the strict repetition of a specific subsequence, and the routine movement index is $R = 1$ and the most relevant conditional order is $O = 1$: although all sites are visited with the same frequency ($P_{ij} = 1/n$, for any $i$, leading to $H_0 = 1$), the occurrence of a visit to a given site in the movement sequence is fully determined by the site visited just before (either $P_{ij} = 0$ or $P_{ij} = P_{i'j'}$, depending on $j$ and $j'$, leading to $H_1 = 0$ for $p \geq 1$). In turn, if sites are visited randomly, one gets $R = 0$ and $O = 0$, as all sites are then visited with the same frequencies, and knowledge about previously visited sites does not help predicting current use ($P_{ij} = P_{i'j'} = 1/n$, for any $i$ and $j$, leading to $H_0 = 1$ for any $p$). In more realistic situations, knowing the last visited site should often not be sufficient to fully determine the next site that will be visited ($H_1 > 0$), and knowing the sites visited at older times may (if $O > 1$) or may not (if $O = 1$) improve the predictability of the next visit.

Unfortunately, reliable estimates of $H_p$ (and therefore $H_{\text{min}}$) can be obtained using Equation 2 only for very long (potentially infinite) sequences, for which the empirical relative frequencies correctly reflect the underlying distribution of the conditional probabilities at any conditional order. In practice, when the conditional order considered $p$ increases, the number of possible strings $S_p$ that have to be considered grows exponentially. With sequences of finite size, some of these strings will appear a single time, which leads to erroneous determinism (because $P_{ij}|S_p$ is wrongly set to 1 or 0, depending on $i$). The conditional entropy thus eventually drops to 0 (more rapidly as the number of different symbols increases) instead of stabilizing at the correct value $H_{\text{min}}$ (Figure 1, plain black line). To counterbalance such false certainties, Porta et al. (1998) proposed a corrected formula of conditional entropy $H_c(p)$ for $p \geq 1$ by adding a noise term corresponding to unconditional entropy weighted by the proportion $\tau_{p-1}$ of strings of length $p + 1$ that occur only once in the whole sequence:

$$H_c = H_p + \tau_{p-1} H_0.$$

Using computer simulations, we showed that this correction usually enables a reliable estimation of $H_{\text{min}}$ (and thus of $R$) from the lowest $H_c$ value (Figure 1, dashed black line). The accuracy of the estimate however decreases when the length of the sequence studied decreases but remains within satisfying ranges (Supplementary Figures S1–S4 in Supporting Information 1). We nevertheless recommend not computing $R$ for sequences with a high proportion of all possible transitions from one site to the next appearing only once, as this may reflect poor sampling of the underlying movement process and will lead $H_c$ to artificially converge toward $H_0$. Moreover, because of possible small fluctuations or in some cases of a tendency of $H_c$ to slightly decrease when longer histories are considered (Figure S5 in Supporting Information 1), the value of $p$ corresponding to the lowest $H_c$ may not provide a reliable estimate of the relevant order of dependency $O$. We therefore consider as satisfying an estimate of $O$ the largest value of $p$ leading to a relevant decrease in $H_c(p)$ ($H_{p-1} - H_c > 0.05$); Smaller decreases are considered as being noise and/or as providing only marginal additional information.

**Detecting the specific subsequences that are repeated**

Repeated subsequences can be detected by building a site-lag upper triangular matrix $L$, where each line represents an incremented lag, partly similar to the way Goto (2003) built a time-lag matrix for mining chorus sections in music. Call $S$ the entire movement sequence of length $N$, $L$ is constructed as follows: For any lag $l$ in $[1, N - 1]$, and integer $i$ in $[1, N - l]$, one sets $L[i, i + l] = 1$ if $S[i] = S[i + l]$, that is, if the site visited at time $i$ is revisited at time $i + l$, and $L[i, i + l] = 0$ otherwise. In this way, series of 1s appear in rows in the matrix—which is otherwise filled with 0s—when repetitions of subsequences occur. For example, in the matrix shown in Figure 2, a series of four 1s occurs in the 7th row, at the 1st to 4th columns. This highlights that a subsequence of length 4, first occurring at the 1st to 4th ranks of the sequence, is repeated at lag 7.

Specific rules can be set to control if similar, but not identical, subsequences are considered repetitions. For instance, in the analyses presented below, for subsequences that were at least 5-site-long, we allowed repetitions to be instances of subsequences that could differ by a single deletion or addition, and we also allowed for 1 site to differ every 3 sites (these rules imply that the number of differences of sites between repetitions of a subsequence of length $n_{\text{site}}$ with $n_{\text{site}} \geq 5$, cannot exceed $(n_{\text{site}}/3) + 1$; see Supporting Information 2, for details). It is then straightforward to calculate the number of occurrences of each subsequence detected as repeated at least once (either strictly or in a similar form, as mentioned above).

![Figure 1](image-url)

**Figure 1**
Conditional entropy $H_p$ depending on the order of dependency considered $p$, for a simulated 1st-order dependency (i.e., Markovian) sequence of length 500, with 10 different sites. Transitions from one site to another are equiprobable, except from sites 1 to 2, 2 to 3, and 3 to 4, where the transition probability is equal to 0.9. Despite the tendency of Equation 3 to over-correct $H_p$ estimates, the minimum value ($H_{\text{min}} = 0.65$) and the relevant conditional order ($O = 1$) are satisfactorily estimated from the lowest value reached by the dashed black line.
To avoid studying short repeated subsequences of little interest, in the analyses below, we retained subsequences of length superior or equal to 3 and repeated at least 3 times. Note that there is no objective rule to decide the minimum length and number of repetitions for a subsequence to be retained. The obvious minimum is a subsequence of length 2, repeated twice, but such very short subsequences are likely to appear often by random and are therefore quite uninformative about the movement process. We therefore chose to consider only subsequences that are at least 3-sites long in the algorithm provided. To illustrate the kind of output our algorithm generates, in Supporting Information 2, we present 2 toy examples where we incorporated a known number of occurrences of known repeated subsequences.

ILLUSTRATIVE EXAMPLES

Theoretical examples
To demonstrate our approach, we first used a very simple movement process, where the individual moves between 5 sites of interest, going to the closest site without backtracking with probability $q$ and selecting the next site randomly with probability $1 - q$. We show that, as expected, the routine index $R$ increases with $q$ (Supporting Information 3, Supplementary Figure S8), and the estimated relevant order of dependency $O$ is usually 0 for low values of $q$ (as the movement process is close to random), 2 for high values of $q$ (as the next visit depends on the current and the previous ones), and 1 for $q = 1$ (as the movement is then perfect traplining). We moreover use this simple process to show that, for a given movement process, $R$ does not depend on the number of sites of interest (Supporting Information 3, Supplementary Figure S9).

In a more complex theoretical example, we considered an environment consisting of randomly distributed resource patches that are depleted by consumption but replenish over time. Six foragers are simultaneously released in the environment and compete for the same resources. They are initially naive and search for food using a correlated random walk and use two memory processes, one to remember visited patches (their location and their expected quality), the other to avoid revisiting patches too soon (before a patch partly replenishes). Every time an individual finishes exploiting a patch, it decides, based on its knowledge of the quality of previously visited patches, either to look for a new one or to revisit a known one. In this latter case, it moves to the patch with the highest expected value, defined as the ratio of the memorized patch quality and the distance that would have to be traveled to reach it. These simple decision rules lead to HR emergence and nonterritorial spatial segregation, as patches exploited by others are perceived as of lower quality and thus avoided (see Riotte-Lambert et al. 2015, for more details). We divided the simulation in 1500 time step long periods to compute the routine movement index $R$ on each of these periods separately. We hypothesized that $R$ would increase over time as the individuals should progressively establish an HR and their movement become more repetitive and that the relevant order of dependency $O$ to describe the movement sequences will at least equal to 1.

The routine movement indices $R$ of the 6 individuals are initially below 0.65, but progressively level up to almost 1 after approximately 50 000 steps (Figure 3a). At this stage, the individuals have established HRs and are performing almost perfect traplining (Figure 3c; a small amount of variability in modeled movement decisions prevents animals from performing perfect traplining). For both the first and the last time periods, the relevant order of dependency $O$ equals 1 for all individuals. In Supporting Information 4, we showed that the initial level of routine movement is significantly lower than expected for an individual that would choose the closest site with probability 0.8, whereas the final level of routine movement is significantly larger than expected from the same null hypothesis.

The increase in movement repetitiveness is also obvious when looking for repeated subsequences: the movement sequence of a typical individual (black movement track in Figure 3, used for demonstration purposes) only contains a limited number of repetitions (3 occurrences each) of 2 short subsequences (Figure 3d and f) during the first 1500 steps, but very long subsequences are repeated during the last 1500 steps (Figure 3e and g).

Real-world example
To demonstrate our approach on a real-world example, we used data from 4 adult black-tailed deer translocated from a...
The study of routine movement behavior has so far been limited to the most obvious cases, like traplining in experimental setups where movement bouts are clearly delimited (Lihoreau et al. 2011; Tello-Ramos et al. 2015). The new conceptual and analytical framework we introduce here makes it possible to characterize the level of routine, the most relevant order of dependency, and the structure of the routine involved in all kinds of recursive movement behaviors.

The level of routine corresponds to the degree of predictability of the movement sequence, that is, to the average confidence about the routine involved in all kinds of recursive movement behaviors. The level of routine corresponds to the degree of predictability of the movement sequence, that is, to the average confidence about the routine involved in all kinds of recursive movement behaviors. The level of routine corresponds to the degree of predictability of the movement sequence, that is, to the average confidence about the routine involved in all kinds of recursive movement behaviors.

DISCUSSION

The study of routine movement behavior has so far been limited to the most obvious cases, like traplining in experimental setups where movement bouts are clearly delimited (Lihoreau et al. 2011; Tello-Ramos et al. 2015). The new conceptual and analytical framework we introduce here makes it possible to characterize the level of routine, the most relevant order of dependency, and the structure of the routine involved in all kinds of recursive movement behaviors.

The level of routine corresponds to the degree of predictability of the movement sequence, that is, to the average confidence about the next site visited, given full knowledge of the sites previously visited. We propose to measure it as $R = 1 - H_{\text{min}}$, where $H_{\text{min}}$ is the minimum conditional entropy. We showed, using simulation examples, that this index appropriately quantifies the level of movement predictability, from random revisitation of places to perfect traplining. Previous studies of repetitive movement either focused on traplining behavior (e.g., Lihoreau et al. 2012, Tello-Ramos et al. 2015), which corresponds to an extreme case easy to quantify, or, for more complex cases, were mostly qualitative (e.g., Janson 1998; Di Fiore and Suarez 2007; Noser and Byrne 2010; Jacoby et al. 2012) because of the lack of a quantitative index such as the...
one we proposed. The most relevant order of dependency $O$ corresponds to the minimum number of the most recently visited sites that have to be known to significantly improve the predictability of the next site visited, indicating that older knowledge is unnecessary or only marginally useful. However, it should be kept in mind that this order of dependency characterizes the movement pattern observed but does not necessarily reflect the memory span used by the actual underlying decision process, which can extend to a series of sites to be visited in a predefined order rather than a single one.

The specific structure of the routine behavior appears through an investigation of the subsequences that are actually repeated. Highlighting repeated subsequences is a key step when studying sequences. This has been the subject of much research in various fields. Most of the algorithms developed so far to identify any possible subsequence without any a priori knowledge were developed for the analysis of 4-symbols DNA sequences using abstract cost parameters and are therefore hardly adaptable to movement sequences and/or require a burdensome parameterization (e.g., Magnusson 2000; Bao and Eddy 2002; Price et al. 2005) or only consider exact repetitions (e.g., Carrascosa et al. 2011). We therefore developed a new, flexible algorithm that detects repeated subsequences with no a priori assumption about their composition and that enables the detection of nonidentical repetitions with a controlled number of differences between repetitions. Our simulated and real-world examples showed that this algorithm works efficiently and provides a useful visualization of routine movements.

The routine movement index should be useful in conservation biology when looking at the fate of translocated animals. In our real-world example, even if the most intensively used areas and the specific structure of the routine movements differed between the 2 periods considered (first 2 months and 6th and 7th months after translocation), the translocated black-tailed deer did not show significant variations in the level of routine movement behavior between the 2 periods. Even if some resource depletion could have occurred between the 2 time periods we compared (September–October vs. February–March), this hypothesis is unlikely, given the very low herbivore densities compared with food availability on this island. HR establishment may in that case have been so

Figure 4
Movement subsequences most repeated by 2 deer (each individual is represented in a row and correspond to deer number 1 and 2 in Supplementary Table S1) during the first 2 months (panels a and c) and 6th and 7th months (panel b and d) after their release, without allowing for consecutive revisits to the same site. Shaded grays represent cumulative utilization distributions (UDs) estimated using the Movement-based Kernel Density Estimation method on those time periods and for those individuals separately. Areas delimited by thin black lines correspond to the upper 25% of the UD s and are used as sites when mining for repeated subsequences. The upper 25% UD areas for the first period are represented as thin dashed black lines in the second period figures for comparative purposes. Black thick lines represent the most repeated subsequences, with arrows representing the order of visits. Deer number 1, panel a: each repeated subsequence is repeated 16 times within the 160-site-long movement sequence, panel b: the subsequence, which corresponds to twice the return trip between the 2 sites, is repeated 7 times within the 59-site-long sequence; Deer number 2, panel c: the subsequence is repeated 10 times within the 179-site-long sequence, panel d: the subsequence, which corresponds to “2, 3, 2, 1, 2, 1,” is repeated 5 times within the 132-site-long sequence.
quick that the expected increase in the degree of routine movement might have taken place on time scales much smaller than the one used here (2 months period), but this is quite unusual. For example, Fryxell et al. (2008) showed that translocated elks require 1–3 years to establish HRs. However, the areas used for 2 months periods by individuals roughly correspond, corroborating the idea that HR establishment has occurred very quickly in this case. This result, along with the simulation example, indicates that the evolution of the routine movement index of translocated animals should thus provide either a reliable way to estimate the time they require to acclimate to their new environment, when this occurs on sufficiently long time periods (as in the simulation example case), or the maximum time required for the establishment of routine movement when this occurs rapidly (less than 2 months in our real-world deer example). The rapidity at which deer routine movement established may stem from the fact that deer were translocated from a poor to a rich environment. As they thus could more easily find food patches than previously, they were not compelled to perform extended exploratory (i.e., random or nomadic) movements.

The routine movement index and associated most relevant order of dependency should prove useful for studying linkages between cognition, foraging strategies, and environments. Although one cannot get a direct access to cognitive processes, one can test hypotheses about the cognitive processes underlying routine movement by comparing the levels of routine between different time periods for the same individuals (as we did with black-tailed deer), experimental treatments, or any other factor of interest. An interesting possibility would be to compare the level of routine behavior between individuals of different age-classes living in similar environments, as this would indicate the extent to which the exploitation of the environment necessitates learning and travel route optimization skills gained through experience and therefore the extent to which the establishment of routine movement patterns really rests on the use of spatial memory. The comparison of routine behavior for different species living in similar environments, as well as species living in very dissimilar environments, would moreover enable the testing of hypotheses on the selective pressures acting on travel route optimization strategies.

Another way to test hypotheses on the cognitive processes underlying routine movement patterns is to compare the level of routine in any actual movement with the level expected from a hypothesized movement process. For example, we showed that the level of routine reached after HR establishment in our simulation model is much higher than the one expected from a Markov process, where the closest site is chosen as the next site visited with a fixed probability (e.g., 0.8; see Supporting Information 4). Routine movement behavior is often considered to be the result of some travel optimization. In particular, studies focusing on trampling in nectarivores showed that repeatedly visiting the same routes is an efficient way to increase the mean intake rate and to reduce its variance by reducing the time spent searching and, in some cases, to increase the chances of preemption (Ohashi et al. 2008; Janmaat et al. 2014). Comparing the routine index and the order of dependency obtained on actual movement with the values expected under more or less strong optimization strategies should be a reliable way to investigate the extent to which the degree of optimality depends on the level of routine movement in cases less stereotyped than those involving trampling.

A limitation of the conditional entropy approach is that the routine movement index for short sequences is noisier than for long sequences. This means that quick changes are hard to detect because they occur through short movement sequences. This may hinder the detection of statistically significant differences of routine movement behavior between groups of individuals or make bigger sample sizes necessary for this purpose. Another critical point in our method is that we considered the sequence of visits to a number of sites without taking into account the time spent within each site. The temporal dynamics of site use may be integrated into the analysis, if needed, by constructing sequences in such a way that there would be one symbol per regular time interval, the symbol corresponding to a given site being repeated as long as the individual remains within this site.

Although our approach was developed to study routine movement behavior, it can readily be used to characterize and quantify other kinds of repetitive behavior. Numerous studies focus on the repetitions of various kinds of behavioral sequences (Martaresche et al. 2000; Lehongre et al. 2008; Desrochers et al. 2010; De Groeve et al. 2016) and could benefit from our framework. Its application in the field of movement ecology appears nevertheless particularly promising to study the link between memory and movement, which is beginning to receive much attention (reviewed in Fagan et al. 2013) and to investigate the fundamental ecological and evolutionary implications that repetitiveness of movement can have. The new conceptual framework and the methods to explore and quantify the degree of routine in movement behavior we provide here should help to unify the study of repetitiveness of movement in species that use space in a much more complex way than trappers. Thus, this framework should allow the testing of numerous hypotheses on proximate and ultimate drivers of the use of memory in movement that were difficult to characterize and quantify so far and could even be applied to the study of other types of routine behavior.

SUPPLEMENTARY MATERIAL
Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING
The Agence Nationale de la Recherche funded the deer translocations via its grant no 2010-BLAN-1718-RAMBI.

We thank Jean-Louis Martin for having organized the deer translocations and Rémi Choquet for insightful discussions on Markov chains. We thank Daniel Fortin and anonymous reviewers for their helpful comments on an earlier version of this manuscript.

Data Accessibility: R scripts (R Core Team 2016) necessary to run the methods are provided by Riou-Lambert et al. (2016a). Analyses reported in this article can be reproduced using the data provided by Riou-Lambert et al. (2016a).

Handling editor: David Stephens

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