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Optimum effort to estimate habitat use when the individual animal is the sampling unit

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ABSTRACT

1. Studies of habitat use in which the individual animal is the sampling unit should ideally sample each individual sufficiently to achieve a stable estimate of its habitat use. Data are typically obtained by radio-tracking, which can be labour-intensive. Hence, optimization of sampling effort is desirable. A method to determine optimum sampling effort is described with reference to an example from a study of Natterer's bat *Myotis nattereri*, in which data were collected by radio-tracking with individual bats followed continuously for entire nights.
2. Habitat use by Natterer's bat was assessed by compositional analysis, which compares the composition of habitats used with those potentially available. Therefore, we plotted running per cent foraging time spent over a range of habitat types against the cumulative foraging time recorded. We visually estimated the optimum sum of foraging time required to determine stable estimates of the composition of habitat use from the plots. Then, by reference to the full-time budget, the total tracking effort expended at the point when this optimum amount of foraging data had been recorded was determined and expressed in units of the number of nightly tracking sessions that had been undertaken to collect that amount of foraging data.
3. Stable estimates of habitat use were attained after a mean of 22 ± 7.7 h of foraging time, which were obtained in a mean of 4.6 ± 1.9 nights of radio-tracking effort. Thus, in this Natterer's bat study, where habitat preference was assessed by compositional analysis, it was appropriate to aim to collect foraging data during five nights of radio-tracking for each bat sampled.
4. The method presented is also applicable to studies where tracking data are discontinuous. A variation of the method can be applied in studies where a Euclidean distance method is to be used for the analysis of habitat use.

Keywords: Chiroptera, compositional analysis, Euclidean distance, habitat preference, *Myotis nattereri*, Natterer's bat, radio-tracking

INTRODUCTION

Modern approaches to the study of habitat use by wild animals correctly identify the individual animal as the appropriate experimental or sample unit (Johnson, 1980; Aebischer, Robertson & Kenward, 1993; Conner & Plowman, 2001) and individual locations as subsamples. Data are typically obtained by radio-tracking, and the sample size is the number of animals from the population that is radio-tagged. Habitat analysis procedures used to assess non-random habitat use include compositional analysis (Aitchison, 1986; Aebischer *et al.*, 1993) and a Euclidean distance approach (Conner & Plowman, 2001). The former method

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uses the composition of habitat usage (i.e. a set of proportions of use across several habitat categories of interest) obtained for each animal, while the latter approach uses mean distances from locations recorded for each animal to each habitat of interest. With both these methods, since the animal is the sample unit, unequal sampling of individual animals does not affect the overall analysis, provided that sampling intensity is sufficient to derive accurate estimates of mean habitat use or that at least the estimates from different animals are equally accurate or stable. Since radio-tracking can be highly labour-intensive, optimization of sampling effort is desirable. A method to determine optimum sampling effort is described here with reference to an example from a case study of Natterer's bat *Myotis nattereri* (Kuhl 1817).

METHODS

Habitat use by Natterer's bat was studied (Smith, 2000; Smith & Racey, 2005) on the border of England and Wales. The study area (51°55′N, 2°57′W) was characterized by a hilly landscape, with elevations from 70 to 680 m above mean sea level. Below about 300–400 m, pasture was the dominant land use with some arable fields and frequent blocks of broad-leaved and coniferous woodland. Above this elevation, the land comprised mostly unenclosed common ground grazed by sheep. The purpose was to obtain data on habitat use that would be suitable for testing hypotheses concerning habitat use by the population. Hence, it was appropriate to use a method in which the sample size equates to the number of animals tracked, while the accuracy with which individual habitat use was estimated would relate to the quantity of foraging data obtained per animal. For each animal, habitat use (and potential availability) was given by a set of proportions describing habitat composition. Compositional analysis (Aebischer *et al*., 1993) was used for the study.

Aebischer *et al*. (1993) recommend sample sizes above 10 individuals, and preferably above 30, to represent a population adequately. However, a trade off is necessary between the effort required to follow a large number of individuals and the duration that each individual can be followed. Ideally, each animal would be sampled sufficiently to achieve a stable estimate of its habitat use to satisfy the assumption that compositions from different animals are equally accurate.

We radio-tracked 37 Natterer's bats from four study areas between mid-May and mid-September during 1995–97 (Smith, 2000; Smith & Racey, 2005). The 'close approach' method (White & Garrott, 1990) was used to obtain estimates of the bat's position and activity (foraging, commuting or roosting), and only data obtained during periods of close radio contact when estimates could be determined to within a 50-m radius were used in further analyses. Individual animals were observed continuously throughout the night with every substantial change in position or activity recorded to the nearest minute. We digitized the data on MapInfo geographical information system (GIS), and entered habitat data on the GIS with habitats categorized into six main types: improved grassland, other grassland, open water, semi-natural broad-leaved woodland, other woodland, and other habitats comprising arable, coniferous plantation, continuous bracken, road and rural development. For each bat tracked, we used standard GIS tools to derive tables of the sum of time spent at each fix and, for foraging fixes, the habitat present at the location.

The foraging time element of the time budgets recorded for each bat varied from 2.0 to 42.4 h (Smith, 2000; Smith & Racey, 2005), and exceeded 30 h for seven bats. We analysed data from these seven bats to determine the optimum tracking time required to achieve stable estimates of habitat use. We exported the data obtained to Microsoft Excel and calculated the running proportion of time spent foraging over each habitat with cumulative foraging time as each successive foraging fix was added. For each bat, we plotted running per cent foraging time spent over each habitat type against the cumulative foraging time recorded, and visually estimated the optimum sum of foraging time required to determine stable estimates of habitat use from the plots. The criteria used in estimating the optimum sum of foraging time were: the point should be the earliest time at which, for all habitats, plots showed no subsequent deviation of more than about ± 5% estimated by eye; the point should be at, or beyond, the inflexion point estimated by eye for plots that seem to be approaching an asymptote. The optimum point was set to the nearest whole hour since the method did not justify any greater precision. The total tracking effort at which this optimum point was reached was determined by reference to the full-time budget, including periods of lost contact and time when bats were engaged in non-foraging activities, and expressed in units of the number of nights that the bat had been tracked at the point when the optimum amount of foraging data had been recorded. Hence, the time required to obtain a stable estimate of habitat use was expressed both as the sum of foraging time recorded and as the number of nightly tracking sessions that had been undertaken to collect that amount of foraging data.

RESULTS

An inspection of plots of the change in composition of habitat use with cumulative time tracked (Fig. 1) revealed that stable estimates of the composition of habitat use were obtained after a mean of 22 ± 7.7 h of cumulative foraging time (Table 1). This represents the optimum sampling effort required to estimate habitat use in the Natterer's bat study when compositional data are to be used in the analysis. The plots in Fig. 1 show only the foraging element of the overall-time budget, but the point at which each night was completed is also indicated. It was found that, allowing for periods of lost contact and time when bats were engaged in other activities, it took a mean of 4.6 ± 1.9 nights to reach stable estimates of compositional habitat use (Table 1).

DISCUSSION

It is generally not practicable to assess tracking results as they are obtained each day, owing to time constraints, and therefore usually the researcher will not know whether stable estimates of habitat use have been achieved, or even the total of foraging time recorded, until it is too late to obtain further data from the tagged individual. Hence, once optimum sampling effort has been assessed, perhaps in a pilot study, the most practical measure of the optimum point at which to stop tracking is the mean number of tracking sessions required to obtain a stable estimate. The mean of 4.6 ± 1.9 nights obtained in the present study indicates that it would be appropriate to aim to collect five nights of data from each bat sampled when habitat preference of Natterer's bat is to be assessed by compositional analysis.

Examination of the plots in Fig. 1 reveals that if these seven bats had been tracked for only five nights each, estimates of habitat use would have been stable for four of the bats, but less accurate for the bats represented in Fig. 1a,b,d where asymptotes for habitat use were reached at 5.4, 8.1 and 5.1 days, respectively (Table 1). Nevertheless, in the absence of more accurate estimates being available, it would be appropriate to include data from all seven bats in compositional analysis (with just the five nights of data available for each), since, as Aebischer *et al*. (1993) note, increasing the number of animals improves the accuracy of the mean, even if the quantity of data obtained from individuals is consequently reduced. Time constraints during radio-tracking studies can be severe, especially when working with highly mobile small animals such as bats that often require continuous tracking of just one individual each night to minimize difficulties of re-finding lost contacts. Problems such as premature loss of tags may result in a suboptimal quantity of data being obtained from some individuals. Inclusion

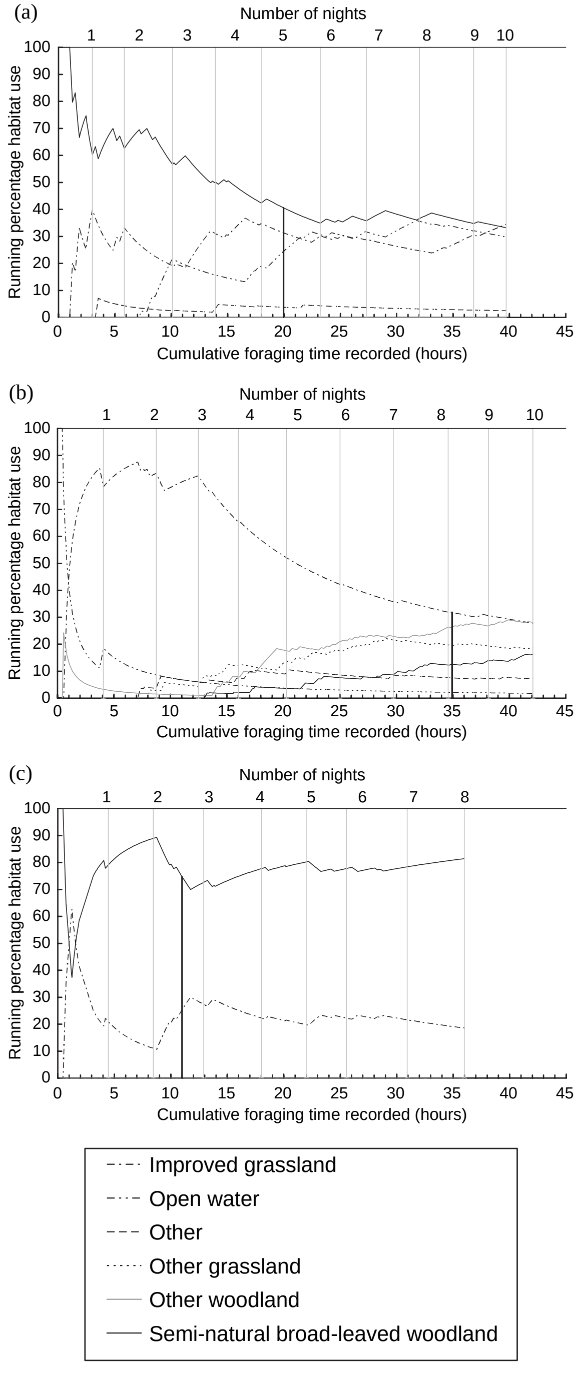

Fig. 1. Plots of running percentage habitat use by Natterer's bats against cumulative foraging time and number of nights tracked for: (a) an adult female tracked for 10 consecutive nights, starting 21 May 1996, (b) a pregnant female tracked for 10 nights out of 17, starting 6 June 1996, (c) a lactating female tracked for eight nights out of 14, starting 12 July 1996, (d) a post-lactating female tracked for nine nights out of 18, starting 8 August 1996, (e) an adult male tracked for seven nights out of 13, starting 27 August 1996, (f) an adult female tracked for six nights out of 11, starting 28 August 1996, and (g) an adult female tracked for five nights out of six, starting 14 August 1997. The time when a stable estimate is attained is indicated by a vertical line beneath the most used habitat with the line placed on the basis of visual inspection/estimation.

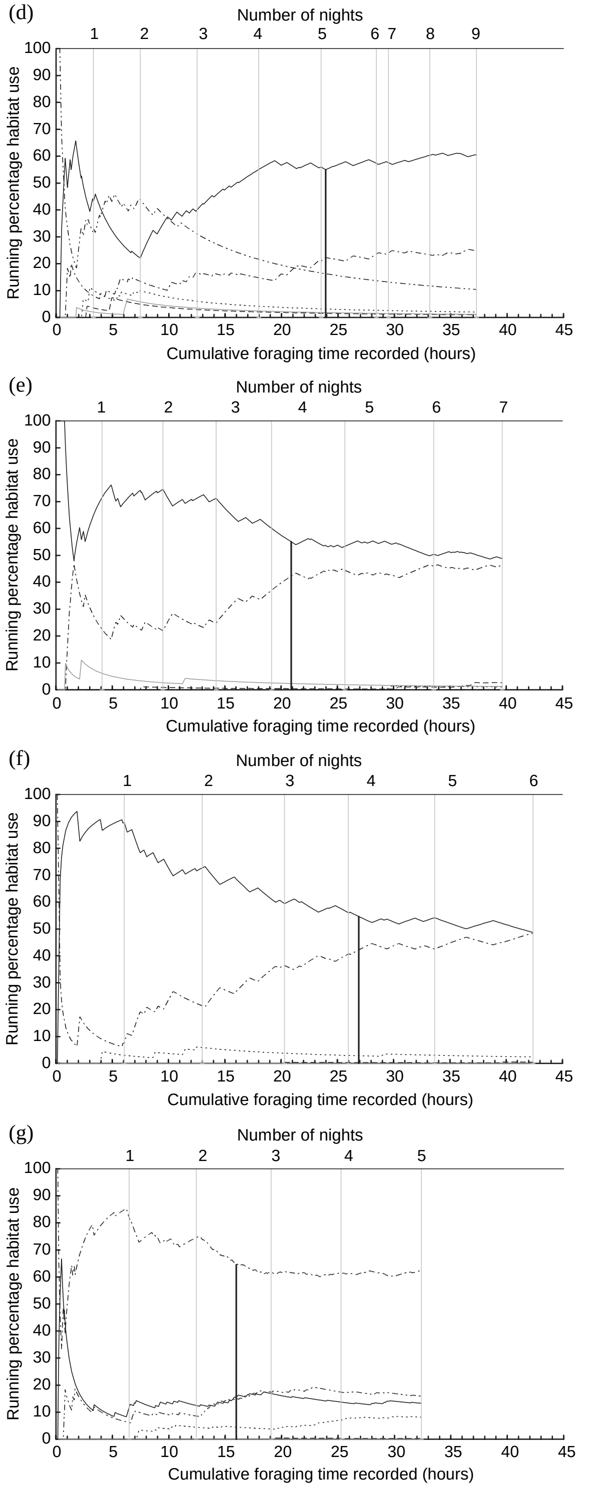

Fig. 1. *Continued*

Table 1. Foraging time recorded for seven adult Natterer's bats and time to obtain stable estimates of the composition of habitat use as determined by visual inspection of plotted data (Fig. 1)

Figure number of plot showing composition of habitat use	Number of nights tracked	Total foraging time recorded (h)	Mean foraging time recorded per night (h)	Cumulative foraging time to obtain stable estimate of habitat use (h)	Number of nights to obtain stable estimate of habitat use
1 (a)	10	39.7	4.0	20	5.4
1 (b)	10	42.1	4.2	35	8.1
1 (c)	8	36.0	6.0	11	2.6
1 (d)	9	37.3	4.1	24	5.1
1 (e)	7	39.7	5.7	21	4.3
1 (f)	6	42.4	7.1	27	4.2
1 (g)	5	32.4	6.5	16	2.6
Mean (S.D.)	7.9 (2.0)	38.5 (3.6)	5.4 (1.3)	22.0 (7.7)	4.6 (1.9)

of data from individuals with habitat use estimates that do not approach stability has the effect of increasing the variance between individuals, so increasing the risk of Type II error in the omnibus test for selectivity of habitat types during compositional analysis (Aebischer *et al*., 1993) and for subsequent tests for significance of difference between habitat rankings. It should not introduce any bias to the ranking of habitat preferences for the population, however, and, on the contrary, should improve the reliability of the population estimate because of the increased sample size of contributing individuals (N. Aebischer, personal communication). Hence it is appropriate to include data from such animals in the analysis so as to maintain the sample size, except where the data deficiency is extreme.

Estimation of the optimum number of tracking sessions required to obtain accurate estimates of habitat use will assist in planning the effort required for radio-tracking studies. There may be wide variation in the efficiency with which habitat use data are collected from different individuals. If it seems to the observer that comparatively little data have been obtained from a particular animal upon completing the optimum number of tracking sessions, the tracking programme should be extended for that animal to minimize the risk of discovering extreme data deficiency after it is too late to obtain more data.

The optimum level of sampling effort will vary with the parameters of the study, including species, reproductive stage, season, year or landscape. Further, sample estimates are likely to be stable only in the context of the individual sampling period: radio-tracking studies generally underestimate the lifetime patterns of animals because the duration of tracking is so brief. Furthermore, if home range estimates are needed, then different methods will be required to assess their stability in relation to the quantity of data collected.

The method presented above is also applicable to studies where tracking data are discontinuous. In the habitat composition plots, the cumulative number of fixes recorded for habitat use is substituted for the cumulative time recorded on the x-axis. Radio locations collected from an animal do not need to be independent, but they must provide an unbiased representation of the trajectory they sample.

In studies where a Euclidean distance method is to be used for habitat analysis, it would be appropriate to use a variation of the method for determination of optimum tracking effort described for use with compositional data above. Habitat use in the Euclidean distance method is assessed using mean distances from locations recorded for each animal to each habitat of interest. The running means of the distance of locations from each habitat can be plotted on the y-axis with the cumulative number of locations represented on the x-axis. The set of habitat plots can be visually inspected in a similar way to that described for compositional data to determine the optimum tracking time.

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