

# Determinism as a statistical metric for ecologically important recurrent behaviors with trapline foraging as a case study

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**Abstract** Patterns of discrete behaviors tied together in specific sequences are essential for the formation of complex behavioral phenomena. Such behavioral sequences can be of critical ecological importance, for example relating to resource acquisition, predator evasion, and sexual selection. The role of sequential behaviors in ecology, however, is understudied, in substantial part due to the difficulty of quantifying complex sequences. Here, we present a modified version of determinism (DET) from recurrence quantification analysis (RQA) as a standard metric for quantifying sequential behaviors. We focus on a case study of trapline foraging, a taxonomically widespread behavioral strategy in which animals repeatedly visit spatially fixed resources in a predictable order. Using a bumble bee movement dataset, we demonstrate how to calculate DET and create and interpret recurrence plots, which visually demonstrate patterns in foraging sequences. We show a new method for statistical comparisons of DET scores and assess the sensitivity of DET to resource density using simulated foraging sequences. We find that DET

complements and offers distinct advantages over previously available methods for many questions and datasets since it does not depend on any particular resource arrangement or experimental setup and is relatively insensitive to resource density. These features make DET a powerful tool for comparing sequential behaviors between differing environments in a range of ecologically important contexts.

**Keywords** Recurrence quantification analysis (RQA) · Recurrence plots · Behavioral sequencing · Bumble bees (*Bombus*) · Fixed action patterns

## Introduction

Patterns of discrete sequential behaviors are essential for the formation of complex behavioral phenomena. Such sequential behaviors can be of key importance for ecological or evolutionary processes, including host–parasite and predator–prey interactions, optimal foraging, and sexual selection. For host–parasite and predator–prey interactions, these behaviors may include sequential grooming behaviors (Fentress and Stilwell 1973; Berridge et al. 2005; Kristan 2014) and patterns of time allocation to foraging versus scanning for predators in birds and mice (Caraco 1982; Maubourguet et al. 2008). Sequential behaviors are also important for establishing daily foraging patterns (Champion et al. 1994), including foraging on different prey or resource types, for example, pollen- versus nectar-focused foraging in bumble bees (Vaudo et al. 2014). Sequential behaviors which drive sexual selection may include the establishment of social dominance (Chase 1982) and complex courtship dances (Barske et al. 2011). Innate sequential behaviors have long been studied in the context of fixed action patterns, where a series of behaviors are completed in response to a distinct stimulus. A classic example is the greylag goose, which

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uses a series of egg rolling motions to return an egg to the nest when an egg is displaced and performs the entire behavioral sequence even when the egg is removed (Lorenz and Tinbergen 1970). Many sequential behaviors, however, are learned plastic behaviors that form in response to environmental stimuli and may greatly vary between individuals.

While a substantial body of work is devoted to the examination of the neurological process of learning sequential behaviors (e.g., Melamed et al. 2004; Rhodes et al. 2004; Jin et al. 2014), their role in ecology is understudied. This is due in large part to the difficulty of quantifying ordered patterns from a time series of behaviors. Though sequential behavioral data have been recorded at set time intervals to examine time budgets, a method in use for decades (Wiens et al. 1970), these data are nearly always analyzed as the proportion of time spent on each activity (Williams et al. 1997; Sabine et al. 2008), which may obscure important temporal patterns. Other studies examining repetitive behavioral sequences only measure the rate of sequence initiation, without quantifying the degree of variation between sequences (e.g., Berridge et al. 2005). From these analyses, it is impossible to statistically test whether a particular sequence order is important for the outcome of the behavior, as opposed to the presence of all the behavioral elements in a random order.

An ideal standard metric of temporal behavioral sequencing should have several features. It should be able to detect imperfect repeats in sequence data, such that the omission or addition of a particular sequence point would not entirely disguise an otherwise perfect sequence. It should be capable of detecting long sequence repeats, rather than only examining very short subsets of sequences, in order to distinguish between long and short sequential behaviors. An ideal standard metric should also be able to distinguish between forward- and reverse-order sequence repeats, since in some cases behavioral sequences can be executed in either “forward” or “backward” directions. Finally, an ideal metric should be broadly applicable to different types of behavioral sequences, beyond a single study system or experimental design. In order to facilitate comparisons across studies, it should be able to quantify sequence predictability without relying on a specific reference sequence. To our knowledge, no widely applied metric for behavioral sequences meets all of these criteria for an ideal standard metric. However, it is important to note that, while these features are important for a standard metric, they may not be desirable for all specific questions and datasets, in which case multiple metrics may be used.

Here, we address the lack of a standard metric by altering and assessing a new metric for behavioral sequencing. We propose determinism (DET), adapted from recurrence quantification analysis (RQA), as a new standard metric and recurrence plots as a tool for sequence data visualization (Zbilut and Webber 1992; Trulla et al. 1996; Marwan et al. 2007). DET is a metric adapted from RQA, which was originally

developed to investigate nonlinear dynamical systems, and has been applied to many fields including engineering, chemistry, astrophysics, and climatology (Marwan et al. 2007).

Though determinism has many of the required characteristics of an ideal standard behavioral sequencing metric described above, to our knowledge, it has not been previously applied to any animal behavior. DET is broadly applicable to many ecologically important sequential behaviors, and we assess DET using the case study of traplining, a foraging strategy where animals foraging on replenishing, spatially fixed resources visit resources repeatedly in a predictable order (Thomson et al. 1997). Traplining is important ecologically since it allows foragers to minimize distance travelled between resources, reduce search times, and improve overall foraging efficiency (Ohashi et al. 2007, 2008; Saleh and Chittka 2007; Lihoreau et al. 2011, 2012a, b). Trapline foraging is also taxonomically widespread, occurring in a variety of bee taxa (Ackerman et al. 1982), as well as in butterflies (Gilbert and Singer 1975), hummingbirds (Gill 1988; Garrison and Gass 1999; Gass and Garrison 1999; Temeles et al. 2006; Tello-Ramos et al. 2015), vultures (Deygout et al. 2009), and many mammals including bats (Gould 1978; Woodsworth et al. 1981; Lemke 1984), opossums (Wooller et al. 1999), rats, and primates (Garber 1988). Traplining behavior is thought to be driven by complex cognitive processes, including spatial reference memory and iterative learning heuristics (Saleh and Chittka 2007; Reynolds et al. 2013).

Traplining represents an ideal case study for quantitative assessment of behavioral sequences because the sequence order is of critical importance and is therefore often recorded in data collection efforts of traplining in contrast to many other behavioral sequence data. Because traplining is sequence dependent, researchers have also considered a number of different metrics for quantifying traplining behavior (Table 1), but as with other behavioral sequences, no metrics have been proposed that meet all the criteria we outline in the previous paragraph.

In this paper, we demonstrate how RQA can be adapted for studying traplining and other sequential behaviors in ecology. We use a publicly available dataset of bumble bee (Hymenoptera: Apidae: *Bombus*) foraging movements (Lihoreau et al. 2012a) to demonstrate how to calculate DET and create and interpret recurrence plots, which visually demonstrate foraging sequence patterns. Using simulated sequences, we demonstrate a new method for statistical comparisons of DET scores, and we assess the sensitivity of DET to resource density.

## Methods

### Case study system

Traplining, a foraging strategy where animals repeatedly visit replenishing, spatially fixed resources in a predictable order, is

**Table 1** Summary of existing metrics for trapline foraging

Existing metrics for trapline foraging				
Name	Description	Advantage	Disadvantage	Citations
Asymmetry index	Measures bias in direction of transitions between pairs of flowers (first developed to test migration)	Can detect basic patterns in bee movements between pairs of flowers	Pairwise comparisons only; would not be useful whenever foragers repeat a trapline in reverse order	Sokal (1991), Thomson et al. (1997)
Skeleton diagrams	Graphical depiction of asymmetrical transitions between pairs of flowers	Good visual summary of foraging movements	Pairwise comparisons only (very short repeats would be considered traplines)	Thomson et al. (1997)
Variation of return cycle	Measures the variance in time or number of flowers it takes for a bee to return to the same point	Most practical measure when sequence data is difficult to collect	No information on identity of flowers visited (two very different paths could be of similar lengths)	Ackerman (1982), Gill (1988), Thomson et al. (1997)
Sequence similarity indices	Similarity of sequences starting and ending with a “terminal flower”	Examines subsets of data longer than pairs of resources	Targets individual pre-specified trapline routes, so difficult to apply when there are many possible routes of interest; may be sensitive to the selection of the terminal flower	Thomson et al. (1997), Lihoreau et al. (2010)
Spatial geometry of routes	Total number of different routes used by a forager between a specified start and end point (e.g., nest entrance)	Simple to calculate if sequence data is known; does not rely on pairwise comparisons	May only be used if resources are not replenishing and their spatial arrangement is fixed; only examines whether sequences are completely identical and cannot distinguish degree of similarity between sequences	Thomson et al. (1997), Lihoreau et al. (2010)

particularly important in two areas of behavioral and ecological research. First, since traplining behavior is thought to be driven by complex cognitive processes, it is commonly used as a model system to study spatial memory and foraging decision-making (Saleh and Chittka 2007; Reynolds et al. 2013). Second, due to the prevalence of the behavior in pollinators such as bees and hummingbirds, traplining is often studied in the context of its functional implications for plant pollination because traplines incorporating flowers of the same species may enhance conspecific pollen transfer and plant reproduction (Ohashi and Thomson 2009).

As with other types of behavioral sequence data, few tools exist to quantitatively assess traplining. While existing traplining metrics (Table 1) can be used to detect basic patterns in foraging movements, none of these metrics satisfies all of the aforementioned criteria of an ideal standard metric. Several of these measures, such as the asymmetry index (Sokal 1991; Thomson et al. 1997), examine bias in the direction of transitions between pairs of flowers, which cannot be used to distinguish between long and short traplines or to detect traplines that may occur in reverse order. Another measure, the variation in return cycle (Ackerman et al. 1982; Gill 1988; Thomson et al. 1997), is based on variability in the time required for foragers to complete a trapline. This may be practical to measure in field studies but does not contain any

information on the sequence of resources visited. Thus, very different sequences with similar completion times would be indistinguishable. Other metrics, including sequence similarity indices (Thomson et al. 1997; Lihoreau et al. 2010), are designed to test the self-similarity of a foraging sequence but are sensitive to which resource is selected as the start and end of the trapline. In terms of behavioral sequences more generally, it may be challenging to select a starting or ending behavior for a grooming sequence or mating dance. Similarity indices also require a previously specified sequence for comparison. One common approach is to compare the similarity of consecutive foraging bouts, but this does not allow for detection of repeated sequences between nonconsecutive bouts. Many metrics may only be used to compare foraging sequences from identical resource layouts, for instance, metrics which quantify the number of different routes taken. Finally, several metrics are specific to particular experimental designs, including the spatial geometry of routes (Thomson et al. 1997; Lihoreau et al. 2010). These often require resources not to replenish during a foraging bout or foragers to return to a home base at the start and end of each trapline. Many other traditional metrics of bee foraging, such as average rank (Ohashi et al. 2007), are not easily adapted to quantifying traplines since they do not depend on the identity of flowers visited in the sequence.

Determinism (see description and calculation below), however, has all the aforementioned properties of an ideal standard metric for behavioral sequencing and offers many distinct advantages over existing metrics.

### Description and calculation of determinism and recurrence plots

Originally developed for nonlinear systems, RQA also has many biological applications, including detection of physiological patterns in heart rate variability (Marwan et al. 2002; Zbilut et al. 2002b), respiratory data (Webber and Zbilut 1996), and brain electrical activity (Thomasson et al. 2001), as well as analyzing amino acid sequences (Zbilut et al. 1998, 2002a; Porrello et al. 2004; Yang et al. 2009). Despite its applications in many different fields, to our knowledge, RQA has not been used to analyze animal behavior.

DET measures sequence predictability by quantifying the number and length of recurrences and series of recurrences. A *recurrence* refers to any time a system returns to an area of phase space which it has previously visited (Marwan et al. 2007). For behavioral sequencing applications, a recurrence occurs when a discrete behavioral action (e.g., a single step in a grooming or courtship sequence) is repeated anywhere in the behavioral sequence. In the case of trapline foraging, a recurrence occurs whenever a forager revisits a resource. A *recurrent series* occurs when sequence elements are repeated in the

same order (in either forward or reverse directions) in different parts of the sequence. DET is based on the proportion of recurrences (i.e., revisited behavioral actions) that belong to a recurrent series of a minimum designated length. In the case of traplining, DET represents the proportion of revisited resources which were visited in the same continuous order in multiple parts of the visitation sequence.

Determinism may be best understood graphically using recurrence plots, which visually depict the behavior of a dynamical system (Eckmann et al. 1987; Marwan et al. 2007). To construct a recurrence plot for traplining, we first assign a unique identification number to each individual resource (e.g., a flower). A resource visitation sequence is then constructed by recording the unique number of each resource in the order of visitation by the forager. We construct the plot by placing the resource visitation sequence on both the horizontal and vertical axes, such that  $x_i$  and  $y_i$  both represent the  $i$ th resource visited (on the  $x$  and  $y$  axes, respectively). A point is placed each time  $x_i = y_j$ , where  $i$  and  $j$  are the  $i$ th and  $j$ th resources visited in the sequence. Since the same sequence is placed on both axes, points always appear on the main diagonal, where  $i = j$ , and the plots are necessarily symmetrical across this diagonal. Points not on the main diagonal represent a revisit to a resource at a different time in the visitation sequence.

Determinism may be calculated directly using a recurrence plot, as follows:

$$\text{DET} = \frac{\text{Number of points above the main diagonal belonging to a contiguous diagonal of length} \geq l}{\text{Number of points above the main diagonal}} \quad (1)$$

where  $l$  indicates the minimum length (measured in number of contiguous points) of a recurrent series in order to be included in the numerator of the DET formula. Since recurrence plots are symmetrical across the main diagonal, we propose calculating DET only for the top half of each recurrence plot. This restriction, which departs from traditional forms of DET, is important for constructing a conservative statistical test of DET using generalized linear models (GLMs) with binomial errors (see “Statistical analysis of determinism” section).

For example, in Fig. 1, the hypothetical forager visited resources numbered:

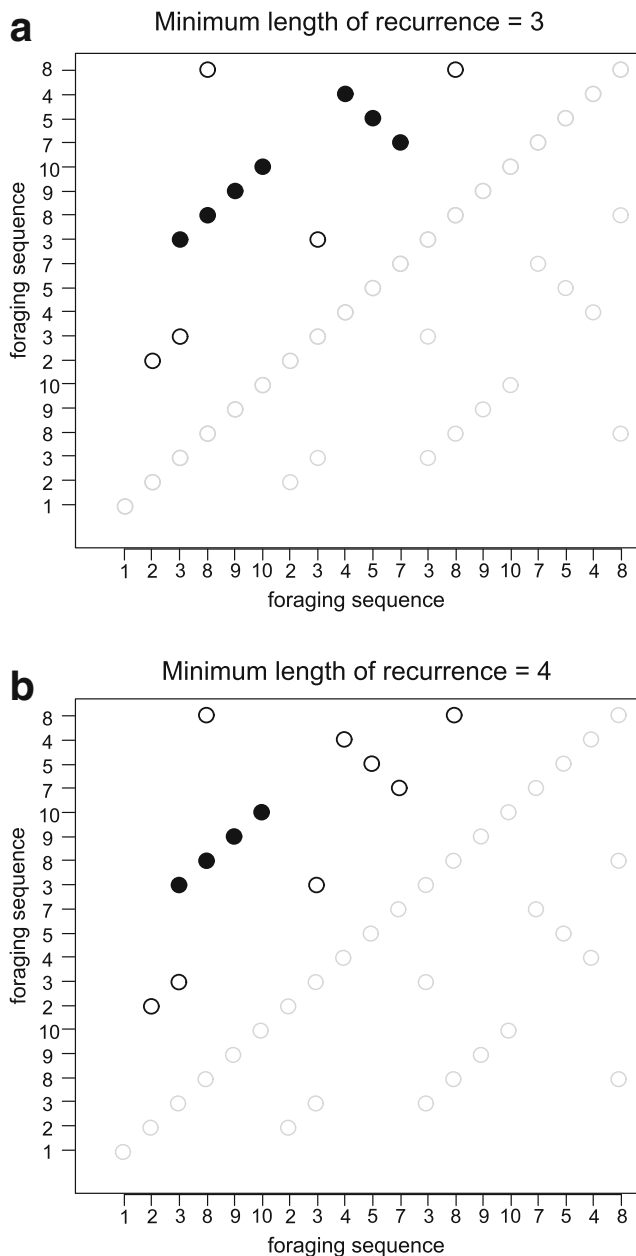
1 2 3 8 9 10 2 3 4 5 7 3 8 9 10 7 5 4 8

beginning with “1” and ending with “8.” Each repeated number represents a revisit to a particular resource (e.g., resource number “8” was visited three times by the forager). We first construct the recurrence plot by placing this sequence on both

the  $x$  and  $y$  axes. A point is placed each time the resource identification number on the  $x$  axis equals the number on the  $y$  axis. Again, since recurrence plots are symmetrical, points on or below the main diagonal are not considered in our calculation of DET (light gray points in Fig. 1). Points above the main diagonal which belong to unbroken diagonals of length  $\geq l$  are included in the numerator of the DET formula (closed points in Fig. 1). The denominator of the formula equals the total number of points above (but not including) the main diagonal.

Increasing the minimum length of a recurrence ( $l$ ) typically decreases DET as it excludes points belonging to shorter diagonals, as demonstrated in Fig. 1. When  $l=3$  (Fig. 1a), the numerator of the DET calculation includes one diagonal consisting of four points and one diagonal of three points:

$$\text{DET}_{l=3} = \frac{4(1) + 3(1)}{12} = \frac{7}{12} = 0.58$$



**Fig. 1** Recurrence plots for a hypothetical foraging sequence with a minimum recurrence length of **a** 3 or **b** 4 points. All points above (but not including) the main diagonal are included in the denominator of the determinism (DET) formula. Closed points, or those which belong to contiguous diagonals (recurrences) of at least the minimum length, are included in the numerator of the DET formula. All gray points are excluded from the calculation of DET, since the plot is symmetric across the main diagonal.  $DET=7/12=0.58$  and  $DET=4/12=0.33$  in **a** and **b**, respectively

DET is dependent on the minimum sequence length, however, and when  $l=4$  (Fig. 1b), the numerator of the

DET calculation only consists of only one diagonal of four points:

$$DET_{l=4} = \frac{4(1)}{12} = \frac{4}{12} = 0.33$$

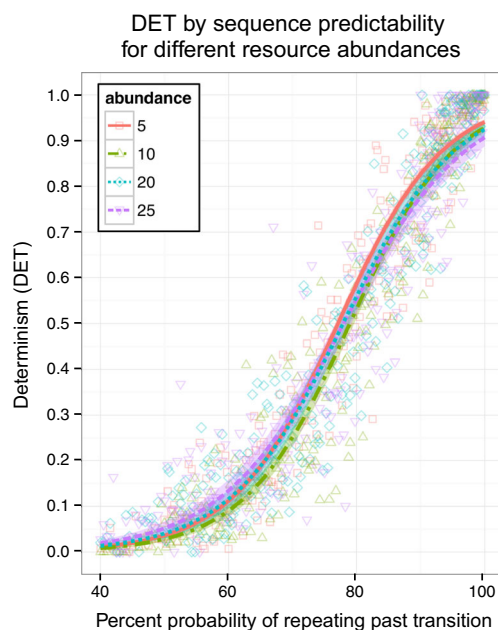
The structure of lines in a recurrence plot indicates when and how often the system returns to the same phase space. Vertical or horizontal lines indicate the system remains fixed in space, such as when a forager repeatedly visits the same resource. Vertical or horizontal lines may be especially important for grooming sequences or mating dances where animals repeat behaviors multiple times in a row before advancing to the next behavior. Diagonal lines indicate repeats in the trajectory of the system, such as when a forager visits resources in a predictable order (i.e., traplining). Perpendicular diagonals indicate a reversal in the order of resources visited in a trapline. Such reverse sequences may be biologically relevant in the formation of optimal traplines, since the optimal route may be used in either clockwise or counterclockwise directions. However, such reverse sequences may not be relevant to all recurrent behaviors, in which case DET may be calculated without including perpendicular diagonals in the numerator of the determinism calculation (see [Electronic supplementary material](#)). Exclusion of perpendicular diagonals may lead to lower estimates of DET, so it is important for users of determinism to document their inclusion or exclusion of perpendicular diagonals in order to facilitate comparisons across studies. Here, perpendicular diagonals are included unless otherwise stated.

## Statistical analysis of determinism

### Analysis of determinism with GLMs

To statistically compare the degree of traplining between two or more resource visitation sequences using DET, we propose the use of GLMs with binomial errors. DET values are typically not normally distributed but instead more closely follow a binomial distribution since each point on a recurrence plot is either a “success” (belonging to a recurrent sequence) or “failure” (not belonging to a recurrent sequence). The use of a GLM with binomial errors allows for modeling nonlinear responses of DET to differing levels of traplining (Fig. 2). Since the statistical power of a binomial GLM depends on the number of counts (or points on a recurrence plot), we have modified traditional DET to only include the top halves of recurrence plots, which are symmetrical across the main diagonal, in order to maintain a conservative statistical test. We should emphasize that the GLM approach is for comparing traplining between





**Fig. 2** Determinism (DET) values ( $l=5$ ) from hypothetical foraging sequences with varying predictability and resource abundance. We generated 1,044 sequences with 100 resource visits each while varying the probability of repeating a transition from an earlier stage of the foraging sequence. The lines of best fit and 95 % CIs were calculated using GLMs with quasi-binomial errors to account for the nonlinear response of DET to sequence predictability. DET significantly increased with sequence predictability and was significantly higher for the case with 25 resources

two or more samples. To test whether or not individuals are “significantly” traplining requires an appropriate null model (e.g., Ohashi et al. 2007), which is beyond the scope of this paper, though DET could be used were such a model available.

To better understand how DET responds to varying levels of traplining, we analyzed DET values calculated from 1,044 simulated foraging sequences (see [Electronic supplementary material](#)) with varying levels of predictability (Fig. 2). To generate simulated sequences, we set a fixed probability that a forager would repeat a past transition, using a short sequence as a reference. To repeat a previous transition, the forager would repeat its behavior from the reference sequence. If the forager failed to repeat the transition, another resource was chosen at random, excluding the current resource and the one which would have led to a repeat transition. As expected, we found a highly significant positive relationship between DET and sequence predictability (Table 2).

### Sensitivity to resource abundance

One potential issue in the analysis of behavioral recurrence data is that determinism could be sensitive to the number of potential discrete behaviors in a sequence, such that it might be inappropriate to compare behavioral sequences of differing

**Table 2** Statistical analysis of DET ( $l=5$ ) in response to changes in the percent chance of repeating a past foraging transition (sequence predictability) and the level of resource abundance

	Estimate	Std. error	<i>t</i> value	Pr(>  <i>t</i>  )
Intercept	−9.34	0.18	−51.234	<2 × 10 <sup>−16</sup>
Abundance 10	−0.29	0.33	−0.88	0.38
Abundance 20	0.5	0.41	1.23	0.22
Abundance 25	1.25	0.42	2.98	0.003
Percent	0.12	0.002	52.5	<2 × 10 <sup>−16</sup>
Percent x Abundance 10	0.001	0.004	0.19	0.85
Percent x Abundance 20	−0.008	0.005	−1.5	0.13
Percent x Abundance 25	−0.02	0.005	−3.28	0.001

We used a GLM with quasi-binomial errors, where the dispersion parameter was estimated as 29.9. Resource abundance was treated as a factor, and an abundance of five resources was set as the reference group. As expected, there was a strongly significant effect of predictability on DET. Compared to an abundance of five resources, DET was significantly greater for 25 resources but not significantly different for 10 or 20 resources. There was a significant interaction between abundance and predictability only for the 25 resource case

complexity. In the context of traplining, sensitivity of determinism to the number of possible resources would likely prevent comparisons across environments with different resource densities. To explore this issue, we analyzed DET values for hypothetical sequences with varying resource abundance (Fig. 2). Using five resources as our baseline, we found that that DET was able to clearly distinguish variation in traplining despite a fourfold increase in resource abundance. This range of resource densities is applicable to the majority of traplining studies, which typically occur in controlled laboratory settings with a small number of resources (e.g., 6 resource points as in Lihoreau et al. 2012a and up to 16 resource points as in Ohashi et al. 2008). Comparisons between extremely large numbers of possible sequence elements (e.g., 50 to 500 resources) may significantly impact DET (see [Electronic supplementary material](#)); however, such large numbers of possible elements are not likely to be required for the majority of ecological or behavioral applications. In rare cases where DET is likely to be sensitive to resource abundance, comparisons across studies are still possible after performing a sensitivity analysis of the effect of resource abundance on DET (see [Electronic supplementary material](#)).

### Worked examples

Here, we demonstrate how determinism and recurrence plots may be used to compare the behavior of one individual before

and after gaining experience on a foraging array or the foraging behavior of different individuals. Recurrence plots were generated using the “fNonlinear” package in R (Wuertz et al. 2013; R Core Team 2014). Calculations of DET were also performed in R, and the corresponding R code is provided in the [Electronic supplementary material](#).

Recurrence plots were constructed using publicly available data from Lihoreau et al. (2012a). This dataset includes foraging data from eight individual bumble bees (*Bombus terrestris*) foraging in an enclosure containing six artificial flowers. Nectar rewards did not replenish and were calibrated such that bees typically visited all six flowers once per foraging bout, and the process was repeated until each bee performed 80 foraging bouts. The foraging data were processed to remove immediate revisits by a bee to a particular flower.

Figure 3 shows recurrence plots of the foraging behavior of a bee (individual (indiv.) 1 from Lihoreau et al. 2012a) after first entering the foraging array and after gaining experience on the array (following 360 floral visits or approximately 60 foraging bouts). The DET calculations for these foraging sequences, with  $l=5$ , are as follows:

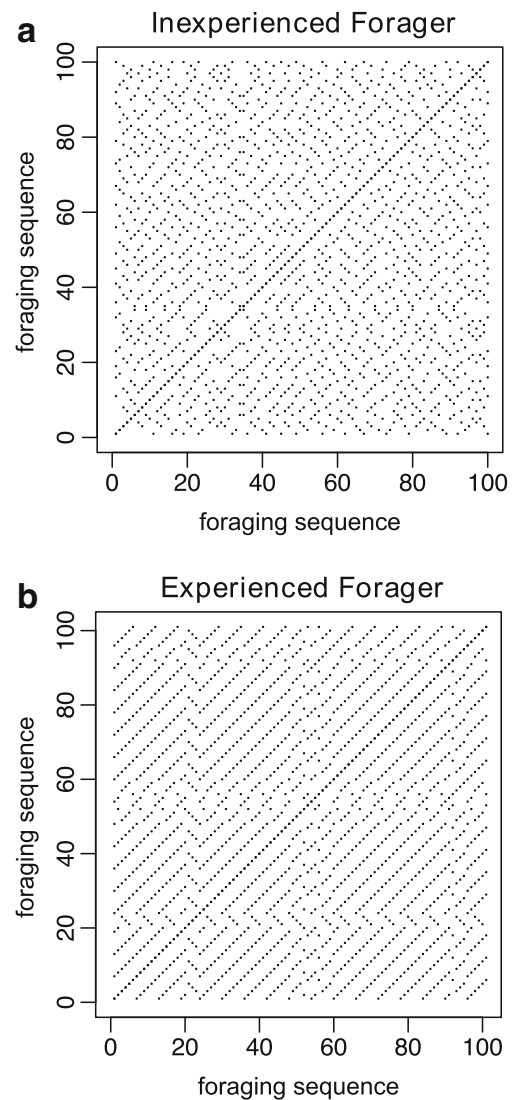
$$\text{DET}_{\text{inexperienced}} = \frac{26}{777} = 0.03$$

$$\text{DET}_{\text{experienced}} = \frac{517}{784} = 0.66$$

Using a generalized linear mixed-effects model with binomial errors, we found that traplining significantly increases after bees gain experience on the foraging array ( $P=4.77 \times 10^{-6}$ ; see [Electronic supplementary material](#) for full analysis).

Recurrence plots are useful to visually compare qualitative differences in traplining. Longer diagonal lines indicate greater predictability in the foraging sequence, corresponding to more numerous and consistent traplines. For the inexperienced foraging trials, all diagonals in the recurrence plot are short, and very few points belong to a long diagonal (Fig. 3a). However, after the forager gains experience, the number and lengths of diagonals in the recurrence plot increase, and most points belong to a long diagonal (Fig. 3b).

In Fig. 4, we use recurrence plots to compare the traplining behavior of four different bees (indiv. 2, 4, 5, and 6 from Lihoreau et al. 2012a) after gaining experience inside a foraging array. The first two foragers shown have very predictable foraging sequences and therefore have high DET values, while the last two foragers have much less predictable sequences and low DET values. Though the pairs of predictable and unpredictable foragers have similar DET values, the recurrence plots reveal qualitative differences in traplining patterns. The recurrence plot for forager three, for instance, has a higher prevalence of diagonals perpendicular to the main diagonal. The percent of points in a perpendicular diagonal (out of all points belonging



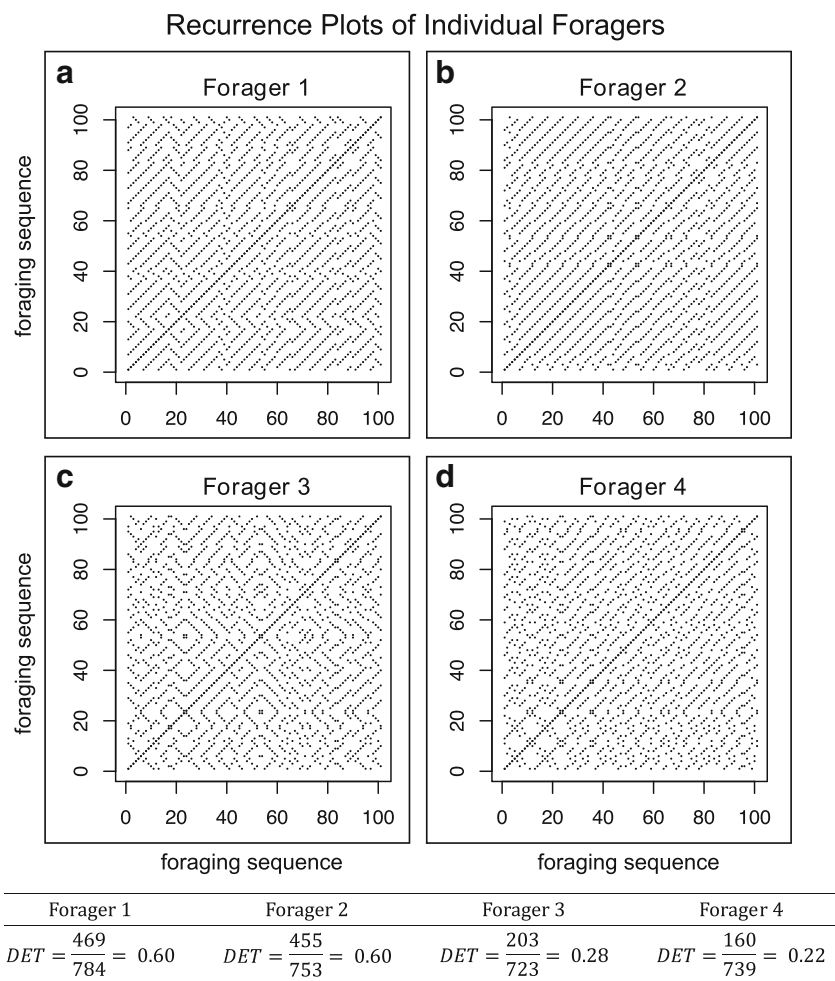
**Fig. 3** **a** Recurrence plot of the foraging behavior of a bee after first entering a foraging array. **b** Recurrence plot of the foraging behavior of the same bee after gaining experience on the array (following 360 floral visits). *Longer diagonal lines indicate greater predictability in the foraging sequence, corresponding to more numerous and consistent traplines* (data from indiv. 1 in Lihoreau et al. (2012a))

to a diagonal of  $l=5$ ) was 40 % for forager 3 and only approximately 2 % for foragers 1, 2, and 4. This pattern indicates forager 3 was more likely to reverse the direction of its traplines. If we do not classify perpendicular sequences as recurrent series, we find that DET is slightly reduced for individuals 1, 2, and 4 (a decrease of 0.02, 0.01, and 0.01, respectively) and greatly reduced for forager 3 (a decrease of 0.12).

## Final remarks

In this paper, we developed a modified version of DET from RQA as a standard metric for quantifying sequential behaviors. We compared DET with existing metrics and analyzed

**Fig. 4** Recurrence plots of four individual bee foragers and the corresponding DET values. The plots show the last 100 flower visits after the bumble bees gained experience on a foraging array (data from Lihoreau et al. (2012a)). Foragers 1–4 correspond to indiv. 4, 2, 6, and 5, respectively, from Lihoreau et al. (2012a). *Longer diagonal lines* indicate greater predictability in the foraging sequence and more consistent traplines (as in **a** and **b**). *Many short diagonals or isolated points* indicate less consistent traplines (as in **c** and **d**). *Lines perpendicular to the main diagonal* indicate a reverse in trapline direction (as is most prevalent in **c**). The corresponding DET values were calculated with  $l=5$



the sensitivity of DET to resource density using simulated foraging sequences in a case study of trapline foraging.

We found that many of the properties of determinism make it a promising metric for comparing sequential behaviors between a range of study systems and experimental designs, which would not have been possible with existing metrics. First, we found that DET is able to detect recurrent patterns over the entire length of a behavioral sequence without relying on comparisons of sequential pairs or other subsets of the behavioral sequence. Second, we found that determinism is relatively insensitive to the number of possible sequence elements, thus allowing for direct comparisons between studies with roughly similar numbers of possible behavioral elements. Third, determinism does not require a specific start or end point or a particular sequence of interest, as is often the case with similarity indices (Thomson et al. 1997; Lihoreau et al. 2010). Fourth, DET is able to detect recurrent sequences from incomplete sequence data, which are the norm in field settings. Determinism also offers additional advantages for particular types of recurrent behaviors, for instance, allowing for detection of sequence repeats in either forward or backward

directions, and the ability to set the minimum length of a recurrent sequence. Recurrence quantification analysis (from which determinism is derived) also offers additional tools (Marwan et al. 2007) which may be useful for quantifying other properties of interest, such as the average length of recurrent behavioral sequences.

One potential shortcoming of determinism, which is also prevalent among existing metrics, is that it may underestimate sequence predictability if there are many imperfections in otherwise consistent behavioral sequences. In such cases, DET can be extended by using modified DNA sequence alignment techniques to minimize the impacts of inserted or deleted elements in behavioral sequences (Waterman 1989; Thomson et al. 1997), a detailed discussion of which is beyond the scope of this manuscript.

Determinism may also need to be complemented with other metrics depending on the question of interest. For example, while DET can be used to detect the overall level of sequence similarity, it would not be used to directly compare an observed sequence with a specific reference sequence. In the case of trapline foraging, DET is



useful to detect traplines following many different routes, but in some specific cases, only one or two particular routes are of interest (Lihoreau et al. 2012a). For these cases, DET may be combined well with sequence similarity indices, which are designed to detect sequence similarity to a particular route (Thomson et al. 1997; Lihoreau et al. 2010). When combined, the two metrics may be used to ask additional questions, such as the proportion of all strong trapliners which are following a particular route of interest.

The straightforward application of determinism and other RQA-derived techniques will promote interest in the role of sequential behaviors important for ecological and evolutionary processes, including sexual selection (Barske et al. 2011), parasite–host interactions (Fentress and Stilwell 1973; Berridge et al. 2005; Kristan 2014), and efficient resource gathering (Lihoreau et al. 2012a; Vaudo et al. 2014). Specifically, the wealth of techniques developed for RQA may be applied to quantifying grooming sequences, complex mating dances, or social dominance displays, as well as sequential patterns of time allocation. The versatility of RQA will enhance the use of sequential behaviors in ecology since it allows for comparisons of sequential behavior between individuals and across multiple studies, taxonomic groups, and environments. For example, sequential behaviors may be used for comparing ecologically important factors, such as perceived predation risk (Caraco 1982) or foraging efficiency, across varying environments. One might also use RQA to test whether the order of sequential behaviors is critically important for the outcome or efficacy of the behaviors, as may be the case for complex mating dances or trapline foraging. In contrast, other sequential behaviors may be equally effective as long as all elements appear in the sequence, as may be the case for sequential grooming patterns. In these cases, functionally similar behaviors may be packaged together in a particular sequence only as a memory tool to decrease the likelihood of forgetting any one behavior. Though sequential behaviors important for ecological process have been traditionally neglected due to the lack of an appropriate metric for many questions and datasets, the versatility of determinism and RQA will enhance their use and potentially lead to important innovations in behavioral ecology.

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