R<small>EVIEW</small>

Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare

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While the incorporation of mathematical and engineering methods has greatly advanced in other areas of the life sciences, they have been under-utilized in the field of animal welfare. Exceptions are beginning to emerge and share a common motivation to quantify 'hidden' aspects in the structure of the behaviour of an individual, or group of animals. Such analyses have the potential to quantify behavioural markers of pain and stress and quantify abnormal behaviour objectively. This review seeks to explore the scope of such analytical methods as behavioural indicators of welfare. We outline four classes of analyses that can be used to quantify aspects of behavioural organization. The underlying principles, possible applications and limitations are described for: fractal analysis, temporal methods, social network analysis, and agent-based modelling and simulation. We hope to encourage further application of analyses of behavioural organization by highlighting potential applications in the assessment of animal welfare, and increasing awareness of the scope for the development of new mathematical methods in this area.

Keywords: fractal analysis; Theme; Markov chains; social networks; modelling; animal behaviour

1. INTRODUCTION

The analysis of behaviour is an area being greatly advanced through the application of mathematical and engineering methods, e.g. modelling (Sumpter 2006), artificial intelligence (Minsky 2006), remote behavioural detection methods (Fowler *et al.* 2001; Troscianko *et al.* 2004), operant equipment (Cook *et al.* 2004) and advanced statistics (Browne *et al.* 2007; Mundry & Sommer 2007). Such methodologies could be of great influence when behaviour is used to make inferences about an animal's welfare, but are currently vastly under-utilized for this purpose. Here, we review advances in the analysis of behavioural organization. We use the term behavioural organization to refer to the arrangement of behavioural states relative to each other in time and space, and in relation to other individuals' locations or behaviour.

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Behaviour is used as a measure of animal welfare because an animal's state can be inferred from its actions. Classically, animal welfare has concerned the identification of negative welfare states; of markers of pain and stress, aggression, boredom and abnormal behaviour (Fraser 2008). Increasingly, there is also an interest in positive welfare states and potential markers of these, such as play and anticipation (Yeates & Main 2008). Many recent studies have focused on individual differences, through studies of personality and coping strategies, and interactions between maternal environment, early environment and later environments (e.g. Ruis *et al.* 2001; Coutellier *et al.* 2009). There is also interest in social interactions, whether positive, negative or neutral, and the effects of these on welfare (e.g. Ruis *et al.* 2001). Behaviour is recorded *in situ* to measure the welfare of animals in a particular environment, or in response to short-term changes in environment or a particular stressor or stimulus. The responses of animals and the choices they make in tests are used to infer the abilities of that animal or

to try to understand what animals want or do not want (Dawkins 2003).

Several basic methods exist for scoring animal behaviour, where behaviour is considered to be a process in which events occur over a continuous time-stream. Behaviour can be recorded continuously or sampled at regular intervals, the behaviour of an individual or group can be recorded, it can be categorized by social interactions, vocalizations, locomotion, activity/inactivity, location or a complete comprehensive ethogram (see Martin & Bateson (1993) for a classic introductory text). In this review we present a simple example dataset of the behaviour of six chickens in a pen to demonstrate each of the mathematical techniques outlined (see boxes 1–4). For full details of the example dataset please see the electronic supplementary material.

A common approach to the study of behaviour in welfare science is to compile a comprehensive ethogram of each discrete type of behaviour. Correlations with other measures of welfare are used to identify behaviour associated with positive and negative welfare states. It is not unusual to find ethograms consisting of a large number of behaviour states, or events. In describing the play behaviour of equids, McDonnell & Poulin (2002) describe 38 states, which they divide into five distinct categories of play. As this example demonstrates, behaviour can be divided and further subdivided into progressively more specific types. Behaviour can also be subdivided into concurrently scored, overlapping behaviour patterns, to account for the possibility that an animal can be performing more than one behaviour at any one time, for example sitting and eating while interacting with a conspecific.

Ethogram approaches focus on discretization: approximating a continuous process by division into discrete parts. These discrete parts are commonly analysed individually, disregarding temporal and structural detail (organization). Often behavioural indicators of welfare show poor correlation with other measures of welfare, particularly physiological measures (Dawkins 2003). Clearly, current behavioural measures of welfare are not ideal and new methods of analysis are needed. There are reasons to believe that analysis of behaviour that incorporates measurement or understanding of behavioural organization might be of particular relevance when it is to be used as a measure of welfare.

The organization of behaviour encodes information on complexity, variability and flexibility, all of which are believed to be important in determining animal welfare. Animals with a large and flexible behaviour repertoire are expected to have better welfare. If an animal has more behavioural options available to them, we expect them to be better able to control their environment, for example they are able to re-prioritize motivations when necessary. A loss in controllability in the environment is linked with chronic stress and hence poor welfare (Wiepkema & Koolhaas 1993). It may be that welfare is compromised when animals are no longer in control and when their adaptive, re-prioritizing abilities have become compromised; when they are no longer able to cope (Bassett & Buchanan-Smith 2007).

Environmental complexity produces neural complexity, in turn producing behavioural complexity. Environmental complexity at the stage of brain development confers a host of benefits: decreasing stress reactivity; improving health and healing; delaying the onset of neurodegenerative diseases; and protecting against development of some forms of abnormal repetitive behaviour (for reviews see Lewis 2004; Fox *et al.* 2006). Many captive animals are reared in barren conditions and then expected to cope with unpredictable stressors. This creates a mismatch between the available behavioural complexity and the level of behavioural complexity that would allow effective coping.
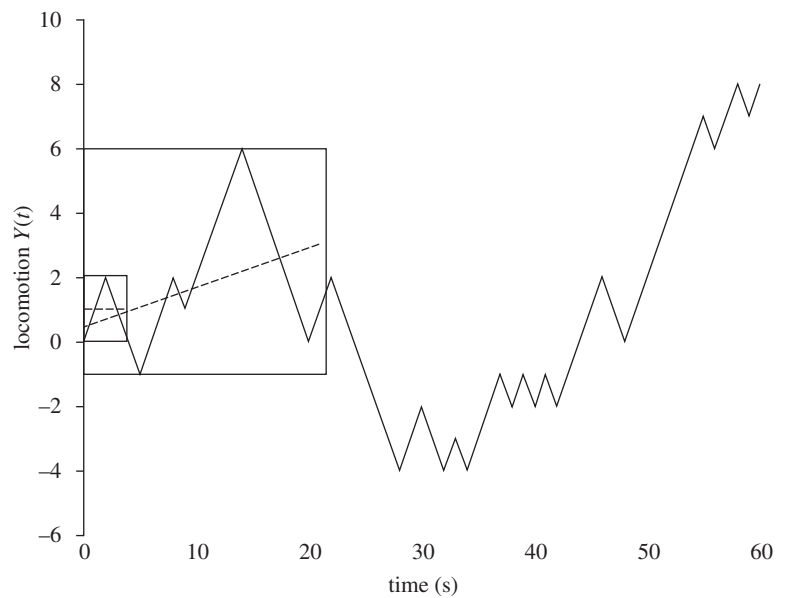
A common outcome of stress is a reduction in the variability of physiological responses. For example, heart rate variability decreases in response to an acute stressor (Visser *et al.* 2002) and the diurnal cortisol profile becomes flattened and less variable in people who are chronically stressed (Miller *et al.* 2007). Since behaviour and physiology are intrinsically linked, it is possible that behaviour will follow a similar pattern. Alterations to the profile of response can be linked under the concept of allostasis, a model of physiological regulation. Allostasis considers that, when an animal is coping with its environment it has a wide regulatory range of mechanisms available, but once it gets into an allostatic state (system overload), the animal is forced into a narrower regulatory range and has an increased chance of veering off into either hypo- or hyper-reactive states (e.g. Wingfield 2005; Korte *et al.* 2007). Under this model, behaviour is expected to become either more or less variable than at baseline in response to stress overload.

One final reason to believe that behavioural complexity is important is that animals devote a large amount of resources through play to ensure they are behaviourally complex. While there are different theories to account for the evolution of play most point towards a more functional, behaviourally complex animal (either socially, physically or in terms of general flexibility; Spinka *et al.* 2001). Play is found universally among mammals and in birds, reptiles and even in an invertebrate (Burghardt 2005). In order to be this phylogenically widespread, play, and therefore also behavioural complexity, must confer significant benefits.

Here we discuss the possibilities that measures of behavioural organization present to welfare science, with respect to four analytical approaches: fractal analysis; temporal analysis (including Markov chains and time pattern approaches); social network analysis (SNA); and agent-based modelling and simulation (ABMS). The methods chosen have the ability either to measure behavioural organization or elucidate the rules that determine the organization, and some can be used to explore the consequences of the organization through modelling and simulation. With the exception of ABMS, this review will primarily concern measurement of behavioural organization. Each section will (i) outline the general principles and practices of each method; (ii) briefly review traditional uses of the methodology; (iii) present some examples of actual and possible applications to the study of animal behaviour and welfare; and (iv) highlight some of the advantages and disadvantages of the techniques.

Box 1. Detrended fluctuation analysis using example data from bird 1.

time (s)	behaviour	$Z(i)$ binary behaviour sequence	$Y(t)$ cumulative binary sequence
0	walk	1	1
1		1	2
2	sit	−1	1
3		−1	0
4		−1	−1
5	walk	1	0
6		1	1
7		1	2
8	sit	−1	1
9	walk	1	2
10		1	3
⋮	⋮	⋮	⋮
55	walk	1	8
56		1	9
57	sit	−1	8
58	walk	1	9
59		1	10
60	end recording	1	11

The cumulative binary behaviour sequence $Y(t)$ (calculations shown in the table) is plotted at 1s time intervals in the line graph to the right. $Y(t)$ is divided into boxes of length b, and regression lines fitted. $F(b)$ is the function of changing box size on regression lines. α values are calculated from the fit of a bi-logarithmic plot of $F(b)$ against b, shown in the adjacent graph. A linear slope $= \alpha = 0.5$. In this example patterns of activity are uncorrelated with time.
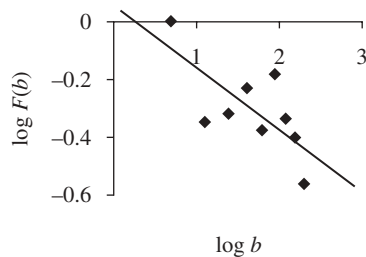
2. FRACTAL ANALYSIS

2.1. Principles

Fractal analysis concerns the effects of scaling on the measurement of a continuous variable. Fractals are shapes with self-similar structure, i.e. that can be decomposed into smaller versions of themselves. Fractal analysis covers a range of methods that examine the degree to which objects or processes are fractal-like or self-similar, by comparing measurement of objects or processes at different resolutions. Fractal analysis can deal with objects and processes; the differentiation being that the former are measured on a physical scale and the latter a temporal scale. The classic example of fractal analysis is Mandelbrot's (1967, cited by Rutherford *et al.* 2004) examination of coastlines. Consider three different profiles of a coastline: one is smooth and could be represented by a continuous fluid line; one is made up of inlets that are formed inside larger inlets and so on; and a third coastline is rugged and craggy in nature. Both the smooth coastline and the inlets coastline have regular patterns, the rugged coastline does not. While the regular structure of the smooth coastline is easily quantified by traditional (Euclidean) geometry, the self-similar inlet coastline is not. Fractal geometry was conceived to be able to mathematically quantify the more complex type of regularity exhibited by the inlet coastline.

There are two types of behavioural data used in fractal analysis: (i) behavioural processes scored on a binary scale and (ii) pathway analysis (using x–y coordinates). Observations of the presence or absence of a state over time form the binary scale, e.g. whether an animal is active or inactive (Cole 1995), or fluctuation between two states (Alados & Huffman 2000). The method of fractal analysis most applied to such time series is detrended fluctuation analysis (DFA) (Peng *et al.* 1994, 1995*a,b*). In DFA, the correlation within binary sequences, $Z(i)$, encoded 1 (e.g. for active), −1 (e.g. inactive or social), is graphically represented using a random walk, plotted as a function $Y(t)$ over fixed time intervals, by summing the previous sequence (box 1). The function $Y(t)$ is divided into series of progressively smaller sections, or boxes, b (i.e. measured at different time resolutions). Optimal box size can be established using the method outlined in Tavazoei & Haeri (2007). A regression line $b(t)$ is fitted to the boxes and a mean taken of the residual variance of the whole sequence for each box size. Finally, the slope of the bi-log plot of the mean residual variance $Y(t)$ and box size (b) is used to calculate the fractal exponent, α, as a function of $bF(b) = b^{\alpha}$. Regression lines should be fitted using the maximum likelihood method since least-square regressions in the log–log domain can lead to biased model estimates (Clauset *et al.* 2007). For a completely random sequence $\alpha = \frac{1}{2}$. As α increases above 0.5, the sequence becomes more self-similar or fractal-like. Lower

α values indicate less regularity in the sequence and the absence of predictable patterns over time (or space in the case of pathway analysis).

For the study of animal pathways, Paulus & Geyer (1993) validated a type of fractal analysis for rats' movements, which compared microscopically recorded events with macroscopic behaviour patterns by partitioning local and mass-scaling exponents, using a filter value, q (analogous to the Lagrange multiplier) so that both high and low local spatial scaling exponents (the fractal dimension based on smaller and larger scales) contribute to the fractal score. Another way fractal analysis has been applied to pathway analysis is as a measure of path tortuosity: where tortuosity is the degree of turning in a given space and time, often used to distinguish between goal-oriented and random search movements. Incorporation of fractality into a model of Brownian motion could yield a model of a random search and while such models do exist (Dicke & Burrough 1988; Sugihara & May 1990), they are yet to be verified (Benhamou 2004).

A final example of the use of fractal analysis is in identifying hierarchical or functional levels of organization in behaviour. Using fractal analysis, Fritz *et al.* (2003) identified three functional levels under different spatial resolutions in wandering albatrosses' flight patterns (although see Edwards *et al.* (2007) for a critique). Under high resolutions, birds were moving in accordance with wind fluctuations; under medium resolutions birds were moving towards food sources, and on larger scales (lower resolutions) flight patterns corresponded with movement between patches. Hierarchical levels can be identified by the consistency in α (the scaling exponent) over a given range of k (resolutions). Outside this range, there will be a shift and a sudden change in the value of α.

2.2. General examples

Fractal analysis found early application in geology, but has many varied applications describing: regularity of heart beats (Yamamoto & Hughson 1991); structure of vocalizations (Pickover & Khorasani 1986); changes in cell mass and complexity (Smith *et al.* 1989); gait and movement analysis (Riley & Turvey 2002); disease spread (Cazelles *et al.* 2007); population dynamics (Hastings & Sugihara 1993); changes in economic markets (Gatti *et al.* 2008); and the structure of particles (Shibuichi *et al.* 1996).

2.3. Animal behaviour applications

Using DFA, more structured temporal sequences of behaviour (i.e. with higher α values) have been interpreted as a sign of stress, and have been observed with the stresses of pregnancy, disease (Alados & Huffman 2000) and exposure to toxins (Alados & Weber 1999). To date, five studies have examined the effects of stressors on temporal regularity of behaviour using DFA as a welfare indicator. One study found laying hens responded to proposed stressors of a novel arena and a restraint procedure with less regular vigilance patterns (lower α values), but did not find changes in response to blood sampling (Rutherford

et al. 2003). In a separate study, there were no differences found between the structure of behaviour in differentially food-restricted broiler chickens (Hocking *et al.* 2007). María and co-workers (2004) found that locomotor patterns of chickens became less regular with age (lower α values) and were significantly altered by food limitation, where patterns became more regular (higher α values). In response to other stressors, a small sand-bath and introduction of strangers, chickens locomotor patterns were less regular (lower α value) and, in the sand-bath, perching and foraging patterns were also less regular (lower α value) and resting was more regular (higher α value). A fourth study examined pigs exposed to a chronic mild stress treatment. It found that pigs had more regular (higher α values) postural behaviour after being exposed to stressors (Rutherford *et al.* 2006). Less regular patterns (lower α values) were found in the movements of quails selected for low stress when compared with high stress in an open field test (Kembro *et al.* 2008). The studies outlined demonstrate that there are not consistent directional relations between stress and the fractal quality of behaviour as Alados supposes. Changes in regularity probably reflect adaptive shifts in the structure of behaviour in response to acute stress, so that the fractal exponent will depend on the type and duration of the stressor applied, the resolution of the behaviour examined, and which behaviour is being analysed.

The fractal dimension of pathways can also be altered by stressors, and this has been studied in fish exposed to toxins (toxins lowered the fractal dimension; Kane *et al.* 2004), and isolated and group-housed rats (isolated rats had straighter movement pathways and more predictable sequences than group-housed controls; Paulus *et al.* 1998). Fractal analysis of pathways could be used to identify animals with low variability in patterns of movement, such as those with locomotive stereotypies.

The potential use of the fractal dimension to identify levels of hierarchical organization is currently being examined in the grazing paths of cows. Early results indicate an effect of group size on the fractality at high resolution (<9 m) and an effect of paddock area at low resolution (>9 m; S. Tada 2008, personal communication). Circadian and ultradian rhythms in activity levels of free-living ruminants have been examined using a similar mathematical method (Scheibe *et al.* 1999). The fractal dimension exhibits consistency at the level of the individual (Rutherford *et al.* 2006), so has potential application in studies of animal personality or coping strategies.

The fractal quality of behaviour could be a valuable addition to behavioural indictors of welfare because it characterizes a type of organization that is frequently exhibited by natural systems: self-similarity. It can indicate how variable behaviour is and can be used to identify layers of behavioural structure. However, to date, links between the fractal quality and other indicators of animal welfare are mixed, and in order to find patterns in changes to regularity further studies are necessary. In order for fractal analysis to be valid much data are required and a lengthy period of time should ideally be measured. Hence, the analysis might be more suited to behaviour processes that can be measured simply in a binary manner but where interest lies in

patterns over an extended time period (e.g. sleep; Lo *et al.* 2004). When the focus of data collection is placed on the quantity of data collected rather than observations rich in detail, such as can be the case for automated methods of behavioural data collection, fractal analysis can help condense large amounts of data.

2.4. Advantages and disadvantages

2.4.1. Advantages

(i) Identifies self-similarity, a type of organization that is commonly exhibited by natural systems but not easily quantified using traditional mathematics.
(ii) Examines long-range patterns, so condenses information from data scored over extended time periods.
(iii) Can identify hierarchical or functional levels of behavioural organization.

2.4.2. Disadvantages

(i) Measures fluctuation between two states, such that types of behaviour must be considered independently.
(ii) Much data are required for valid fractal analysis.
(iii) As with many welfare indicators, it can be difficult to interpret in relation to welfare. There is no simple relationship between the fractal quality of behaviour and stress.

3. TEMPORAL ANALYSES

3.1. Principles

Behaviour is a continuous process and yet often when it is analysed it is separated into discrete events where structural detail, such as temporal arrangement, is ignored. Temporal analyses retain information on structure, effectively reconstructing events into meaningful sequences. We outline two such analyses below: Markov chain-based methods and time-pattern methods.

3.1.1. Markov chain methods. A Markov chain is a series of events where the next event depends only upon the current state, or short chain of states. The Markovian property is used to determine sequential organization or determinism, by considering transitional probabilities between states (Gillespie 1992). In contrast to fractal analyses, which consider long-range correlations, Markov chain-based methods are concerned with the pattern of contiguous states: which specific state follows which. The number of discrete states (or greatest number of states) that best predicts the next state is the order of the chain. When only transitions from one event to the next are considered, this is known as first order. It may be the case that second- (three sequential events), third- (four sequential events), or even fourth- (five sequential events) order chains better fit behavioural data. In practice, real behavioural data rarely meet the requirements of tests of high-order dependencies because there are many combinations of transitions

between behavioural elements which will not be observed (Haccou & Meelis 1992). States can be grouped together so that lower order chains can be constructed from higher order ones (for method see Cane 1959).

The most basic Markov model is a discrete-time, finite chain with constant transitional probabilities. Although there is not the scope to discuss these in detail, readers should be aware that other Markov-based models exist, which may be more suitable for behavioural data (for review of Markov models see Barbu & Limnios 2008). These include: continuous-time Markov models, although these are often based on a discrete-time approximation (Yin & Zhang 2005); hidden Markov models, where the state is unobservable but observable states can be used to infer the hidden state (e.g. foraging behaviour might be used to infer hunger); or semi-Markovian models, where the transitional probability depends in part on the current state, but also on another property such as the time spent in that state.

Markov chain methods are bottom-up, since more global features of the data are constructed or measured from the observed data, and as such can be computationally challenging. The computation is challenging because transition matrices between behavioural states can rapidly become large when all combinations of behavioural states are considered. In the earlier example of play behaviour in horses (McDonnell & Poulin 2002), there were 38 types of play behaviour. Possible combinations of transitions between these play types are: 1444 first-order; 54 872 second-order; and 2 085 136 third-order chains. This type of computation is possible but time-expensive.

3.1.2. Time-pattern approaches. Some pattern metrics use a more efficient top-down approach, applying global rules such as data-mining algorithms to observed time-series data. Many time-pattern algorithms have been formulated (e.g. SPADE, Patin *et al.* 2007; PrefixSpan, Pei *et al.* 2001) and while it is generally agreed that such algorithms have wide applications, to date their application to the study of behaviour has been limited. There has been some time pattern-based software development specifically focused on behaviour. Magnusson's Theme programme (Noldus Information Technology, Wageningen, The Netherlands) is by far the most widely applied to the study of animal behaviour and hence we focus on this methodology here. Other softwares designed for analysis of behaviour, such as GSEQ (Bakeman & Quera 1995), or the application of the time-pattern algorithms derived from data-mining techniques, could have similar utility in the study of behaviour sequences.

Theme decides on time patterns using pattern-detection algorithms based on: (i) the order of events; (ii) the time distances between them; (iii) events relative position on a time scale; and (iv) the probability of each event occurring (Magnusson 2000, 2005). Because the algorithms consider the duration and length of time between events, Theme can also detect patterns with an intervening event. If the between- or within-event duration is considerably longer or shorter than other observations of the pattern, it becomes unrecognizable by the algorithm and will not be counted as a time pattern, just as a sentence

would become unintelligible if phonemes were slowed or quickened beyond a threshold level (Magnusson 2005).

To identify time patterns, the first stage is to establish the bout criterion interval, where a bout is defined as a temporal cluster of events, and all events within that bout make up a time pattern. Theme's pattern-detection algorithm searches for the longest time between the end of element X1, which lasts a duration d1, and the beginning of the next element X2, which lasts a duration d2, with the constraint that X2 appears after X1 within time frame $[t+d1, \ t+d2]$ significantly more than expected given that X2 has a constant probability of occurring n times, randomly distributed throughout the observation period $[t1, t2]$. The processes are repeated with the newly identified time patterns treated as elements until no more time patterns are found (for more details, see Magnusson 2000, 2004, 2005). The sensitivity of the pattern-detection algorithm can be altered using various parameters entered by the experimenter (see Magnusson 2004; electronic supplementary material in Bonasera *et al.* 2008); however, there exists no objective procedure for determining these parameters.

3.2. General examples

Markov models have been used widely in genomics and phylogenetic analysis (Larget & Simon 1999; Krogh *et al.* 2001) and in artificial intelligence where they are used both for analysing original behaviour and then regenerating it artificially (Brand *et al.* 1997). The Markov property is a central mathematical model, and contributes to statistical (Hastings 1970) and computational advances (Keller-McNulty *et al.* 1991). Briefly, other examples of Markov-based analyses include: particle structure and movement (Hannenhalli & Russell 2000); analysis of disease spread (McBryde *et al.* 2007; Keeling & Ross 2008); meteorology and climate analysis (Valdez & Young 1985; Young 1994); distribution and movement of plants and animals (Miall 1973); analysis of speech and acoustics (Hawes & Foley 1973); and sequence analysis of sports footage (Leonardi *et al.* 2004).

Unlike other methods in this review, Theme's time patterns were specifically designed to analyse behaviour. Outside of animal behaviour, Theme has been used in the analysis of sports sequences (Borrie *et al.* 2002; Jonsson *et al.* 2006); in human psychology and psychiatry research (Grammer *et al.* 1998; Lyon & Kemp 2004); and to understand patterns in language (Anolli *et al.* 2005).

3.3. Animal behaviour applications

The application of Markovian methods is not new to the study of behaviour or welfare (e.g. Cane 1959; Wechsler & Bachmann 1998). Markov chains are mentioned in classic behavioural methods texts (Martin & Bateson 1993; Slater 1993). Markov models have previously been used in animal welfare science to understand eliminative behaviour (Wechsler & Bachmann 1998) and oral/nasal/facial activity in pigs (Dailey & McGlone 1997). Pigs were found to follow a pattern of 'enter dunging area, sniff, posture, defecate, urinate and sniff', when eliminating and had fewer transitions that involved the top of the snout when feeding outdoors than when feeding indoors. Such details could be

useful in the design of housing systems or to understand development of abnormal feeding behaviour. A Markovian method, the χ^2 test for sequential dependency (Haccou & Meelis 1992; also see box 2), has been applied to repetitive behaviour in captive starlings (Asher *et al.* 2009). Starlings were found to have less-repetitive behaviour patterns in large and medium-sized long-shaped cages. They have also been used to analyse perseveration in the Gambling task, an operant task examining flexibility in pattern learning, in animals and humans (Garner *et al.* 2003).

Theme has been used to study human–animal interactions (Kerepesi *et al.* 2005, 2006), behaviour in feed-restricted hens (Merlet *et al.* 2005; Hocking *et al.* 2007) and feeding behaviour in chicks (Martaresche *et al.* 2000). Most recently, a study of drug-induced stereotypic behaviour in mice used Theme as a method of objectively quantifying stereotypy (Bonasera *et al.* 2008).

For both methodologies permutation methods need to be applied to test the likelihood of obtaining the observed pattern under randomness given environmental and behavioural constraints (visual inspection is recommended for this comparison in Theme). To this end, we suggest the use of Monte Carlo methods to account for impossible and improbable transitions, an approach taken by Bonasera and co-workers (2008). While temporal analyses could be applied to almost any study of behaviour, the obvious usage is scoring repetitive behaviour, which is more deterministic because it is predictable in time and space.

3.4. Advantages and disadvantages

3.4.1. Advantages

(i) Retains information concerning structure; order in the case of Markov chains, and order and timing in the case of time patterns.
(ii) Groups discrete behaviour events into patterns according to their co-occurrence.

3.4.2 Disadvantages

(i) Requires investment to determine which model best suits behavioural data, e.g. in which order of analysis to use in Markovian methods and in Theme how to decide the criterion levels of all different variables.
(ii) Care needs to be taken to ensure that baseline randomness is controlled for, given real-word constraints.

4. SOCIAL NETWORK ANALYSIS

4.1. Principles

Formally, a social network consists of a finite set of nodes and the relations defining them: where a node (or actor) is a social entity; an edge (or tie) is a defined linkage between two nodes; and a relation is a collection of edges of specific kind among members of a group. SNA theorists have developed a set of concepts and parameters that enable the researcher to characterize and

Box 2. Testing the Markov property using the χ^2 test for sequential dependency on the direction of movements of bird 1 from example dataset.

(i) number of transitions from A to B (Matrix M_k)

moves from

	right	left	up	down
right	2	4	1	
left	3	2		1
up		1	1	
down	1			1

moves to

$$C_X = \sum_a \sum_b \frac{(n_{AXB} - n_{AX}p_{XB})^2}{n_{AX}p_{XB}} \quad (2.1)$$

where n is the number of occurrences of a particular transition, e.g. n_{AX} is the number of transitions of A to X, and p is the probability of that transition occurring, which is estimated by p_{XB}/n_X. The calculation in based on the typical χ calculation of observed (n) and expected values (NP).
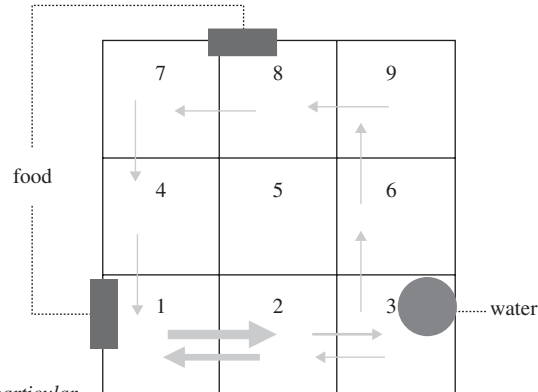
Direction of bird 1's movements in pen notionally divided into squares 1–9.

(ii) number of transitions in the form A-right-B

		A		
	right	left	up	down
right		1 (1.33)	1 (0.33)	
left	1 (1)	2 (2)		
up				
down	1 (0.33)			

B

(iii) number of transitions in the form A-left-B

		A		
	right	left	up	down
right	2 (1.71)	1 (1.42)		1 (0.57)
left	1 (0.86)			
up			1 (0.29)	
down				

B

(iv) number of transitions in the form A-up-B

		A		
	right	left	up	down
right			1 (0.5)	
left				
up		1 (0.5)		
down				

B

(v) number of transitions in the form A-down-B

		A		
	right	left	up	down
right				
left				1 (0.5)
up				
down	1 (0.5)			

B

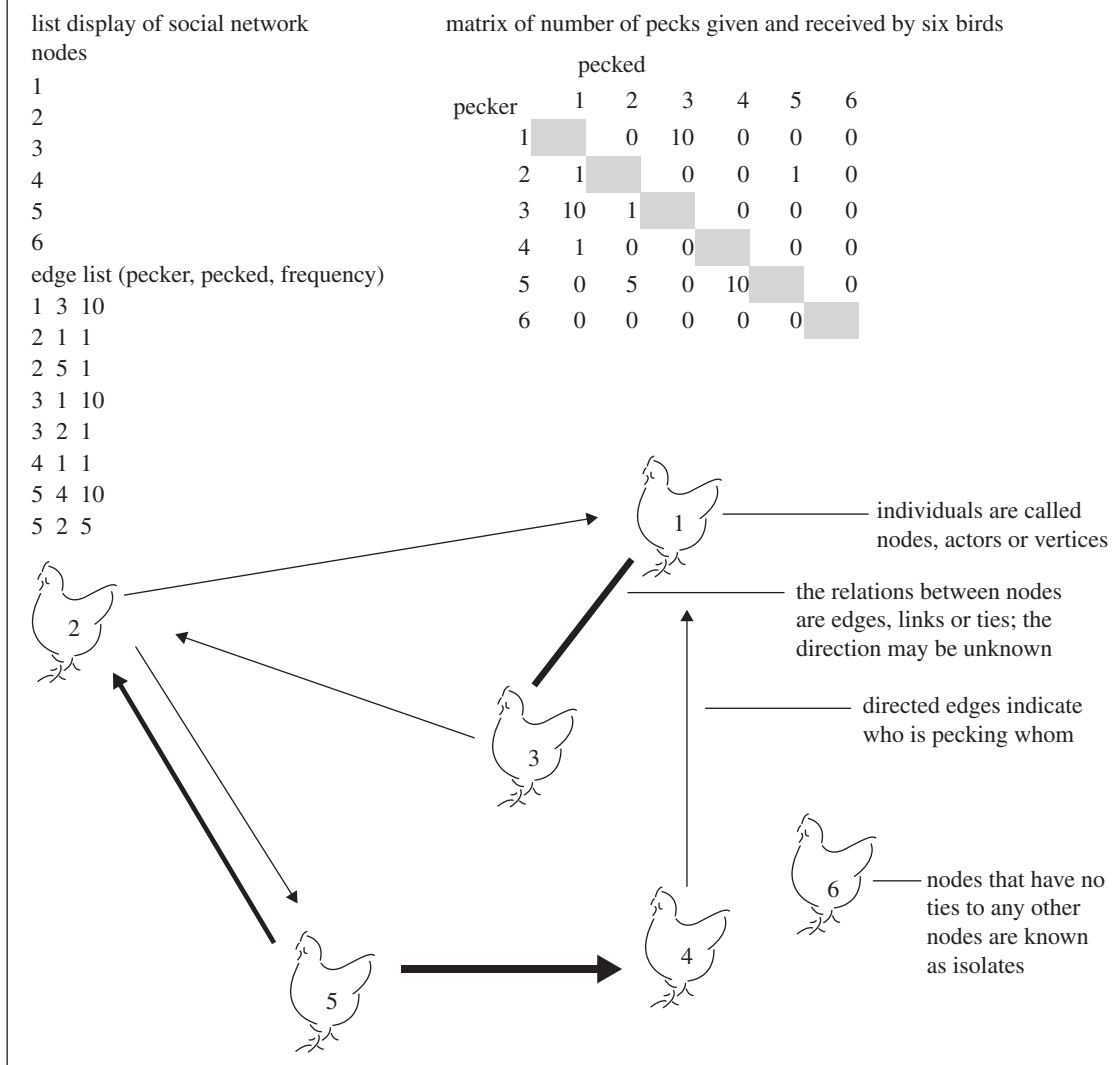$$df = \sum_X (m - k_x - 1)(m - l_x - 1) \quad (2.2)$$

where m is all possible acts, k_x and l_x are the number of transitions towards and from X that equal zero respectively.

Observed directional transitions of the first (i) and second order (ii–v) with expected values in brackets. The χ^2 statistic calculated from equation (2.1) = 2.81 is less than the critical value in χ distribution tables for degrees of freedom from equation (2.2) = 10, so we can conclude there is no evidence of sequential dependency in direction of movements in bird 1. Although it should be noted that due to small values in transitional matrices the assumptions of the χ^2 test were not met and the example is for illustration purpose only.

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compare each member of the network systematically, detect relevant subgroups within a network as well as characterize the network as a whole (see box 3 or for review Hanneman 2005). Wasserman & Faust (1994) describe five key aspects of social networks: (i) models, theories or applications are expressed in terms of relational concepts; (ii) nodes and their relationships are viewed as interdependent rather than independent; (iii) edges between nodes allow the transfer or flow of resources (e.g. information or infection); (iv) the network structure provides opportunities or constraints in individual action; (v) structure is conceptualized as a lasting pattern of relations among nodes.

Depending on the choice of data collection, social networks can be complete, partial or ego-centric. A complete network contains all possible nodes and edges within a population. This can be time-consuming, lead to large, unwieldy datasets and there is potential for missing data. An ego-centric network focuses on a sample individual from a random population and examines all the edges that node has with other individuals in the population, although sampling errors and lack of representativeness can result in a reduction in validity. Partial networks are usually based on snowball-sampling, focusing on the edges between one node and others in the population and then gaining information

Box 3. Social network analysis illustrated by fictitious network of chicken feather pecks.

list display of social network
nodes
1
2
3
4
5
6
edge list (pecker, pecked, frequency)
1 3 10
2 1 1
2 5 1
3 1 10
3 2 1
4 1 1
5 4 10
5 2 5

matrix of number of pecks given and received by six birds

	pecked					
pecker	1	2	3	4	5	6
1		0	10	0	0	0
2	1		0	0	1	0
3	10	1		0	0	0
4	1	0	0		0	0
5	0	5	0	10		0
6	0	0	0	0	0	

individuals are called nodes, actors or vertices

the relations between nodes are edges, links or ties; the direction may be unknown

directed edges indicate who is pecking whom

nodes that have no ties to any other nodes are known as isolates

on the interactions of those nodes and so on. Data collected using snowball methods can be more difficult to analyse (due to sampling biases).

After data collection, analyses centre on the transformation of raw data into network data. An analytical requirement of SNA is that the number of nodes and the period of time examined are finite, and therefore SNA often represents a snapshot of a network bound in space and time, in what is called the 'boundary-specification problem'. Bounding the network to a limited number of nodes requires defining the relevant interactions in topological space. Dynamic network models are increasingly being developed (e.g. Vernon & Keeling 2009, where nodes were farms) to capture rare but important contacts between nodes.

The mathematical foundations of SNA are the graph, statistical and probability theories. Graph theory provides appropriate representation of network data in the form of matrices where all possible combinations of interactions between a set of actors can be represented (box 3). Statistical and probability models are used to test theoretical propositions and allow the

model to show some error or lack of fit. Network data are considered to be interdependent and rarely normally distributed, hence parametric methods cannot be applied. Formal statistical tests based on permutation and bootstrapping procedures are now well established to allow testing of hypotheses and the measurement of type 1 errors. Multiple relationships within and between networks can also be tested using specific statistical models like random graph models (for a description of the most important quantitative models for analysing network data, see Carrington *et al.* 2005).

4.2. General examples

Social sciences developed the network framework as early as in the 1930s and became popular in the 1950s to study human social behaviour (Moreno 1934; Scott 2000). The uses of SNA are diverse in social sciences and some recent ones include: examining flow of information within an organization for management purposes (Nerkar & Paruchuri 2005); modelling fundamental biological theories, such as the evolution of language (Ke *et al.* 2008),

or the spread of innovations (Goldstone *et al.* 2008); and investigating conflicts of interest among authors and potential reviewers (Aleman-Meza *et al.* 2006). Physicists and mathematicians have realized the potential of this methodology to explore the network structure of natural phenomena (Watts & Strogatz 1998), including biological systems, such as yeast genetic interactions and protein interactions (Tong *et al.* 2004; Zhang *et al.* 2008).

4.3. Animal behaviour applications

Animal interaction data that are typically collected include counts of particular type of interaction or proximity, both either with or without identification of individuals. There are many methods for analysing such data other than SNA that have typically centred on standard statistical tests (e.g. odds ratio of being involved in an interaction, tests of association, comparisons of group means) or multiple regression techniques (Minta 1992; Hardy & Field 1998). Such approaches can become laborious if many individuals or groups are involved, and individuals or groups are not statistically treated as interdependent. The type of information that can be extracted from interaction data without individual identification is limited. For instance, counts of aggression may not be representative of group aggression, but rather due to one or two aggressive individuals. Spatial distribution scores (such as nearest neighbour (Henderson *et al.* 2001) or cluster scores (Collins *et al.* in preparation)) are a useful measure of global positioning but do not provide details of the nature of any interactions. For example, are animals close because they are fighting or performing affiliative behaviours? When individuals are identified standard methods do not provide the flexibility that SNA does. For instance, dominance hierarchies typically rely upon a linear relation between all animals within a group which is consistent between contexts. Calculation of dominance hierarchies can be difficult and unreliable without many dyadic interactions (Poisbleau *et al.* 2006). SNA requires identification of individuals, which can be difficult in large groups; however, it does present a number of advantages over the methods outlined above: it has a network rather than a linear structure allowing for fluidity and dynamics in relations; it treats animals as interdependent accounting for the fact that the behaviour of one animal in a group affects the behaviour of another; it recognizes different layers of relational structure and can be used to define groups and subgroups (Wolf *et al.* 2007); it can examine the interactions within and between groups and elucidate the stability of social networks over time (e.g. Drewe *et al.* 2009). Social networks may be constructed from positional or more detailed analyses of behavioural interactions.

After its early application to the social behaviour of primates (Sade 1972), SNA has seldom been applied to animal networks until recent years (Lusseau 2003; Lusseau & Newman 2004; Croft *et al.* 2005; Sundaresan *et al.* 2007; Manno 2008). Recent reviews (Krause *et al.* 2007; Wey *et al.* 2008) and a newly published textbook (Croft *et al.* 2008), written specifically for behavioural biologists, synthesize the literature available on

applications of this methodology. To date, and to the best of our knowledge, the only study of social networks in the field of animal welfare investigated captive primates (rhesus macaques, *Macacca mulatta*; McCowan *et al.* 2008). The conclusions of this study were that aggression could be minimized to prevent severe outbreaks of deleterious aggression in group-housed macaques through the understanding of social behaviour using SNA.

There are two primary reasons that suggest that SNA has utility in the study of animal welfare: (i) to understand transmission probabilities, and (ii) to understand the direct impact of social relations upon welfare. Much of the abnormal behaviour that concerns welfare scientists, such as tail-biting, feather pecking and stereotypic behaviour, spreads either actively due to social learning, or passively through animals encountering a wounded tail or damaged plumage. SNA could improve understanding of behavioural transmission. For example, in large commercial groupings SNA could be used to estimate the number of animals in a group that are likely to encounter each other within a given time-frame. It could also be used to study the effects of mixing animals or removing an individual or individuals from a stable social structure, such as occurs in many commercial pig and cattle farms, on a large scale during culling activities, and in wildlife relocation (e.g. Williams & Lusseau 2006). A key benefit of SNA is its ability to examine simultaneously more than one type of social interaction. Further, the influence of external environmental processes such as rainfall on the interaction patterns of individuals may be examined using SNA (Drewe *et al.* 2009). The network approach therefore complements other more commonly used techniques for the study of animal behaviour.

It has been established for many years that a network of social relationships is one of the most important determinants of quality of life in humans. For example, Berkman & Syme (1979) showed a strong relationship between social network and life expectancy. This has been supported by later studies (e.g. House *et al.* 1988) and meta-analyses (Uchino *et al.* 1996), which further suggest that the quality of relationships is important, as well as the quantity. Social housing has been found to affect rats' and pigs' ability to deal with stressors (Ruis *et al.* 1999, 2001). The importance of social housing and 'stable social groups' is recognized as important in determining animal welfare, for example recommendations for the care of animals in research frequently state that animals should be socially housed wherever possible. However, at present, we do not have a sufficient understanding of what constitutes a good social network as regards promoting good welfare, for any single captive species.

4.4. Advantages and disadvantages

4.4.1. Advantages

(i) Organizes relational data assuming that individuals are interdependent and members of a super-structure called a social network.

(ii) Allows the analysis of relational data at different levels accounting for the interdependency of the data items.

(iii) Analysis may be performed at individual, group or population level.

4.4.2. Disadvantages

(i) Alternative statistical techniques are required, i.e. parametric methods cannot be applied.

(ii) The elements of the network must be defined in time and space, hence identifying individuals is essential.

(iii) Impact of missing network data on analytical results is difficult to assess.

5. AGENT-BASED MODELLING AND SIMULATION

5.1. Principles

ABMS or individual-based modelling and simulation is a type of computation using independent autonomous individuals or 'agents' to describe a system as a whole. The approach is bottom-up and generative. The rules that describe the entire system's behaviour are qualitatively different from those that govern its constituent units and yet the rules governing the units produce the rules of the system (Vicsek 2000). A set of rules or heuristics entered by the author of the model determine how the agents 'behave' and the emergent group behaviour of the agents is revealed. Models can be based on real data and the best validated models are those that are not only based on parameters from real datasets, but are also tested on independent datasets for robustness (Bryson *et al.* 2007). If the model accurately describes observed behaviour of real animals then the logic of the programme (the heuristics, parameters and their relative weighting) is supposed to reflect causal mechanisms. In reality a model can only reveal whether the heuristics and parameters entered are sufficient to generate observed behaviour. ABMS is used to describe how a system functions by subjecting the theoretical individual (agent) to a wide range of environmental conditions and observing the effects, at both the individual and population level. This is achieved by running simulations. The simulations reveal the consequences that arise from the combination of heuristics and parameters.

There is no standard ABMS methodology. The problem to be investigated, and, to a large extent, the author's style, will decide the form the model takes (see box 4 for worked example). This flexibility is a major advantage of ABMS, but also a significant drawback because there is no set precedent (although for suggestion of unifying framework see Grimm *et al.* 2005) and therefore is open to error. Authors may construct models with parameters which they believe to correspond to some real world parameter which actually corresponds to something else. Watts (1998) identifies three stages for models of movement behaviour: (i) initialization, to determine parameters and heuristics; (ii) refinement,

to run simulations with different features, check the model mimics real behaviour and alter parameters/heuristics where necessary; (iii) validation, to compare the model with real systems and assess the predictive ability of the model. ABM heuristics are often borrowed from other areas of science; for instance, the Hills equation, which is more frequently used to describe protein molecule binding, has been used to model flock behaviour (Collins & Sumpter 2007). Some models incorporate artificial neural networks or genetic programming, or endow agents with motivations or emotions (Watts 1998; Abu Maria & Abu Zitar 2007; Broekens *et al.* 2007). They could also incorporate the other methods outlined in this review; for instance, we include basic information about social relations in the example of ABMS in box 4. ABMS can allow for heterogeneity in populations, therefore incorporating behavioural ecology and game theories concerning evolutionary stable strategies (Maynard-Smith 1972). It should, however, be noted that complicated models requiring parameter values for many different effects and relationships are more likely to contain errors and simulations will be subject to large variation. Conversely, complex models can be more intuitive to build, and once built can be reduced to a simplified form. Models that are too complex to analyse analytically can be evaluated using hypothesis testing (Bryson *et al.* 2001).
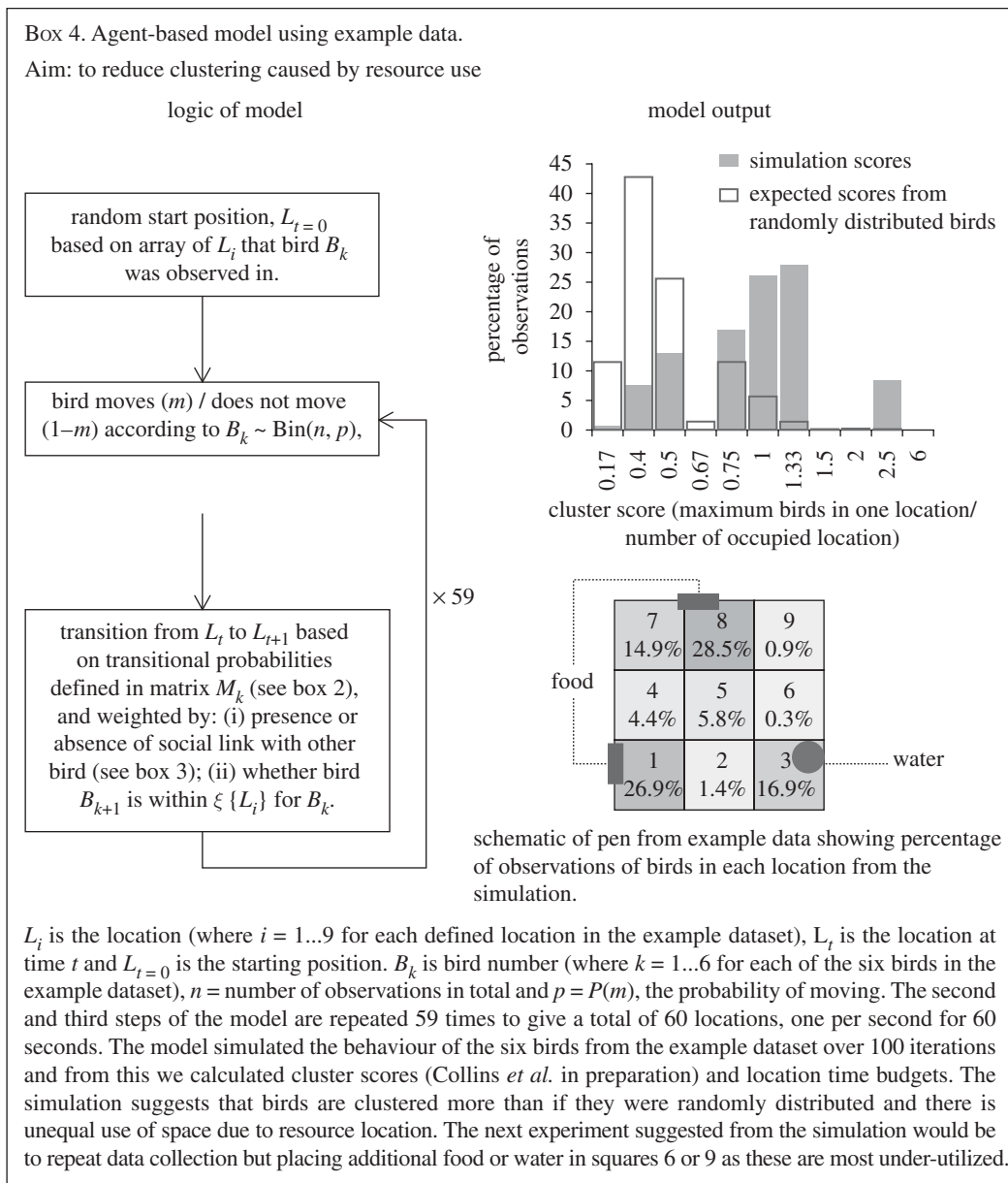
5.2. General examples

ABMS has been used to describe: financial markets (Jefferies *et al.* 2001); bacterial growth (Ben-Jacob & Levine 2006); evolutionary and social processes (Macy & Willer 2002; Bowles & Gintis 2004); and disease dynamics (Eubank *et al.* 2004; Yang *et al.* 2008). It is also a growing part of software design (Jennings 2000).

5.3. Animal behaviour applications

Agent-based models differ from more traditional analytical models that are top-down and at population level. Some such models have been applied to animal welfare; for example, Grafen's (2002) State-free optimization model is concerned with motivation in choice tests and Rands *et al.*'s (2003) work on foraging pairs has implications for obesity in domesticated species such as the horse. Animals have also been modelled as consumers, making choices between resources, using an approach loosely based on microeconomics (Kirkden & Pajor 2006).

The most extensive use of ABMS in animal behaviour is in the study of collective behaviour with examples in insect societies, fish schools and human crowds. The visualization of animal agents in simulated environments has led to their description as animats, the first example of which was Reynold's boids that could mimic behaviour of flocks, herds or schools using just three simple rules-of-thumb (Reynolds 1987). Examples of ABMS in animal welfare have almost exclusively considered the effects of physical environment on farm animal behaviour: the effect of lighting on broiler chickens (Kristensen *et al.* 2006) and the effect of space and resource availability in pigs and broilers (Stricklin *et al.* 1995, 1998; Gonyou *et al.* 1997; Collins & Sumpter 2007). As making real-life

Box 4. Agent-based model using example data.

Aim: to reduce clustering caused by resource use

logic of model

model output

random start position, $L_{t=0}$ based on array of L_i that bird B_k was observed in.

bird moves (m) / does not move ($1-m$) according to $B_k \sim \mathrm{Bin}(n, p)$,

$\times 59$

transition from L_t to L_{t+1} based on transitional probabilities defined in matrix M_k (see box 2), and weighted by: (i) presence or absence of social link with other bird (see box 3); (ii) whether bird B_{k+1} is within $\xi \{L_i\}$ for B_k.

cluster score (maximum birds in one location/ number of occupied location)

7 14.9%	8 28.5%	9 0.9%
4 4.4%	5 5.8%	6 0.3%
1 26.9%	2 1.4%	3 16.9%

food

water

schematic of pen from example data showing percentage of observations of birds in each location from the simulation.

L_i is the location (where $i = 1...9$ for each defined location in the example dataset), L_t is the location at time t and $L_{t=0}$ is the starting position. B_k is bird number (where $k = 1...6$ for each of the six birds in the example dataset), n = number of observations in total and $p = P(m)$, the probability of moving. The second and third steps of the model are repeated 59 times to give a total of 60 locations, one per second for 60 seconds. The model simulated the behaviour of the six birds from the example dataset over 100 iterations and from this we calculated cluster scores (Collins *et al.* in preparation) and location time budgets. The simulation suggests that birds are clustered more than if they were randomly distributed and there is unequal use of space due to resource location. The next experiment suggested from the simulation would be to repeat data collection but placing additional food or water in squares 6 or 9 as these are most under-utilized.

changes to the physical environment is costly, such models are appealing and the number and scope of environments tested can far exceed those that could be tested in the real world.

Much scope exists in application of ABMS from behavioural ecology (and other areas) to animal welfare and for conversion of analytical type models into agent-based ones. For instance, Inglis & Langton's (2006) analytical model accounts for the finding that behavioural complexity reduces in response to environmental complexity. An extension to this model could examine the effects of environmental complexity on group behaviour and test these predictions on group-housed animals. White & Smith (2007) demonstrated how ABMS can be used to evaluate the existing behaviour scoring methods. Since the methodology exists to incorporate genetic programming into ABMS, the phenotypic effects of selective breeding could be examined, thus moving towards the goal of breeding animals that cope better with captive environments. Used as

Monte Carlo methods, simulations could be utilized to make statistical inference and distinguish between hypotheses. For instance, in recent work we compared clustering behaviour observed in real hens with simulated hens which spent the same proportion of time in each location as our real hens (Collins *et al.* in preparation) in a method similar to that used in box 4. We were able to ascertain that hens were being socially cohesive and were not just clustering due to shared resource use.

5.4. Advantages and disadvantages

5.4.1. Advantages

(i) Can run experiments in number and varieties that would be impossible in the real world, thus reducing costs and the number of animals required.

(ii) Can be used to understand the complexity of systems and predict the effects of a large number of variables.

5.4.2. Disadvantages

(i) There is an absence of a coherent framework.
(ii) Complicated models can be unreliable unless relationships between parameters are well understood.
(iii) Models are essentially best estimates if they are not testable, or based on real data.

6. DISCUSSION

Collection of behavioural data is considered standard in the assessment of animal welfare and yet is not exploited to its full potential. Animal behaviour is complex, with simultaneously occurring, differentially contributing processes that do not follow simple linear patterns. Through this review it has become apparent that we currently know very little about the relation between deep structural characteristics of behaviour and animal welfare. We cannot be certain of the utility of behavioural organization methods when compared with typical ethogram approaches, but this can only be elucidated with a more consistent body of empirical evidence.

In addition to the potential advantages of analysis of behavioural organization in assessing welfare, such methods can also directly impact upon welfare. Group-housing of animals used in research could be encouraged by the application of SNA because it can control statistically for the fact one animal may have an impact upon another. Simulations, such as those used in ABMS, require fewer animals and allow experiments to be conducted in number and variety impossible in the real world.

Some of the methods mentioned are based on a bottom-up generative approach and others on top-down rules. Bottom-up approaches can be computationally expensive but may be expected to be particularly useful when there is much variability between individuals and the interactions between them. Top-down approaches, even stochastic ones, treat each individual unit in the same manner and therefore are likely to have most utility when animals share similar behavioural patterns and priorities.

Each of the techniques mentioned in this review captures a different aspect of complexity: fractal analysis captures long-range organization; temporal methods capture short-term behaviour patterns and the determinism of these patterns; SNA captures social complexity; and ABMS can decompose complex behaviour into heuristic rules. For certain data types it is possible that more than one of the methods outlined could be correctly applied. Hocking *et al.* (2007) used the Theme program and DFA to analyse the behaviour of feed-restricted broiler chickens. Theme was found to complement traditional ethogram analysis but DFA was less useful, possibly due to differences in the range of these analyses.

For ease of comparison we have briefly summarized the type of data that could be inputted into the four methods of analysis and the possible outputs (table 1). Comparisons between the methods are probably best explained using examples. While the

Table 1. Comparison of inputs and outputs of methods of analysing behavioural organization.

analysis	input	output
fractal analysis	most usually binary (1,0) data or x–y coordinates from scan sampling	measures self-similarity patterns in data along a random to organized continuum
temporal analysis	discrete behavioural events measured along a continuous time scale	can measure the predictability of chains of events and identify and measure chains of events
social network analysis	presence/absence or frequencies of interactions or associations between individuals in a group	information concerning social structure and individuals' position within this structure
agent-based modelling	model of a system of autonomous parts driven by parameters from real data	deconstruction of systems into heuristic parts and simulations to predict effects of changes to the system

four methods in this review have not been applied to the same behavioural data they have all been applied to the study of football, for example: the fractal dimension of player two-dimensional coordinates on a pitch has been found to be higher (i.e. behaviour is more regular) when teams were defending (Kim 2006); more consistency has been found in the t-patterns of international football over club matches (Borrie *et al.* 2002); Brazilian football players were found to be a small-world network (Onody & de Castro 2004); and an ABMS performed well in simulated football matches and could be extended to predict effective strategies against specific teams (Jolly *et al.* 2007).

We used the same example dataset throughout this review to illustrate the use of different methods. It is hoped that these examples provide an intuitive understanding of the methods outlined rather than a true reflection of how these techniques might work in practice. In box 1 we calculated the fractal dimension of activity in a single bird and found a low fractal exponent. This indicates that the birds' activity was randomly distributed over time. In order to be able to offer a true interpretation we would need to find the time distribution of activity in birds in stressful and non-stressful situations. However, the bird fractal dimension demonstrated that the bird had variability in behaviour which shows it is not limited to the simple motor patterns associated with abnormal repetitive behaviour. In box 2 we demonstrated a lack of Markovian determinism in the sequences of direction moved by one hen. Again this suggests the bird is not limited to repetitive movement. From all birds in the dataset, we visualized the structure of relations between

birds using a sociogram in box 3. All but one of the six hens pecked or were pecked by another bird. If this were a real dataset with multiple groups examined it would be interesting to examine the progression of pecking over time or look at the effects of the overall social network structure or individual position within the network on pecking behaviour. Finally, in the ABMS we simulated the movements of birds based on heuristics from the example dataset. The simulated birds were clustering more than expected at random and under-utilized certain areas of the pen that did not contain resources.

Animal behaviour, like many natural and man-made systems, is complex and multi-dimensional. The principles for understanding the complexity of systems transcend traditional scientific disciplines and therefore research on complex systems is likely to be most effective by taking a multi-disciplinary approach. The four types of analysis outlined in this review were either developed or have since been utilized for purposes other than behavioural analysis. Developments in behavioural analysis will continue to become increasingly important alongside advancements in physics and engineering (e.g. Spink *et al.* 2001; Kramer & Kinter 2003; Pack *et al.* 2007; Donohue *et al.* 2008) that are continuing to improve the quantity, and sometimes quality, of behavioural data collected. Through this review we hope to have encouraged a multi-disciplinary approach to behavioural analysis and illustrated some of the realized and potential advantages such an approach may bring.

GLOSSARY

Bootstrapping: A method for making statistical inference based on repeated randomly sampling from an actual sample.

Bottom-up: A strategy for information processing derived from piecing together component parts.

Euclidean: An area of mathematics relating to standard geometry based on the mathematician Euclid's axioms.

Monte Carlo methods: A suite of heuristic mathematical techniques where possible random variation in all parameters is examined and can be used to assess the cause of observed effects.

Random permutations: The random ordering of discrete items.

Random walk: A sequence of random movements of fixed step length where each movement depends only on the direction of the previous movement.

Top-down: Information processing based on decomposition of a system into component units. The opposite of bottom-up.

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