A maximum likelihood approach for identifying dive bouts improves accuracy, precision and objectivity

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Summary

Foraging behaviour frequently occurs in bouts, and considerable efforts to properly define those bouts have been made because they partly reflect different scales of environmental variation. Methods traditionally used to identify such bouts are diverse, include some level of subjectivity, and their accuracy and precision is rarely compared. Therefore, the applicability of a maximum likelihood estimation method (MLM) for identifying dive bouts was investigated and compared with a recently proposed sequential differences analysis (SDA). Using real data on interdive durations from Antarctic fur seals (*Arctocephalus gazella* Peters, 1875), the MLM-based model produced briefer bout ending criterion (BEC) and more precise parameter estimates than the SDA approach. The MLM-based model was also in better agreement with real data, as it predicted the cumulative frequency of differences in interdive duration more accurately. Using both methods on simulated data showed that the MLM-based approach produced less biased estimates of the given model parameters than the SDA approach. Different choices of histogram bin widths involved in SDA had a systematic effect on the estimated BEC, such that larger bin widths resulted in longer BECs. These results suggest that using the MLM-based procedure with the sequential differences in interdive durations, and possibly other dive characteristics, may be an accurate, precise, and objective tool for identifying dive bouts.

Keywords: Antarctic fur seal, diving behaviour, foraging behaviour, foraging patch, pinniped.

Introduction

Many seabirds and marine mammals dive in bouts (Gentry et al., 1986; Huin & Prince, 1997; Kato et al., 2003); i.e., most of their dives occur in rapid

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succession, while the remaining are separated by longer intervals. Dives occurring in the same bout tend to resemble each other more than those occurring in different bouts. Based on their characteristics (e.g., mean dive depth and time spent at the bottom of the dive), bouts can be associated with a particular activity, such as travelling or foraging (Lea et al., 2002). Numerous studies use dive bouts to infer instances of a forager exploiting discrete prey patches (Boyd, 1996; Mori et al., 2002; Harcourt et al., 2002; Mori & Boyd, 2004a), because food resources are patchily distributed (Wroblewski et al., 1975; Croxall et al., 1985) at scales that organisms respond to (With & Crist, 1995; Wu & Loucks, 1995). Depending on the scale(s) at which food resources display patchiness (Wiens, 1976; Levin, 1992), the same argument is applied more generally to most animal behaviours associated with foraging, in both terrestrial (e.g., Schaefer & Messier, 1995; Munger, 1984; Rotenberry & Wiens, 1998) and aquatic environments (e.g., Kruuk et al., 1990; Fauchald, 1999). Therefore, it is essential to accurately and objectively identify behavioural bouts in studies of foraging ecology of aquatic and terrestrial predators. This can be achieved by determining a bout ending criterion (BEC), or how long an interval between two successive dives should be to assign them to different bouts.

The theory and methods used to determine the BEC have been reviewed elsewhere (Slater & Lester, 1982; Tolkamp & Kyriazakis, 1999). Events occurring in bouts are thought to be generated by a combination of two or more processes operating on progressively larger time scales. At the smallest scale, events are separated by similar and brief intervals. Events separated by markedly longer intervals define different groups of events (or bouts), thereby distinguishing the scale at which one process generates individual events from that generating bouts. Processes of both types are thought to follow a random Poisson distribution, where the intervals between them are described by a mixture of exponential distributions (Slater & Lester, 1982). Defining the BEC is, therefore, a problem of finding the time intervals that separate each process from the others.

Methods for searching the BEC include log-survivorship and log-frequency analysis (Gentry & Kooyman, 1986; Sibly et al., 1990). Boyd (1996) developed an iterative method to group dives into bouts by comparing the inter-dive duration of a given dive with the mean of those preceding it, considering it as part of a new bout if these values differed significantly. More recently, Mori et al. (2001) suggested another method, termed sequential differences

analysis (SDA hereafter), based on log-frequency analysis. The BEC in this method could be estimated using the absolute differences between interdive durations, rather than the interdive durations themselves. If the occurrence of dives can be described by a mixture of Poisson distributions, the mean interdive duration should be the same for all bouts (Karlis & Xekalaki, 2005). However, in cases where dive bouts are considered as instances of a diver foraging in patches, interdive duration is expected to vary between bouts because it is closely related to dive depth (Houston & Carbone, 1992; Carbone & Houston, 1996; Boyd, 1997), which in turn depends on prey species composition and determines foraging patch quality for the predator (Thompson & Fedak, 2001). Mori et al. (2001), therefore, pointed out that previous methods may erroneously assume that mean interdive duration is common to all bouts; an assumption that can be avoided with SDA.

Although SDA has been useful in studies of foraging behaviour (Mori, 1998; Mori & Boyd, 2004b; Mori et al., 2005), it is based on fitting a nonlinear model to the logarithm of frequencies of absolute differences in interdive durations, and possibly other dive characteristics (e.g., dive depth). SDA relies on the construction of a histogram, using the midpoints of each class as the independent variable (Sibly et al., 1990). Therefore, a certain level of subjectivity is involved in the selection of class widths, and some information is lost by summarizing data from each class with a single value. Furthermore, class widths must be adjusted, or a weighting scheme must be implemented, to avoid empty classes. There are currently no objective criteria for dealing with these problems. Johnson et al. (2006) recently pointed out that the choices made throughout this procedure can have large influences on the BEC.

Some of these issues have been raised by Langton et al. (1995), and proposed to address them by using a maximum likelihood estimation method (MLM hereafter) for defining the BEC. This approach uses the information in the entire dataset of intervals between events. Unfortunately, the method has not been adopted to identify behavioural bouts in general, and dive bouts of marine predators in particular, where understanding spatiotemporal variation in prey distribution and quality is of major interest. Our aim was, therefore, to demonstrate the usefulness of this approach in this field, incorporating the concept used in SDA to avoid the assumption of invariant mean dive characteristics between dive bouts. We used time-depth recorder (TDR) data from lactating female Antarctic fur seals (*Arctocephalus gazella* Peters,

1875), during their foraging trips to sea, to compare models of the frequency of differences in interdive duration fit using SDA vs. those fit using MLM.

Methods

Data were obtained from lactating female Antarctic fur seals at La Mare aux Elephants (MAE; 46°22′29″S, 51°40′13″E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001-02 (4 December-25 March) and 2002-03 (1 December-16 March) breeding seasons.

Instrumentation and measurement of diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005). Briefly, lactating females were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, WA, USA). TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. Instruments were left on the seals for 1 to 11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer, where analyses of the resulting time series of dive data were performed using custom written software, available as GNU R (R development Core Team, 2007) package diveMove (Luque, in press). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e., continuous depth readings) was available for at least 6 h. This limit was selected to exclude short excursions to sea for activities other than foraging, because these contained isolated shallow dives and mainly surface behaviour.

Dives were defined as departures from the surface to depths $\geq$ 4 m plus the ensuing return to surface. Dives to shallower depths were not considered because they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the

instrument (Beck et al., 2000). Dives were, thus, described by their duration, maximal depth, and interdive duration.

For the purposes of this paper, data from the first recorded foraging trip to sea of four randomly selected individual seals were used in subsequent analyses. The models described below were fitted to each seal's dive record separately because foraging trip durations varied between them, and to avoid effects of interindividual variation in diving behaviour masking bout structure.

Identifying bouts using SDA

The variable used for defining bouts with SDA- and MLM-based methods was the absolute difference in interdive duration (t); the time between a dive and the preceding one. This procedure is based on a log-frequency analysis described in detail by Sibly et al. (1990) and further developed by Mori et al. (2001). Briefly, the first step of the method consists of creating a histogram of t, with the frequencies expressed as a logarithm. Because large values of t are considerably less frequent than small ones, some class intervals may have a frequency of zero, leading to the erroneous representation of frequencies in larger class intervals. To correct for this effect, the frequency of class intervals following intervals with zero frequency was divided by the number of preceding empty intervals plus one. The logarithm of the frequencies of all class intervals where frequency > 0 is, thus, considered a function of the midpoint of the intervals.

The distribution of t is assumed to be a mixture of two random Poisson processes; a fast and a slow one (Sibly et al., 1990). The fast process represents the small time scale at which individual dives occur, while the slow process represents the large time scale where bouts are distinguished. Therefore, the relationship described above can be defined as the sum of both processes:

$$y = \log[N_f \lambda_f e^{-\lambda_f t} + N_s \lambda_s e^{-\lambda_s t}] \tag{1}$$

where y is the logarithm of the frequency of any given t; the subscripts $_f$ and $_s$ denote the fast and slow processes, respectively; N is the number of interdive intervals occurring in each process; and λ represents the probability of an event occurring in a given process per unit time (Sibly et al., 1990). Initial values for the N and λ parameters must be obtained in order to fit this

negative exponential function. The broken-stick method was used for this purpose, following Sibly et al. (1990).

The BEC defining the threshold between the two Poisson processes can be obtained from equation (1):

$$BEC = \frac{1}{\lambda_f - \lambda_s} \log \frac{N_f \lambda_f}{N_s \lambda_s} \tag{2}$$

To assess the effect of the choice of histogram bin widths on the estimation procedure, the model was fit, and the BEC calculated using bin widths from 5 (i.e., the sampling resolution) to 50 s.

Identifying bouts using MLM

Langton et al. (1995) suggested that equation (1) did not consider that the total number of events observed should be equal to $N_f + N_s$, and, hence, that the model can be simplified by expressing one of these parameters as a function of the other. The authors presented also a maximum likelihood estimation method using all observed data, rather than a histogram of these, to describe the frequency of any given event. The log likelihood of all the N_t absolute differences in interdive duration can be expressed as:

$$\log L_2 = \sum_{i=1}^{N_t} \log[p\lambda_f e^{-\lambda_f t_i} + (1-p)\lambda_s e^{-\lambda_s t_i}] \tag{3}$$

where p is a mixing parameter representing the proportion of fast to slow process events in the sampled population. The parameters from equation (3) must be estimated numerically, hence an optimization procedure is required using appropriate initial values. These values were obtained by first maximizing a reparameterized version of equation (3) using a logit transformation of the p parameter, and a logarithm transformation of the λ parameters. Initial values for this reparameterized model were in turn calculated as for the SDA (i.e., by using the broken-stick method). Such transformations stabilized the variance in the parameters, and rescaled them to avoid difficulties with the optimization algorithm. The parameter estimates obtained from this procedure were untransformed, and used as initial values for maximizing equation (3). Therefore, parameter estimates and their standard errors were obtained in their original scales.

The BEC in this case was estimated analogously to equation (2):

$$BEC = \frac{1}{\lambda_f - \lambda_s} \log \frac{p\lambda_f}{(1-p)\lambda_s} \tag{4}$$

Comparison between methods

Models describing the distribution of interdive differences in dive duration (t) should accurately predict t's relative cumulative frequency. The expected relative cumulative frequency (f_c) of t can be calculated from parameters in models (1) and (3) using:

$$f_c = 1 - pe^{-\lambda_f t} - (1-p)e^{-\lambda_s t} \tag{5}$$

Thus, f_c for the range of observed t, and the actual relative cumulative frequency distribution of t were also calculated. The observed and expected relative cumulative frequencies of t were plotted simultaneously against t (logarithmically transformed) to compare the fit of the two models to data, as proposed by Langton et al. (1995). Differences in model outcomes, relative to observed cumulative frequencies, were tested by comparing the squared residuals (observed – predicted values, squared) between the models with a paired Student's t-test (Zar, 1996).

Standard errors (SEs) for each parameter estimate provided a measure of the precision of each fitted model, and hence that of the estimated BEC. Bias was compared using simulated data generated with chosen mixing (p) and probability (λ) parameters. Based on the mid-range of observed data for all four seals, the mixing parameter was set to 0.7, and values for the probability parameters were set to 0.05 and 0.005 (λ_f and λ_s, respectively). Thus, one thousand values for t were simulated 100 times with these values, by generating a mixture of two random samples with exponential distribution ($f(\lambda_x, t) = \lambda_x e^{-\lambda_x t}$): one with $\lambda_x = 0.05$ if a random uniform variable x ($1 \geqslant x \geqslant 0$) from the total of 100 was <0.7, and another with $\lambda_x = 0.005$ otherwise. Each simulated mixture was fit with both models, using the respective methods described above. The bias of the estimates in the simulations, with respect to the true value for the parameters, were subsequently calculated and compared. All data manipulations and computations were done in the GNU R statistical system and programming language (R development Core Team, 2007).

To compare the effect of each method on interpretations of the behaviour of study animals, each seal's dive record was divided into bouts using

the estimated BECs. The mean and variance of bout duration and interval between bouts was calculated and compared between models for each seal using Wilcoxon rank-sum and Fligner–Killeen tests, respectively (Conover et al., 1981).

Results

The number of dives observed for each seal varied from 910 to 1881 (Table 1). Probability parameter (λ) estimates from these samples were larger using MLM compared to those obtained through SDA. Conversely, the mixing parameter (p) was consistently smaller using MLM, and the total number of interdive intervals ($N_f + N_s$) was largely overestimated using SDA. As a result of these differences, estimated BECs were markedly larger using SDA, by factors ranging from 2 to 6 (Table 1). SEs of estimated parameters were generally smaller using MLM. More importantly, the total number of bouts identified for each seal was considerably smaller when using SDA (Table 1).

Varying the bin width for creating the histograms used in SDA resulted in systematic changes in most parameters: estimated BECs and numbers of interdive intervals (N_f and N_s) increased, but λ_f tended to decrease. SEs of estimated parameters increased as class bin widths were increased (Table 1). Using the narrowest bin width for the sampling interval programmed for TDRs (5 s), variation in estimated BECs among seals was larger using SDA (range 91.3-191.2 s) than MLM (range 43.8-59.5 s).

Estimated and observed cumulative frequencies differed for high but non-asymptotic t values, regardless of the model (Figure 1). However, such departures were larger for models fit through SDA. Models fit through MLM followed the observed cumulative frequencies more closely, although they underestimated these frequencies for large t values (Figure 1). The sum of squared residuals from MLM-derived frequencies (relative to observed) ranged from 0.06 to 0.09, and from 0.5 to 1.0 for SDA-derived frequencies. The difference between models was significant for all seals (Figure 1).

Bias of estimated parameters from models of simulated t values were 0.001, 0.0002, 0.00002 when fit through MLM, and 0.031, −0.0028, −0.0010 when fit through SDA (p, λ_f, λ_s, respectively). Thus, biases were smaller, and variation for each parameter was smaller for MLM estimates, particularly in the case of λ_f estimated using this method (Figure 2).

Table 1. Estimated parameters and bout ending criteria (BEC) (mean $\pm$ SE) from a model of sequential differences in interdive duration, using a maximum likelihood estimation method (MLM), and a log frequency analysis (SDA). Results from four different choices of bin widths (s) were used for the SDA approach. The number of dives observed for each seal is in parenthesis.

MLM[a]		SDA[b]			
		5 s	10 s	20 s	50 s
Seal 1 ($N = 1081$)					
p	0.65 ± 0.025				
N_f		3070 ± 477	6480 ± 1300	$13\,500 \pm 3800$	$36\,700 \pm 15\,600$
N_s		803 ± 95.7	1370 ± 177	2270 ± 390	4720 ± 1220
λ_f	0.069 ± 0.006	0.021 ± 0.003	0.020 ± 0.003	0.018 ± 0.003	0.016 ± 0.004
λ_s	0.005 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0003	0.002 ± 0.0003	0.002 ± 0.0004
BEC	51.1	191.2	209.6	249.6	289.3
Bouts	339	126	116	103	88
Seal 2 ($N = 910$)					
p	0.63 ± 0.026				
N_f		2440 ± 427	5090 ± 1170	$10\,700 \pm 2910$	$29\,900 \pm 10\,800$
N_s		1120 ± 102	1960 ± 203	3420 ± 433	7390 ± 1270
λ_f	0.060 ± 0.004	0.023 ± 0.003	0.022 ± 0.004	0.019 ± 0.004	0.017 ± 0.004
λ_s	0.004 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	59.5	156.8	173.9	202.4	237.9
Bouts	320	186	168	146	139
Seal 3 ($N = 1881$)					
p	0.74 ± 0.014				
N_f		5230 ± 1220	$10\,500 \pm 2990$	$22\,800 \pm 8890$	$90\,800 \pm 53\,200$
N_s		1550 ± 127	2850 ± 285	5420 ± 725	$14\,000 \pm 2630$
λ_f	0.096 ± 0.004	0.047 ± 0.007	0.042 ± 0.008	0.041 ± 0.010	0.044 ± 0.014
λ_s	0.004 ± 0.0003	0.003 ± 0.0002	0.003 ± 0.0002	0.003 ± 0.0003	0.003 ± 0.0003
BEC	43.8	91.3	100.2	105.7	110.0
Bouts	478	287	276	270	270
Seal 4 ($N = 1164$)					
p	0.080 ± 0.015				
N_f		3140 ± 736	6120 ± 1690	$12\,900 \pm 4230$	$47\,400 \pm 24\,000$
N_s		906 ± 82	1530 ± 152	2760 ± 303	6570 ± 1050
λ_f	0.083 ± 0.004	0.046 ± 0.007	0.038 ± 0.006	0.034 ± 0.007	0.036 ± 0.009
λ_s	0.004 ± 0.0003	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0002	0.002 ± 0.0003
BEC	56.6	96.7	118.9	134.8	140.9
Bouts	223	169	156	144	132

[a] The log likelihood function is shown in equation (3).

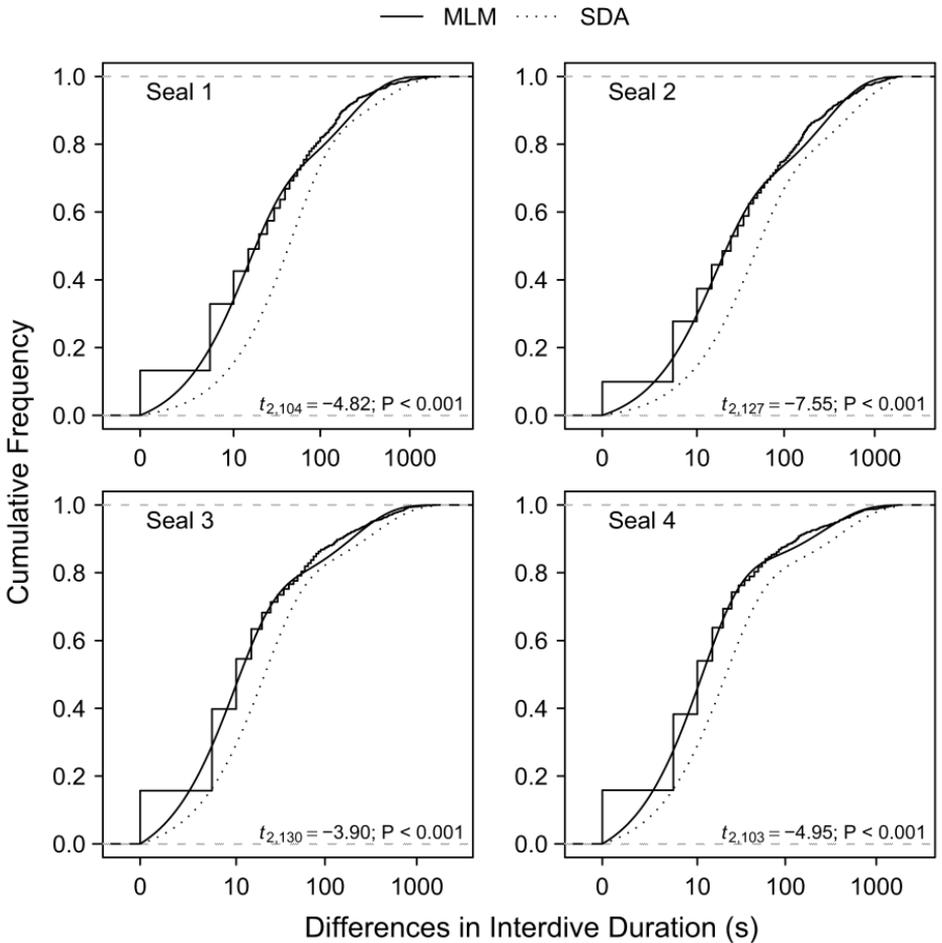[b] Columns represent four different choices of class interval width for fitting equation (1).

Figure 1. Relative cumulative frequencies (observed as a stepped function; estimated as the smooth lines) estimated through the maximum likelihood estimation method (MLM) were in better agreement with observed data than those estimated through log frequency analysis (SDA). A bin width of 5 s was used to fit the model through the log frequency analysis. Results of paired Student's t-tests comparing the squared residuals between models are also shown.

Variance in the duration of bouts was significantly larger (Fligner–Killeen $\chi^2 = 50.9, 10.9$ and 13.6, seals 1, 2 and 3, respectively; $p < 0.001$ all cases) when SDA with a 5 s bin width was used (Figure 3), except for one seal ($\chi^2 = 3.0$, $p = 0.08$; seal 4). Similar results were observed for postbout duration (Fligner–Killeen $\chi^2 = 22.2, 16.6, 25.2$ and 18.2, seals 1, 2, 3 and 4, respectively; $p < 0.001$, all cases). Median duration of bouts (Wilcoxon
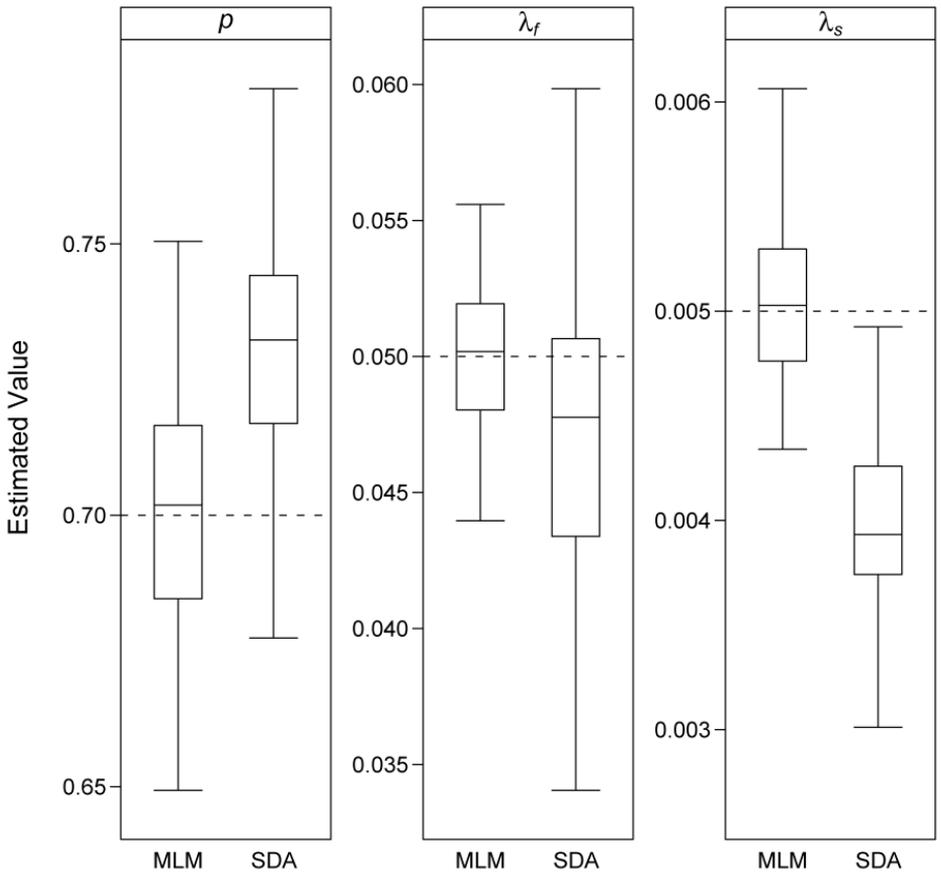
Figure 2. Bias of estimated parameters from 100 simulations of differences in interdive duration were smaller using the maximum likelihood estimation method (MLM), than with the histogram method (SDA). The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, $1.5 \cdot$ interquartile range away from the box by the whiskers. The dashed lines indicate the true values of each parameter for all simulations.

$U = 654, 1976, 6254$ and 1220, $p < 0.05$, all cases) and postbout duration (Wilcoxon $U = 1327, 1570, 6356$ and 1048, $p < 0.05$, all cases) were also significantly larger when using SDA (Figure 3). The mean number of dives per bout was concomitantly smaller when using MLM (range 7.4-15.8), than when using SDA (range 11.5-20.1). Furthermore, the number of isolated dives varied from 158 to 323 when using MLM, whereas it varied from 54 to 170 when using SDA.
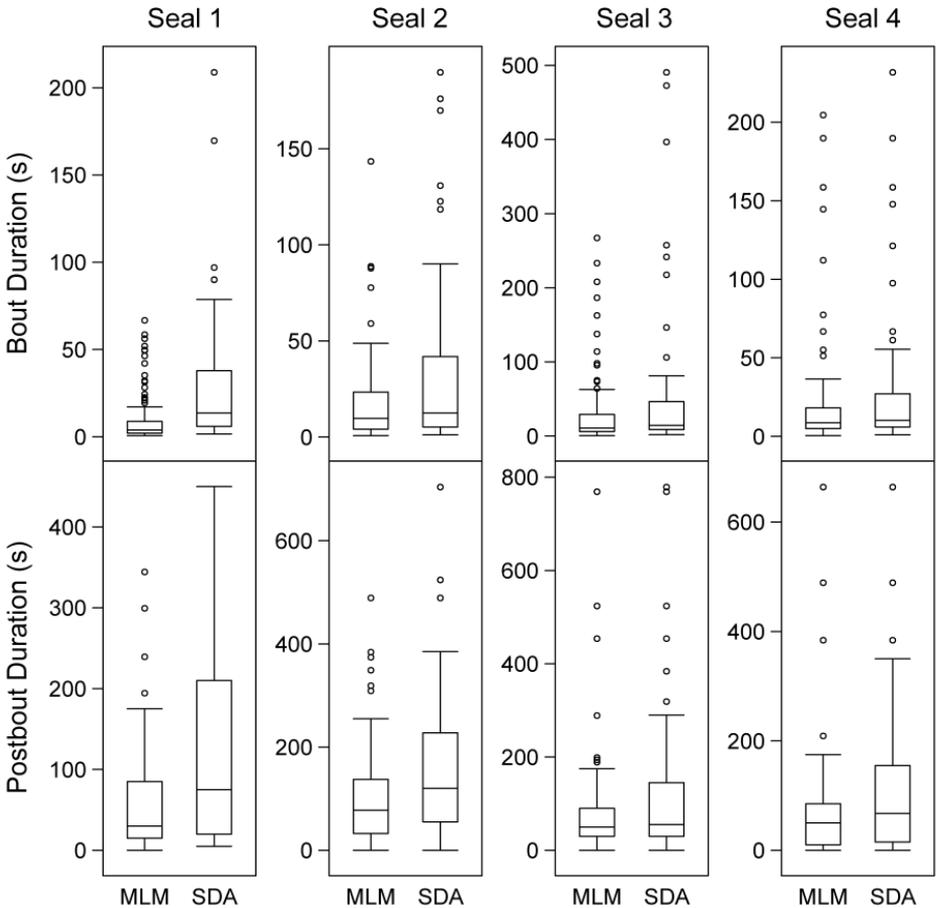
Figure 3. The median and variability of bout and postbout durations were significantly larger when using a log frequency analysis (SDA), compared to the maximum likelihood estimation method (MLM). Only bouts with at least 2 dives are shown. The median is indicated by the horizontal solid line; the interquartile range by the box; and the value that is, at most, 1.5 · interquartile range away from the box by the whiskers.

Discussion

There are several advantages to using the MLM approach for defining the BEC, compared to other methods. Langton et al. (1995) showed that it provides more precise parameter estimates than log-frequency analysis (Sibly et al., 1990) by using all the information in the data, and that methods based on log-frequency analysis may include some subjectivity in the choice of histogram bin widths, which form the basis of the model. Despite these advantages, MLM approaches remain unused for identifying foraging bouts,

and dive bouts in particular, where methods based on log-frequency analysis are predominantly selected for this purpose. Our results support and extend the conclusions in Langton et al. (1995), and suggest that SDA (Mori et al., 2001) may be improved by using this approach.

Because the BEC is defined in terms of the parameters of a mixture of Poisson distributions, its accuracy depends on how well the fitted models describe observed data. The MLM estimates of the model performed better than SDA at describing the cumulative frequency distribution of t. This was evident with real data from all four randomly selected seals. In contrast, expected cumulative frequency distributions based on SDA estimates showed large deviations from observed data, resulting in serious overestimation of the number of interdive intervals within or between bouts. This condition was reproduced in the simulated data, and suggests it is a property of equation (1) fit to the sequential absolute differences in interdive duration. Langton et al. (1995) found a bias in the opposite direction when fitting equation (1) to the interval between events; i.e., $N_f + N_s$, was underestimated. These problems were avoided using MLM.

Differences between methods in their ability to predict observed cumulative frequencies were associated with large differences in estimated BECs. BECs determined through SDA were at least twice as large as BECs determined through MLM. Furthermore, simulated data suggest that BECs estimated through MLM are more accurate and precise than those estimated using log-frequency-based analyses. Such large differences between methods have not been previously shown, and the consequences for any study of foraging ecology based on diving behaviour can be important. Indeed, the number of bouts identified for each seal was considerably larger using MLM, providing finer temporal resolution of the animals' activity at sea. These differences lead to different interpretations of patch structure and characteristics (e.g., Boyd, 1996; Harcourt et al., 2002; Mori & Boyd, 2004a; Mori et al., 2005), where the BEC is used to determine different scales of foraging. Most notably, the temporal scale at which prey patches are encountered by the forager is smaller with the more accurate MLM approach.

Our results showed that increasing the bin widths for constructing the histograms required for identifying bouts based on log-frequency analysis result in larger BECs. A similar effect has been shown for identifying different scales of movement of ungulates (Johnson et al., 2006) using this technique. In our study, we varied the choice of bin width, from a minimum determined

by the sampling resolution to 10 times this value, and found associated increases in BEC estimates of approximately 50% using the largest bin widths. There are no guidelines for choosing appropriate bin widths when using this approach, but Sibly et al. (1990) recommended increasing the bin width of longer, infrequent, intervals. However, using larger bin widths resulted in larger estimates of the BEC. Regardless of the method used for selecting the histogram bin widths, it is not clear what procedure was adopted in any particular analysis of dive bouts, as proxies of patch structure. Therefore, it is difficult to evaluate conclusions about scales of foraging, optimal diving behaviour, and prey patch quality.

Despite the increased accuracy and precision of the MLM approach, some departures from the model were observed. All model fits to real data resulted in underestimation of the cumulative frequency for high but non-asymptotic values of t (see equation (1)) in all seals. Reasons for this departure are not clear with the available data, but may be related to the assumptions of the model. The distribution of intervals, or absolute differences between successive intervals, within each of the two Poisson processes is assumed to be random (Sibly et al., 1990). Therefore, the observed underestimations may indicate departures from this assumption. Large departures from a two-process model, similar to the one in equation (1), have been documented for very brief and very long intervals between meals in dairy cows (Tolkamp et al., 1998). Tolkamp et al. (1998) argued that the departures could be explained by the cows' level of satiety, and proposed an alternative model to account for this effect. However, Tolkamp et al. (1998) studied the feeding behaviour of cows with almost unlimited access to food, which differs from conditions encountered by free-ranging fur seals and their prey. That departures from the model occurred only for $t >$ BEC supports this assertion. Therefore, it is difficult to assess the role of satiety levels in the departures from the model without independent measurements of prey ingestion, and distribution of prey patches.

The arguments and principles in favour of the MLM approach for identifying bouts not only apply to analyses of diving behaviour, but also to analyses of other foraging behaviours that are likely to reflect the spatiotemporal distribution of foraging patches (Wu & Loucks, 1995). For instance, log-survivorship plots of the number of steps taken by kudus (*Tragelaphus strepsiceros* Pallas, 1766) (Owen-Smith & Novellie, 1982) and by muskoxen

(*Ovibos moschatus* Zimmermann, 1780) (Schaefer & Messier, 1995) between feeding stations have been used to identify different scales of food patchiness. Johnson et al. (2002) used the same methods, considering movement rates between successive woodland caribou (*Rangifer tarandus caribou* Linnaeus, 1758) location estimates as analogous to interdive durations in this study, and determined that ungulate movements within patches were strongly influenced by predation risk. Therefore, the improvements in accuracy achieved through MLM methods can bring new insights into foraging behaviour theory. In particular, accurately defining the time spent by animals in and between foraging patches is critical in models of optimal foraging (Stephens et al., 1986).

Whereas foraging behaviour bouts can provide a temporal proxy for foraging patches, the spatial location of those patches must be determined through animal movement data. Considerable efforts have been made to understand animal movement in relation to resource distribution, under the premise that animals move optimally through their habitat so as to maximize long-term energy intake rate (Fauchald, 1999; Fortin, 2002; Fauchald & Tveraa, 2003; Klaassen et al., 2006). The concept of first-passage time; the time taken for an animal to cross a circle of a given radius along its path (Johnson et al., 1992), has been useful for defining spatial scales at which predators concentrate foraging effort (Fauchald & Tveraa, 2003). Fauchald & Tveraa (2003) argued that the scale at which predators are most likely to display area-restricted search behaviour is equal to the radius at which variance in first-passage time is highest. However, this decision is based on the horizontal displacements of animals alone, and may not only reflect feeding activity (Robinson et al., 2007). Therefore, animal movement analysis techniques (e.g., first-passage time) combined with methods for accurate identification of behavioural bouts that can subsequently be attributed to foraging activities, may offer a better assessment of where and how animals exploit food resources.

The SDA procedure (Mori et al., 2001) improved upon previous methods of dive bout detection by removing the assumption of homogeneous dive bout characteristics. This assumption was considered inadequate, as animals may adjust their diving behaviour depending on the characteristics of the patch in which they forage (Mori et al., 2002, 2005). We suggest that the method can be further improved by adopting the MLM approach, which

avoids the limitations associated with methods based on a histogram of observed data. Using this procedure to identify bouts based on other dive behaviour characteristics, in addition to differences in interdive duration (Mori et al., 2001), is possible, so more detailed information on foraging patches might be inferred. This approach may, thus, be a powerful tool to help understand foraging behaviour and prey patch characteristics more accurately.

Acknowledgements

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