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FORUM

Unrealistic animal movement rates as behavioural bouts: a reply

CHRIS J. JOHNSON, KATHERINE L. PARKER, DOUGLAS C. HEARD* and MICHAEL P. GILLINGHAM

*Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC, Canada, V2N 4Z9; and *Ministry of Environment, 4051 18th Avenue, Prince George, BC, Canada, V2N 1B3*

Summary

1. Johnson *et al*. (*Journal of Animal Ecology*, 2002, **71**, 225–235) proposed a technique for stratifying the movements of ungulates into small- and large-scale behaviours. They identified movement paths for woodland caribou and fitted a nonlinear curve to the log-frequency of movement rates. They assumed that slow small-scale movements were correlated with foraging activities in patches and faster large-scale movements occurred when caribou moved between patches.

2. Nams (*Journal of Animal Ecology*, 2006, **75**, 298–302) reviewed the assumptions and tested the technique presented by Johnson *et al*. (2002). Simulated animal movements resulted in rates inconsistent with the data of Johnson *et al*. (2002) and the distribution necessary to fit the nonlinear curve. Nams (2006) challenged animal movement as suitable for the technique and concluded that sampling interval would confound results.

3. We evaluated Nams's (2006) criticisms with movement data collected for caribou, moose and mountain goat. All three species demonstrated the required distribution of movement rates and sampling interval had little influence on the criterion used to identify scales of movement for a range of woodland caribou data. In addition, we tested the sensitivity of the curve-fitting model to the width of the frequency interval for the log-frequency plot of movement rates. We noted bias in the rate criterion, but the scalar relationship was consistent among interval widths.

4. The discrepancy in movement data presented by Nams (2006) and Johnson *et al*. (2002) is likely the result of different movement processes. The movements of simulated animals did not encompass the full range of behaviours typically observed for ungulates. Our analyses and those of Nams (2006) provide little evidence to universally reject the nonlinear curve-fitting model and the results of Johnson *et al*. (2002). However, we caution against blind application of the technique, as not all movement processes are suitable and the scale of movement must be consistent with the scale of the behaviour.

Key-words: animal movement, frequency distribution, global positioning system, movement rate, Sibly.

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Introduction

Many ecological phenomena vary across time and space. That variation can be inherent to the process or pattern of interest or a function of our perspective (Dungan *et al*. 2002). These scalar problems are not new to ecologists, but continue to influence research in many fields of study. Wildlife ecologists, for example, often are interested in identifying and understanding factors that influence the movements of individuals and how those movements affect the distribution and abundance of populations at alternate spatial and temporal scales. With this in mind, we developed and

Correspondence: Chris J. Johnson, Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC, V2N 4Z9, Canada. E-mail: johnsoch@unbc.ca

tested a technique presented in Johnson *et al.* (2002) that relates the movement of individual animals to the size and composition of patches of resources.

We used location data for woodland caribou *Rangifer tarandus caribou* Gmelin to investigate the relationship between animal movement and scalar behaviours. We hypothesized that scalar responses of ungulates to patch heterogeneity were indicated by a nonlinear distribution of slow and fast movement rates. Alternatively, nonscalar behaviours were characterized by movement rates distributed as a monotonically decreasing linear function. Our hypothesis was premised on fine-scale observations of foraging caribou (Johnson, Parker & Heard 2001), black-tailed deer *Odocoileus hemionus sitkensis* Cowan (Parker *et al.* 1999), and theoretical expectations for large ungulates responding to patchy environmental resources in a hierarchical fashion (Senft *et al.* 1987).

We used a previously developed curve-fitting model (Sibly, Nott & Fletcher 1990) and movement paths collected for woodland caribou to test our hypothesis. Where the log of movement rate frequencies resulted in a nonlinear concave function (i.e. resembling a broken stick), the model identified a breakpoint (r_c) between slow and fast movements (Fig. 1). More frequent slow movements occurred on the steep phase of the function and were assumed to occur while an individual was foraging within a patch. The fast movements occurred on the less steep portion of the curve and were assumed to occur when an animal was moving between foraging patches. A random distribution of movement rates produced a linear log frequency plot and was the result of an animal moving in an environment with less defined patch boundaries.

We used GPS collars deployed on individual caribou to collect movement data, which we fitted to the nonlinear curve fitting model. Because collars frequently missed a location due to receiver interference, we standardized all movement distances to rates of movement (Johnson *et al.* 2002). We fit a two-scale, a three-scale, and a simple linear model to the data. Akaike's Information Criterion and explained variation were used to test for scalar or nonscalar movements. Where scalar movements were observed, we used logistic regression to contrast environmental features traversed by caribou during small- and large-scale movements. Sensible differentiation of those features was evidence that the curve fitting procedure identified meaningful patterns in the data relative to caribou behaviour.

In his review and critique of Johnson *et al.*'s (2002) application of the nonlinear curve fitting model, Nams (2006) used a number of simple algorithms to simulate animal movement and then tested for the required distribution of rates. Nams (2006) concluded that the method presented by Johnson *et al.* (2002) was flawed on two accounts: movement rates did not meet the distributional assumptions of the technique and the measurement of movement rate was confounded by sampling interval. Although we acknowledge that these are important considerations, Nams's (2005) methods and test are out of context with the data and type of inference presented by Johnson *et al.* (2002).

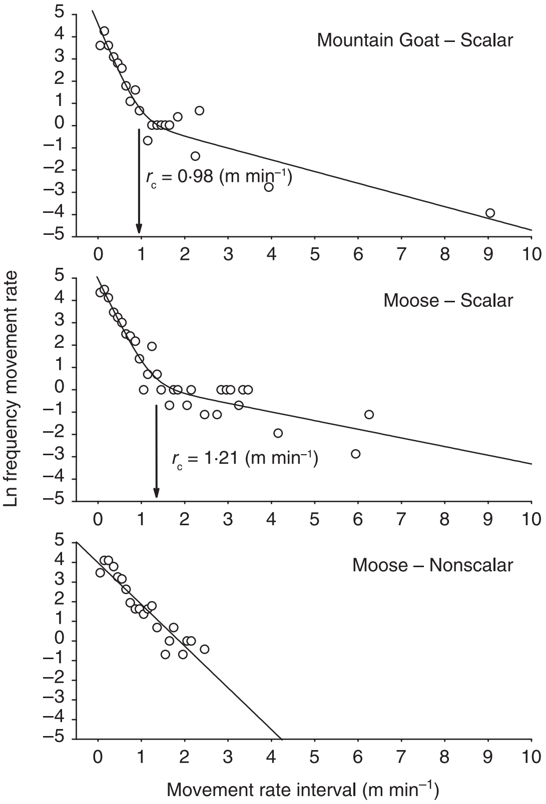

Fig. 1. Scalar and linear log frequency plots of movement rates for a mountain goat and moose collected during winter in British Columbia, Canada. The rate criteria (r_c) were calculated using the nonlinear curve fitting procedure described by Johnson *et al.* (2002). Monitored goats did not demonstrate nonscalar movements.

DO MOVEMENT RATES SATISFY THE DISTRIBUTIONAL ASSUMPTIONS OF THE TECHNIQUE?

The applicability of the curve-fitting model to animal movement is ultimately dependent on the distribution of data. Following Nams' (2005) argument, our hypothesis, and the mathematics of the technique, the frequency distribution of movements must represent the sum of at least two exponential distributions generated by Poisson processes. When plotted as a log frequency, these data should be distributed as a concave or 'broken stick' function. Starting with this fundamental requirement, Nams (2006) simulated 'animal' movements, both scalar and nonscalar, to search for this distribution. Because none of the results approximated a concave or negative linear function, Nams (2006) concluded that the technique and the examples provided by Johnson *et al.* (2002) were unsound. One or even many exceptions to the required distribution, however, are not proof that all applications are invalid. Lack of fit of some set of empirical data is not necessarily evidence that the technique is universally flawed. As with other statistical procedures, such as linear regression, we might test a relationship between two factors, but ultimately reject that hypothesis. Johnson *et al*. (2002) did not report or imply that all animal movements across all spatial and temporal scales fit the model. They devoted a major portion of their text to examining this question as well as providing ecological rational for the application of the curve-fitting procedure to their data.

The log frequency plot for one woodland caribou by season, approximating the concave function, was presented in Johnson *et al*. (2002). In support of the general applicability of this expectation, we produced log frequency plots of movement rates for moose *Alces alces* L. and mountain goats *Oreamnos americanus* de Blainville. As with the application to woodland caribou, location data were collected with GPS collars (Poole & Heard 1998; Parker & Gillingham unpub. data). We generated distributions for six mountain goats and 12 moose for the winter season. In all cases, the log frequency plots approximated a concave or linear distribution (Fig. 1) and none resembled Nams's (2005) simulated data. Nams's (2005) simulations appear to represent different movement processes than those demonstrated by caribou, mountain goats and moose.

Nams (2006) noted that his 'simulations only created patterns in spatial scale' and that Johnson *et al*.'s (2002) data 'included not only position, but time'. This temporal component is an important attribute of real animal behaviour. Simulated random and scalar walks developed by Nams (2006) were premised on continuous movement with variation in the tortuosity of the path. Such movement processes inherently exclude the full range of behaviours that one might expect from animals foraging in patches, including smaller slower steps while selecting bites, ruminating and loafing, or faster steps during movements between patches or migration among seasonal ranges. Ungulate's activity budgets are dominated by these slower behaviours (Bunnell & Gillingham 1985) and hence the observed distribution of rates for caribou. Most of the animals simulated by Nams (2006) demonstrated relatively more fast movements and his algorithms allowed for continuous movement only. Such behaviour is possible over limited spatial and temporal frameworks, but untenable across the full range of behaviours demonstrated by even simple animals, such as zooplankton (Seuront *et al*. 2004).

Nams (2006) questioned the appropriateness of dividing continuous movement paths into discrete events. Based on a strict definition of the curve-fitting model, we must assume that intra- and interpatch movements are independent occurrences generated by a Poisson process. Movement, however, is a set of correlated behaviours. Although the data deviate from the strict definition of a Poisson process, we note that others including Sibly *et al*. (1990), Berdoy (1993), and Gillingham, Parker & Hanley (1997) also ignored this assumption. Most serially repeated animal behaviours, such as foraging, are not discrete events. Berdoy (1993), for example, used the technique to delineate foraging bouts by monitoring the time between visits of brown rats *Rattus norvegicus* Berkenhout to a feeder. Those visits also were unlikely independent. The implications of nonindependence of behavioural events for model fit and statistical inference are unclear. Lack of independence is not immediate grounds to reject a statistical model (Diniz-Filho, Bini & Hawkins 2003), but this is a question requiring further research.

Nams (2006) attributed the discrepancy between his simulations and Johnson *et al*.'s (2002) observed data to violations of the assumed statistical distribution of the curve-fitting procedure. More likely, the real issue is incomparable movement processes generated by Nams (2006) and observed by Johnson *et al*. (2002). The log frequency plots presented in Fig. 1 are a simple summary description of data from free-ranging animals, and differ substantially from animals simulated by Nams (2005).

IS MOVEMENT RATE A FUNCTION OF SAMPLING INTERVAL?

Nams (2006) provided evidence that movement rate is biased by sampling interval. As we sample a movement path more intensively, we record more detail, net displacement is greater, and rate increases. Also, an animal's ability to move quickly is restricted to a finite distance, which can be exceeded across large sampling intervals. The potential for such bias is well reported in the literature (see Reynolds & Laundré 1990; Codling & Hill 2005). Johnson *et al*. (2002) recognized the potential for such sampling bias and tested and then constrained their observations to a sampling interval of ≥ 3 h and ≤ 16 h, across which no differences could be detected (Fig. 2). Furthermore, the majority of data presented (81%) had a sampling interval of 3 or 4 h. Thus, appropriate steps were taken to minimize the confounding effects of sampling interval on pooled movement rates. Even where a consistent interval is possible (i.e. no failure in GPS collar to record a location), the choice of appropriate sampling interval is an important consideration. As the interval increases, our ability to detect finer-scale responses to patch structure decreases. Johnson *et al*. (2002) constrained their inferences to general differences in movement frequency and rate between the feeding site, the foraging patch, which contains multiple feeding sites, and migration type movements. For most caribou, they were unable to fit a model that represented a three-scale process (*sensu* Berdoy 1993).

We revisited data from caribou to examine this issue in more detail. Although interanimal differences in rate criteria may exist, sample size constraints required us to pool the movement rates for four of the five caribou monitored during winter with similar rate criteria (042B, 1D2B, 772B, B91A; Johnson *et al*. 2002). We

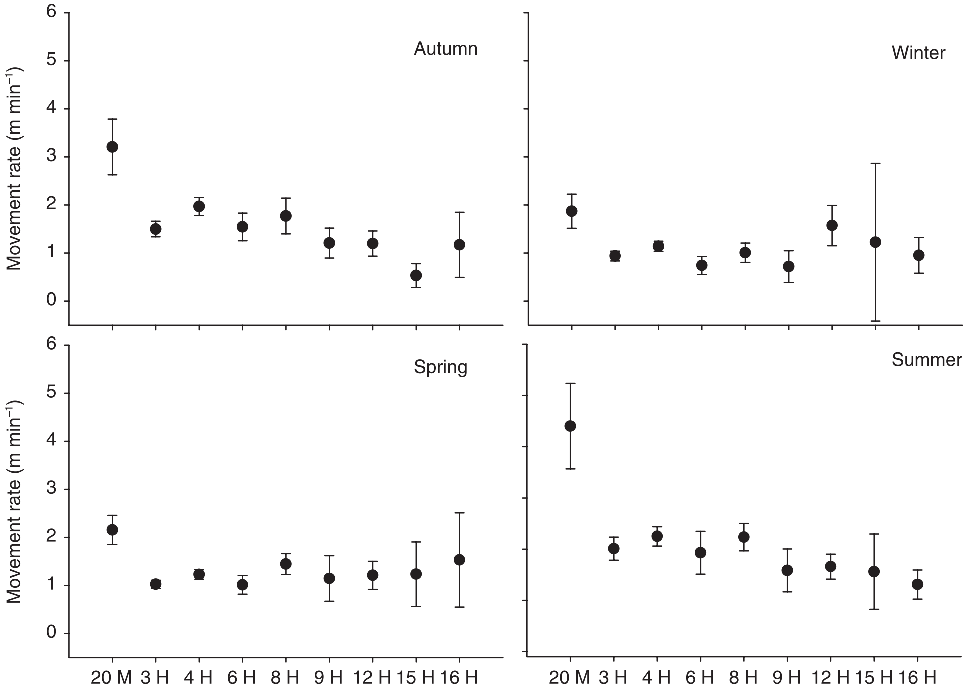

Fig. 2. Autumn, winter, spring and summer movement rate estimates for 20-min to 16-h sampling intervals of GPS collars deployed on woodland caribou in British Columbia, Canada. Data represent means and associated 95% confidence intervals.

stratified movement rates into 4-, 8- and 12-h intervals. For the latter two intervals we rarified the data (i.e. excluded 4- or 8-h locations) to further increase sample sizes. This resulted in 107 movement events for the 12-h interval. To maintain equal sample sizes among comparisons, we randomly selected 107 events from the 4- and 8-h intervals. We then generated the log frequency plots and fit the nonlinear model to the data for each of the intervals. For the three sets of movement data, the log frequency plots were consistent with a concave distribution and the predicted rate criteria were similar. These results suggest that at intermediate scales of movement typical for woodland caribou (i.e. 4–12 h), the technique is robust to change in sampling interval (Fig. 3).

Choice of sampling interval of animal movement is subjective, but can be guided by study objectives in combination with observed variation among intervals (Fig. 2). An issue not addressed by Nams (2005), but even more challenging to practitioners of Johnson *et al.* (2002) and the classic application presented by Sibly *et al.* (1990) is the choice of frequency interval (i.e. bin) to construct the log frequency plot. We should define bins with a width sufficient to illustrate variation in the frequency of rates across the range of data, but not too wide to provide insufficient data points to fit the curve. Neither Sibly *et al.* (1990) nor Berdoy (1993) provide guidance for defining bin size. Unlike movement rates, temporal observations have the advantage of predefined units such as a second, minute or hour, but these are still subjective and might not meet the precision of the data or the study objectives.

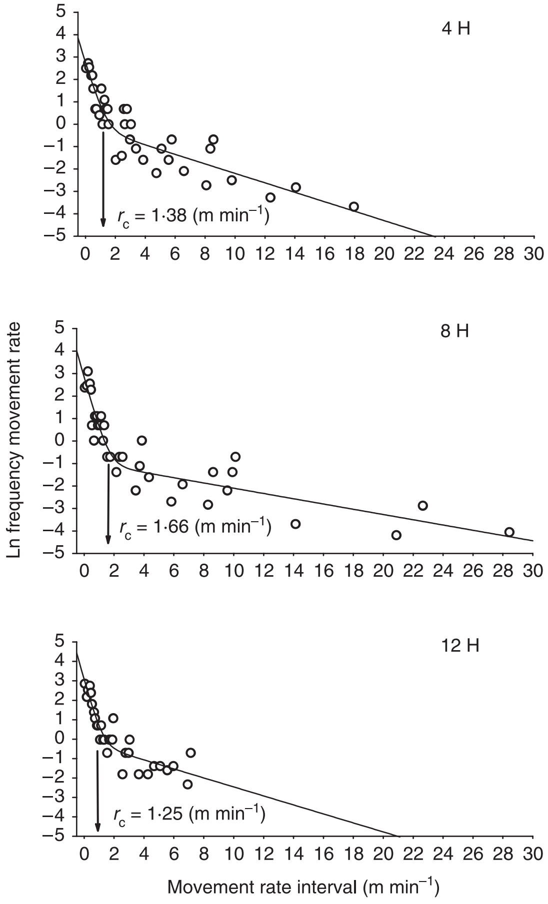

Fig. 3. Log frequency plots and rate criteria (r_c) for movement rates generated from GPS collars deployed on four woodland caribou in British Columbia, Canada. Animal location data were sampled at 4-, 8- and 12-h intervals.

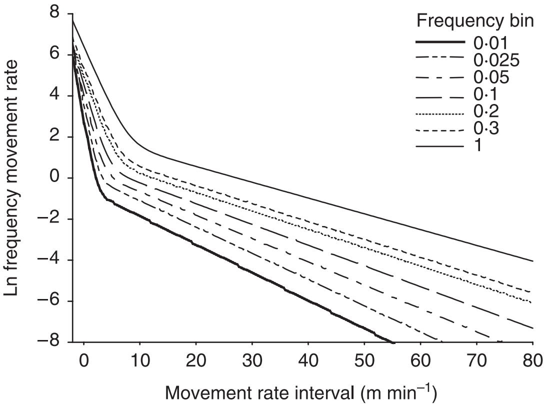

Fig. 4. Model fit in relation to variation in the size of the rate interval (i.e. bin) used to generate the log frequency plot. Movement rates were generated from combined locations of four woodland caribou in British Columbia, Canada.

Given their sample sizes and objective to fit a three-process model, Johnson *et al.* (2002) chose a frequency interval of 0·01 m min^{-1}. We used the aggregated data of winter locations for the four caribou presented in Fig. 3 and tested the sensitivity of their application to choice of bin width. We generated log frequency plots and calculated the rate criteria for bin widths of 0·01, 0·025, 0·05, 0·1, 0·2, 0·3 and 1·0 m min^{-1}.

Although the log frequency plots revealed two-process models with similar model fit, we did find bias when calculating the rate criteria (r_c; Fig. 4). Following a 100-fold increase in the size of the bin, we calculated rate criteria that ranged from 2·22 (95% confidence interval = 1·99–2·52) to 7·85 (6·21–10·17) m min^{-1}. Depending on landscape heterogeneity, this bias could limit absolute predictions and relationships between patch size and movement. Ultimately, continued inflation of the rate criteria will lead to a transition from a scalar to a nonscalar process. Our sensitivity analysis suggests that this is unlikely for most cases, but bias will increase the threshold used to identify large-scale movements associated with landscape features such as corridors. Considering the sample sizes and the range of rates observed for caribou, moose and goats (Figs 1, 3 and 4), bins of 0·01 or 1·0 m min^{-1} are likely too small and large, respectively, for most applications of Johnson *et al.* (2002) to ungulate movement data. With 300–400 movement vectors, small bins (e.g. 0·01 m min^{-1}) would produce too many frequency intervals with one observation and large bins (e.g. 1 m min^{-1}) would provide too few data points to reliably fit a curve. Even given these extremes, however, the curve-fitting model is still robust to comparisons among animals and seasons and to the identification of scalar and nonscalar relationships.

IS *ANIMAL MOVEMENT RATES AS BEHAVIOURAL BOUTS* A 'TEST' OF JOHNSON ET AL. (2002)?

Nams's (2005) test of the curve-fitting model was premised on the observed outcome of movement simulations. The simulated animal movements and observed data for woodland caribou, however, are generated by fundamentally different processes. Furthermore, simplistic movement algorithms such as correlated random walks typically serve as null models against which observed data are compared. The model serves as a learning tool to assess how real behaviour varies from the theoretical. In reality, we rarely find good correspondence between observed movements and model predictions, even for arthropods or other taxa that are observed within a relatively limited spatial and temporal context. For example, Cain (1985), Wallin (1991), and Morales & Ellner (2002) found poor fit between random walk models and the movements of invertebrates. Bergman, Schaefer & Luttich (2000) reported that correspondence of observed movements of caribou with a predicted random walk was not consistent and it was highly scale-dependent.

A true test of Johnson *et al.* (2002) would require additional data describing movements of caribou relative to patch boundaries. In order to pass such a test, the majority of slow movements, as identified by the nonlinear model, should occur within a foraging patch. In the absence of those data, Johnson *et al.* (2002) related movement paths to environmental features and used logistic regression to contrast slow and fast movements identified with the rate criteria. For example, relative to interpatch movements, caribou movement vectors identified at the intrapatch scale were more likely to be associated with land cover types that provided foraging opportunities (Johnson *et al.* 2001). Recently, other researchers working with another population of woodland caribou also have successfully fitted the nonlinear model and reported differences in habitat features found at locations identified as intra- and interpatch movements (Saher & Schmiegelow 2005). Although the precision and accuracy of the technique is still to be established, this evidence suggests that it is useful for identifying ecologically meaningful patterns.

More study is required to define precisely the ecological conditions that produce the observed patterns in the data presented by Johnson *et al.* (2002). These patterns might be related to patch boundaries or even social behaviour, although the interactions with the scale of observation are unclear. None the less, the nonlinear model is useful in guiding our investigations toward fundamental ecological processes and stimulating or contributing to the development of other approaches for identifying the behavioural scales of movement (Fauchald & Tveraa 2003; Franke, Caelli & Hudson 2004).

Although, we do not believe Nams (2006) represented movement data for free-ranging caribou, it provides some general confirmatory evidence for important issues highlighted by Johnson *et al.* (2002). It also lends general support for Gautestad & Mysterud's (2005) contention that animals from many taxa fail to meet the expectations of simple movement and distribution models (e.g. random walk, diffusion). These authors concluded that we must work to develop and apply new ecologically realistic frameworks for simulating and understanding animal distribution. We agree.

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