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Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of environment and tracking systems

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Summary

1. How and at what spatial scale(s) animals change their movements in relation to their environment is central to several topics in ecology and conservation, including foraging ecology, habitat selection and dispersal. A method (first-passage time analysis, FPT) has recently been proposed to measure changes in movements through the landscape, as an index of search effort at the pertinent spatial scales. This method seems largely applicable to an increasing number of studies using satellite, radio-tracking or global positioning system (GPS), but its limits have not yet been assessed.

2. Here I used several movement simulations to examine the ability of FPT analysis to detect area-restricted search (ARS) according to different changes in movements, different patch structures and tracking accuracy.

3. FPT analysis was able to detect changes in movements when both speed and sinuosity changed, or when the animal reacted to patch boundaries. It was also able to detect ARS within the same path at several spatial scales in patches (nested or not) of different sizes.

4. Tracking accuracy affected the detection of ARS by FPT analysis. With the widely used Argos system, a minimum of 13 locations in effective ARS was necessary to detect this behaviour; seven when velocity filtering was applied. Similarly, spatial error in location affected the estimation of the ARS scale value, but the application of velocity filtering reduced this effect.

5. Comparisons between a real GPS track and pathways simulating the Argos error showed that the time-sampling rate of locations (due to satellite-pass frequency) decreased the probability of detecting ARS at small scales (<10 km), while the spatial error decreased this probability by >50% across the whole range of scales. A velocity filter enabled significant reductions in this effect.

6. *Synthesis and application.* Within limits, FPT analysis is highly suitable for animal movement analysis, either to quantify habitat use, or to determine the scale most relevant for describing an ecological system or factors affecting movement decisions. In anticipation of increasing applications of FPT analysis in applied ecology, I provide recommendations for the use of the technique with several tracking methods.

Key-words: animal movement, area-restricted search, Argos satellite tracking, first-passage time analysis, GPS tracking, habitat-use quantification, spatial scale

Introduction

Understanding how organisms explore and exploit their environment is a central topic in ecology, and the assessment of factors affecting their movements and habitat use is of great value for conservation. Since the early 1990s there has been an exponential increase in animal-borne satellite-tracking studies using the Argos system (Coyne & Godley 2005) and, more recently, global positioning systems (GPS). Data sets produced using these technologies are autocorrelated in time and space, and pose some analytical problems when studying habitat use (White & Garrott 1990). Rather than eliminating some information about animal movement contained in these data sets (for example, by subsampling every x hours), recent methods enable this dynamic aspect to be accounted for fully. These methods consider changes in animal movement as a

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response to heterogeneity in the environment resulting from the interaction between animal decisions and landscape properties (Morales *et al*. 2005), and enable the assessment of underlying ecological mechanisms. Fully accounting for movement is crucial to understanding the links between the behaviour of individuals and landscape-level problems in fundamental ecology (Lima & Zollner 1996), and is essential for conservation and population management (Rushton, Ormerod & Kerby 2004). Furthermore, this approach enables the definition of pertinent scales of interaction between animals and the environment, at which ecological processes operate (Fortin & Agrawal 2005), indicating ecologically meaningful management units in fragmented landscapes.

Analysing animal movement follows naturally the development of tracking technology combined with the use of geographic information system tools. It is expected that this new 'toolbox' will be used increasingly in ecological and conservation studies, especially because it leads to quantitative understanding of the connection between moving animals and increasingly fragmented landscapes, as well as, ultimately, the consequences of fragmentation for populations (Morales *et al*. 2005). Analyses of movements are based on the premise that, as the environment is not spatially uniform, animals should react to habitat features and spend more time in areas where resources are more abundant. When resources are distributed in patches (*sensu* Fauchald 1999), the searching activity of foragers should be concentrated in these high-density areas (e.g. Kareiva & Odell 1987). Thus movements of animals should follow the structure of the environment, exhibiting, for example, a behaviour called area-restricted search (ARS). ARS might arise where an animal increases its turning rate and/or decreases its speed, or where it reacts to changes in resource density (i.e. patch boundary) to stay in the patch (Benhamou & Bovet 1989; Fauchald & Tveraa 2003).

Considering that resources can be distributed in a nested patch hierarchy (Johnson 1980; Kotliar & Wiens 1990), animals should be able to respond to patches at several spatial scales (Fauchald 1999). To understand habitat selection and how organisms exploit their environment, it is crucial to identify the scales of environment–animal interactions (Johnson 1980; Levin 1992), particularly in nested scale systems where large-scale patterns tend to mask fine-scale ones (Fauchald, Erikstad, & Skarsfjord 2000). Novel methods have been used recently to study scale-dependent movements (Johnson *et al*. 2002; Fauchald & Tveraa 2003; Fritz, Saïd & Weimerskirch 2003; Nams 2005). First-passage time analysis (FPT; Fauchald & Tveraa 2003) has allowed the description of search effort at scales where an animal adopts an ARS behaviour in interaction with a patchy environment. This analysis is based on calculation of the time taken by an animal to cross a circle with a given radius. This circle is moved along the path of the animal with increasing radii as a scale-dependent measure of search effort. FPT analysis has been used successfully on various species in many ecosystems, using different tracking techniques. These include satellite-tracked seabirds (Fauchald & Tveraa 2003; Pinaud & Weimerskirch 2005; Suryan *et al*. 2006), GPS-collared elks (Frair *et al*. 2005), and theodolite-tracked bottlenosed dolphins (Bailey & Thompson 2006). It is expected that FPT analysis will be increasingly used, especially for highly migratory, endangered species (Suryan *et al*. 2006); however, the limits of the technique have yet to be fully explored.

Despite their potential value for ecologists and conservationists, the efficiency of techniques including FPT analysis is still under debate, and there remains a need to understand better the limits of their application (Johnson *et al*. 2006; Nams 2006). Here I present results of different movement simulations to test the limits of FPT analysis. Animals can modify their searching behaviour in different ways, or encounter patches of different sizes, resulting in heterogeneous ARS at different spatial scales during the same movement path (Fauchald 1999). Using different movement simulations, I test (i) the ability of FPT analysis to detect different modes of animal searching behaviour; (ii) the ability to detect ARS behaviour in an environment presenting patches of different sizes; and (iii) the effect of tracking accuracy and time-sampling rate on ARS detection by FPT analysis, especially with the Argos system. As an applied example, FPT analysis is applied to a GPS path of an at-sea, foraging black-browed albatross, *Thalassarche melanophris* (Temminck), a highly migratory, endangered seabird species (IUCN 2006). Finally, I provide recommendations for the use of FPT analysis in studies using different tracking systems.

Materials and methods

FPT ANALYSIS

First-passage time analysis is based on calculating the time taken by an animal to cross a circle with a given radius. Calculations of FPT are repeated along the path of the animal by moving the circle at distance d and for increasing radii r. The relative variance $S(r)$ in FPT is then calculated for the whole path, given by var[log(FPT)], where $t(r)$ is FPT for circle of radius r, and is log-transformed to make the variance $S(r)$ independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003). Maxima in the plot of $S(r)$ in relation to r will suggest the presence of ARS behaviour and indicate the scale, r, at which the animal increased its search effort (Fauchald & Tveraa 2003). FPT analysis can then be used as a scale-dependent measure of search effort, with high FPT values corresponding to high effort.

DETECTION OF DIFFERENT SEARCH MODES BY FPT ANALYSIS

In order to test whether FPT analysis is sensitive to different modes of searching, I simulated a virtual animal moving in an environment with circular patches of a given size. When outside a patch, the animal adopted a relatively straight correlated random walk (CRW) with two spatial units (2 km) moved per time unit (10 min, with a constant speed of 12 km h^{-1}) and a distribution of turning angles between successive moves taken from a Von Mises distribution with $K = 250$. The Von Mises distribution is a circular normal distribution, with larger K values representing straighter movement paths (Fisher 1993). The simulation started with the animal outside a patch. Once in a patch, the animal adopted a searching behaviour.

I tested four different modes of searching within a patch: (i) REFL: the animal was reflected by the boundaries of the patch with a probability of 0·9; (ii) SIN: the animal adopted a tortuous CRW with an increase in sinuosity ($K = 5$); (iii) SP: the animal adopted a slow CRW by decreasing its speed with a step length of 0·5 km; and (iv) SINSP: the animal changed both its speed (slow CRW with a step length of 0·5 km) and its sinuosity (tortuous CRW with $K = 5$).

In order to test the influence of patch size (relative to step length), this simulation was performed for each search mode with five different patch radii: 5, 10, 20, 30 and 50 km (2·5, 5, 10, 15 and 25 times the step length), with each path simulated for 400, 500, 600, 800 and 1000 steps, respectively. Patches were distributed regularly in the environment, with an interpatch distance of four times the radius to avoid interference between patches. For each combination of search mode and patch radius, 200 paths were simulated. FPT was calculated every 0·5 km for r varying from 2 to 100 km.

DETECTION OF ARS FOR DIFFERENT PATCH SIZES

To explore the scale dependencies in $S(r)$ in an environment with patches of different sizes, I simulated ARS associated with circular patches of two different radii (10 and 30 km). As these dependencies in FPT variance could differ in a nested patch structure (Fauchald 1999; Fauchald & Tveraa 2003), two different patterns were simulated. In the exclusive patch structure (ES) simulation, small patches were located strictly outside large patches, with a minimal distance of 90 km between centres. In the nested structure (NS), each small patch was included completely in a large patch, with a minimal distance of 90 km between the centres of large patches (to avoid interference between patches). In each type of simulation, 1000 paths (of 700 steps each) were simulated according to Fauchald & Tveraa (2003): an organism performed CRW and ARS behaviour (REFL mode, $K = 15$) when visiting a patch. This strategy allowed the animal to search across the whole patch area, keeping the correspondence between the patch radius values and those observed in ARS scale with FPT analysis. FPT was calculated every 0·5 km for r varying from 2 to 100 km.

EFFECT OF ARGOS TRACKING ACCURACY, FILTERING AND ARS INTENSITY

I simulated a 'theoretical' path with an ARS and added spatial noise due to measurement error to generate a typical observed path according to the error of the tracking system. First, I took parameter values from a study on seabirds using the Argos system as a reference, then extended this approach to take into account spatial errors from other systems.

First, the theoretical path simulated a virtual animal moving in a straight line (500 km in total). The animal started at a constant speed of 30 km h^{-1}. At the mid-point of the trip (250 km), it stopped for a variable duration (see below) and then moved again at 30 km h^{-1}. This stop simulated an ARS behaviour at very small scale (where $r \rightarrow 0$ km), meaning that, after adding a simulated spatial error in location, the apparent movement around this position was wholly due to the error of the tracking system. The stop (ARS behaviour) duration was set to 1, 2, 3, 5, 7, 10 and 15 h, increasing the number of fixes involved in ARS. Then I simulated typical results obtained from an Argos satellite-tracking study by applying an 'Argos noise' to these paths. This procedure was simulated 1000 times for each ARS duration, generating 7×1000 paths. Argos noise was considered with two components (Argos 1996): (i) a satellite-pass frequency giving an expected number of locations per day with a different proportion for each localization class (LC) given by Argos; (ii) a spatial error according to each LC, following a normal distribution in longitude and latitude (Vincent *et al*. 2002; Jonsen, Flemming & Myers 2005). In these simulations, parameter values (see Appendix S1 in Supplementary Material) were chosen according to a mid-latitude data set ($n = 234$ locations) on wandering albatross *Diomedea exulans* (L.) in Kerguelen Island (Pinaud & Weimerskirch 2007). Locations were chosen randomly to obtain an average of 16 locations per day (1·5 locations per hour), corresponding to a survey situated at a latitude of 45° (Argos 1996). The spatial error was applied to each location simulating the Argos accuracy: co-ordinates in longitude and latitude of the Argos location were taken from a normal distribution centred at the true location with a standard deviation set for each LC (given in Appendix S1). To study the effect of removing locations with low accuracy, I applied an iterative forward/backward averaging filter to all locations in the focal path (McConnell, Chambers & Fedak 1992). A velocity V_i was associated with the ith location:

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2,\, j \neq 0}^{j=2} (v_{i,i+j})^2} \qquad \text{eqn 1}$$

where $v_{i,j}$ is the velocity between successive locations i and j. This velocity filtering was applied to the 7000 paths. Locations with $V_i > 100$ km h^{-1} (value for wandering albatross, Weimerskirch, Salamolard & Jouventin 1992) were rejected. FPT was then calculated every 0·5 km for radius r varying from 1 to 200 km.

To generalize the effect of location accuracy on estimation of ARS scale by FPT analysis, I created a second set of simulations of a virtual animal moving in a straight line (speed 30 km h^{-1}) for 200 km with a stop of 10 h in the middle. Locations were taken every 30 min. Normal error was applied to these locations, with a standard deviation (mimicking the location accuracy of various tracking systems) ranging from 20 m to 20 km (60 simulations in total). FPT analysis was then applied.

APPLICATION OF ARGOS NOISE TO AN ALBATROSS PATH

In order to detect the effect of Argos accuracy on FPT analysis using real movement data, I applied FPT analysis (i) to a real path obtained from a GPS tracking study on a seabird; and (ii) to this real GPS path with Argos noise added by simulation. In early January 2004, during the brooding period, a breeding black-browed albatross at Kerguelen Island was fitted with a GPS logger (GPS receiver with an integrated antenna and 1-Mb flash memory, Newbehavior company; Steiner *et al*. 2000). The GPS path, with locations and instantaneous speed recorded every 10 s with a precision of few metres, was taken to be the 'theoretical' path (Appendix S2), and FPT was calculated every 1 km for radius r varying from 1 to 100 km.

In a second step, an Argos noise was applied to the subsampled GPS path to reproduce 200 typical Argos paths, using the same procedure and parameters as described previously. To detect the effect of each Argos component on ARS detection (effect of an infrequent satellite pass, effect of spatial error and effect of velocity filtering), FPT analysis was applied to these 200 paths at different steps of the simulation (see an example in Appendix S3): (i) corresponding to the path with Argos time-sampling rate only (with GPS accuracy but 1·5 locations h^{-1} on average); (ii) corresponding to the path with both Argos time-sampling rate and spatial error (typical Argos track); and (iii) the same as (ii) but with the application of velocity filtering (filtered Argos track). FPT was calculated every 1 km for scales from 1 to 100 km.

Table 1. Results of first-passage time analysis of simulated paths with an effective area-restricted search in different patch structure, indicating the percentage of simulated paths showing one and two peaks of variance and the scales of these peaks

	Exclusive patch structure		Nested structure	
Number of detected peak of variance	One	Two	One	Two
Walks with detected peak (%)	39·6	53·8	46·2	51·3
Scale of detected peak (km)	31·9 ± 15·4 53·6 ± 9·3	22·6 ± 7·0	37·2 ± 12·0 48·0 ± 8·8	22·9 ± 5·3

STATISTICS

Each simulated path was inspected to confirm that ARS behaviour in patches was effectively present and that high FPT values (indicating ARS) matched with presence in patches. With this inspection I was able to make the distinction between two kinds of error (type I and II) that one can make using FPT analysis: identifying wrong ARS scales (e.g. one scale when there is none) or missing existing scales (for example 0 instead of 1). Normality and homoscedasticity were tested when using parametric tests, and non-parametric statistics were used when appropriate. Unless stated otherwise, values are reported as means ± 1 SD and statistical significance was considered to be $P < 0·05$. All statistics and programming used R ver. 2.1.1 (R Development Core Team 2005).

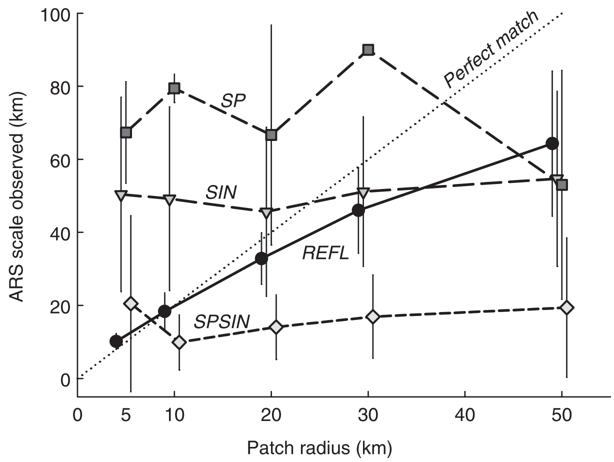

Fig. 1. The results of simulations to estimate area-restricted search (ARS) scales by first-passage time (FPT) analysis according to different patch radii and different modes of searching movement (see text for details). Dotted line indicates a perfect match between patch radius and value of ARS scale given by FPT analysis.

Results

DETECTION OF DIFFERENT SEARCH MODES BY FPT ANALYSIS

In 202 of 4000 initial simulations, the animal did not enter the patch, thus showing no effective ARS behaviour. FPT analysis revealed a peak of variance in 34 of these 202 cases with an average ARS scale of 76·5 ± 17·3 km, indicating a false detection of ARS of 16·8%.

The ability of FPT analysis to detect ARS behaviour was significantly dependent on the searching mode adopted by the animal, but not on the patch radius (ANOVA, proportion of ARS detected as dependent variable with arcsine transformation, effect of SearchMode: $F_{3,12} = 299·9$, $P < 0·001$; PatchRadius: $F_{1,12} = 1·07$, $P = 0·32$; interaction: $F_{3,12} = 2·31$, $P = 0·12$). On paths presenting effective ARS behaviour, the REFL mode showed more efficient detection: FPT analysis detected at least one peak in variance on 99·0% of cases, with 99·9% of these paths matching between the effective and the observed ARS. For the other searching modes, these values were for mode SIN, 59·9 and 85·5%; for mode SP, 4·6 and 79·5%, and for mode SPSIN, 93·8 and 97·6%, respectively.

For paths where a match was observed between the effective and observed ARS, the observed ARS scales differed significantly according to searching mode (ANOVA, $F_{3,2320} = 564·6$, $P < 0·001$) and patch radius ($F_{1,2320} = 607·1$, $P < 0·001$) with a significant effect of the interaction ($F_{3,2320} = 216·0$, $P < 0·001$). The estimation of ARS scale by FPT analysis when the animal was reflected by the patch boundary was particularly relevant, with observed ARS scales close to the diameter of the patch radii (Fig. 1). Considering the other searching modes, this correspondence between the ARS scale and patch radius was unclear (with a large variance in ARS scale), especially when considering the mode with a change in both speed and sinuosity.

SIMULATING ARS IN DIFFERENT PATCH STRUCTURES

283 (28·3%) and 821 (82·1%) paths in ES and NS arenas, respectively, presented an effective ARS behaviour in both patch sizes for the same path (two examples of each structure shown in Appendix S4). Using these paths, I assessed the detection of ARS behaviour by FPT analysis when the animal visited several patches that differed in size. FPT analysis clearly showed peaks of variance in FPT (see examples in Appendix S4) related to ARS behaviour in around 50% of cases (Table 1). This relationship can be illustrated by plotting FPT (at the scale corresponding to each peak of variance) as a function of time elapsed since departure (Fauchald & Tveraa 2003), as shown in Appendix S5. Changes in FPT can be related to the occurrence of ARS behaviour and presence in patch, indicated by an increase and large values of FPT. This correspondence was found for simulated paths in both ES and NS structures and also when several small patches (up to four) were nested in one large patch. Simulations with different radius ratios between the small and large patches (30 and 5 km or 30 and 20 km, for example), showed that the distinction between the

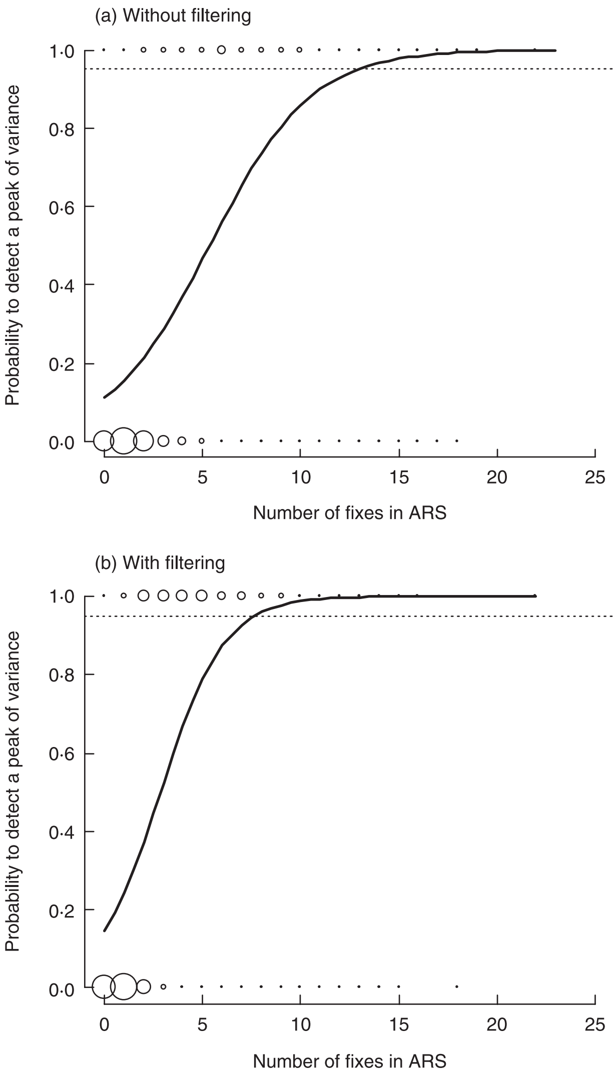

Fig. 2. Effect of the number of Argos locations gained during an area-restricted search (ARS) bout on the probability with which a peak of variance is detected using first-passage time (FPT) analysis (a) without and (b) with location filtering. Solid lines indicate results of logistic models. Diameters of circles are proportional to the number of tracks. Dotted line indicates a probability of 0·95.

two peaks of variance was not perceptible for a radius ratio from 2 : 1 to 1 : 1 (in this simulation for small patches of radius >15 km).

EFFECT OF LOCATION ACCURACY, ARS INTENSITY AND ARGOS FILTERING

When Argos noise was added to the path of a moving animal, the probability with which ARS behaviour was detected increased with the number of Argos fixes during the period of ARS behaviour (logistic regression with non-filtered locations: $d.f._{1,6998} = 2163{\cdot}1$, $P < 0{\cdot}001$; Fig. 2a). To detect ARS behaviour with a probability of 0·95, at least 13 locations were required during the ARS. Using filtered locations, this value decreased, reaching a minimum of seven locations in ARS

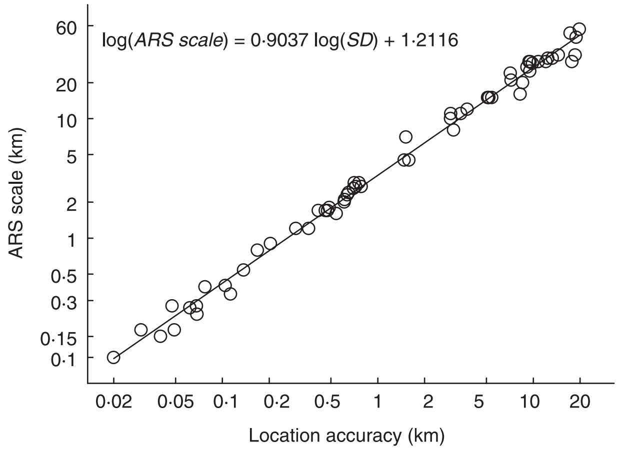

Fig. 3. Effect of location accuracy (log scale) on the estimation of area-restricted search (ARS) scale by first-passage time (FPT) analysis (log scale), as revealed by 60 simulated paths with different location accuracy.

(logistic regression with filtered locations: $d.f._{1,6998} = 2883{\cdot}7$, $P < 0{\cdot}001$; Fig. 2b). For paths with only one peak of variance before filtering (with an effective ARS, $n = 1671$), the peak of variance occurred at a spatial scale of 23·89 ± 25·31 km. Filtering reduced this noise by 8·11 ± 24·27 km (paired comparison without and with filtering, Wilcoxon signed rank test, $V = 5707{\cdot}5$, $P < 0{\cdot}001$). Simulations for a larger range of location error values indicated that the estimation of ARS scale from FPT analysis was significantly dependent on the location accuracy (linear model, $F_{1,58} = 8148$, $P < 0{\cdot}001$, adjusted-$R^2 = 0{\cdot}993$; Fig. 3).

COMPARISON BETWEEN GPS AND ARGOS PATHS

FPT analysis of the albatross GPS path revealed the presence of ARS behaviour at three spatial scales (Fig. 4a): 3, 14 and 80 km. Search effort was quantified at precisely the correct spatial scales in relation to the environment (Fig. 5). First, this individual moved rapidly from the colony and increased its search effort at a scale of 80 km on the edge of the Kerguelen plateau, 120 km away from the colony. In this area it increased its search effort in four areas at a scale of 14 km and two areas at a spatial scale of 3 km.

Taking the GPS path as a basis for comparison (see example in Appendix S3), the time-sampling rate due to Argos satellite passes introduced a biased detection in ARS (see example in Fig. 4b), with a lower proportion of simulations with an ARS detected at the 3-km scale (Fig. 6a). The spatial error introduced by the Argos system decreased the proportion of ARS detected at the three spatial scales by more than 50% (Fig. 6a). Velocity filtering attenuated this effect by retrieving 75% of ARS detected.

The ARS scale identified by FPT in the presence of simulated Argos noise was compared with the true value of ARS scale from the GPS path. Infrequent time-sampling rate from Argos introduced a noise in the estimation of the ARS scale value, especially for ARS performed at small scales relative

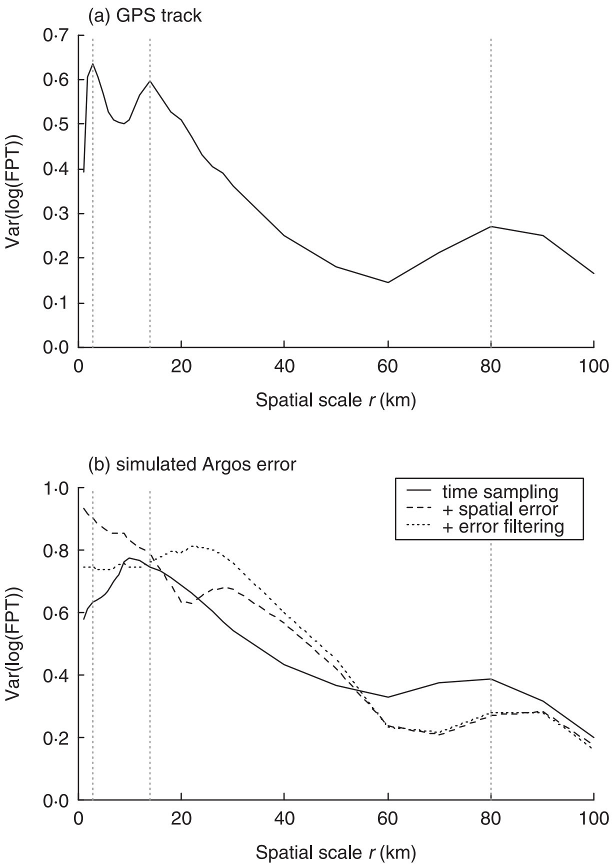

Fig. 4. Variance in spatial scale indicated by first-passage time (FPT) analysis of (a) a GPS path of black-browed albatross from Kerguelen Island; (b) the same GPS path where Argos noise is simulated with different components: solid line, time-sampling rate component only; dashed line, time-sampling rate and spatial error components; dotted line, time-sampling rate and spatial error components with velocity filtering.

to the accuracy of the tracking system, <10 km here (Fig. 6b). On average, values of the ARS scale detected after the application of spatial noise reproducing the Argos time-sampling rate were lower than those detected after application of the Argos spatial error, but were still close to the true ARS scale given from FPT analysis on the GPS path. At the 3-km scale, the effect of spatial error introduced by the Argos system was more important, leading to an overestimation of ARS scale (for spatial error, 11·00 ± 11·63 km; after filtering, 9·16 ± 3·76 km; ANOVA, $F_{2,20} = 3{\cdot}81$, $P = 0{\cdot}04$).

Discussion

The results of this study show that FPT analysis is an efficient method of studying animal movement with various systems like Argos and GPS. FPT analysis can reveal changes in movement, suggesting spatial scales of important interactions of the animal and its environment. FPT analysis can also quantify search effort as an index of habitat use by animals tracked in the wild, even if patches differ in size or are present in a nested structure.

EFFECT OF SEARCHING MODE AND STRUCTURE OF THE ENVIRONMENT

In their initial simulations to test the ability of FPT analysis to detect ARS behaviour, Fauchald & Tveraa (2003) considered ARS only in patches of the same size, with an animal being reflected by patch boundaries. My results show that FPT analysis is also able to detect changes in different movement parameters (speed and sinuosity). In the same movement path, ARS behaviour in patches of different sizes can be detected. It has been shown empirically that, while searching, animals change both their speed and sinuosity in contact with a high density of resource, or react to the patch boundary when perceiving it (Benhamou 1992). FPT analysis is able to detect changes in movements in these two search modes. A clear correspondence exists between the ARS scale and the patch radius when the animal adopts a 'patch-boundary reflectance' search mode (Fauchald & Tveraa 2003), but this was not true when the animal changed both speed and sinuosity, because the patch area is not necessarily covered totally with this mode. Caution is thus essential when trying to relate scale of search to patch size in this case.

In my simulations, peaks of variance were observed at values close to the diameter of simulated patches in >50% of cases. Results were similar when small patches were nested in large ones. Peaks of variance in both patch sizes were not detected in all cases (≈50%), mainly because of differences in ARS intensity. In fact, the probability with which ARS behaviour is detected depends on the number of locations recorded during this behaviour (see below), and could explain the inability of FPT to detect all ARS events. As this method is based on the detection of clear peaks in variance plotted against spatial scale, definition of the ARS scale is less accurate when the search effort increased at several spatial scales close in magnitude. Here, large patches were three times larger than small ones, allowing a clear detection of peaks of variance. In the case of patches of different sizes but closer in diameter (ratio from 2 : 1 to 1 : 1), this detection was less effective with less obvious peaks of variance.

EFFECT OF TRACKING SYSTEM ACCURACY

Simulations demonstrated that location spatial error and, to a lesser extent, sampling time interval affected the detection and quantification of ARS behaviour. These effects were also related to the duration of ARS behaviour: longer bouts of ARS behaviour and higher numbers of locations increased detection by FPT analysis. ARS events had a lower probability of detection at small scales relative to the tracking system accuracy (e.g. <10 km for Argos) because of their short duration (which leads to less-efficient description by the tracking system). Nevertheless, small spatial-scale events can be detected if their duration is long enough to enable sufficient locations during the bout. The effect of velocity filtering can be interpreted as a reduction in spatial noise (Vincent *et al.* 2002), leading to a clearer distinction between travel (higher speed and lower turning rate) and search (lower speed and

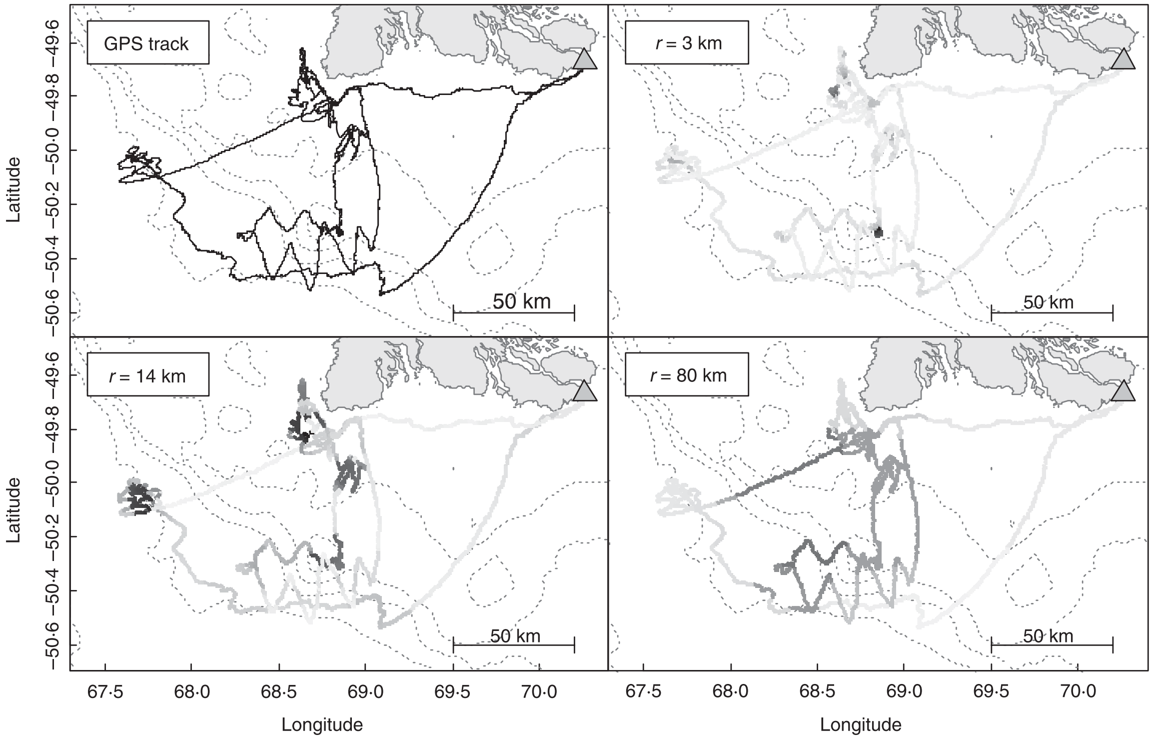

Fig. 5. GPS path of a black-browed albatross from Kerguelen Island (top left) and corresponding search effort as revealed by first-passage time (FPT) analysis (Fig. 4a) at different spatial scales: 3 km (top right), 14 km (below left) and 80 km (below right). Grey triangle indicates colony on the coast of Kerguelen Island (grey). Bathymetry isolines (–2000, –1500, –1000, –500, –200 m) are represented by dotted lines. Grey intensity on the track refers to search effort: darker grey, the more intensive search effort.

higher turning rate). This increases the probability of ARS detection by FTP analysis.

Estimating ARS scale using FPT analysis depends significantly on location accuracy (see equation in Fig. 3). The relationship derived here (Fig. 3) is helpful only where accuracy remains relatively constant for each location (the same error distribution with the same parameters); this is not the case for the Argos system, where accuracy depends on the location class (Argos 1996; Vincent *et al.* 2002). For Argos-derived paths, I found that the resolution of FPT analysis was, on average, 24 km, which was close to the higher spatial error of Argos system in the study. This finding seems consistent with studies providing information about error measurements (Fauchald & Tveraa 2003; Frair *et al.* 2005; Pinaud & Weimerskirch 2005; Bailey & Thompson 2006). This means that an affective ARS at a smaller scale (say 5 or 10 km) could be detected, but ARS scale will be overestimated at an average value of 24 km.

The simulated example was based on an animal searching in a marine environment, but conclusions can be applied easily to terrestrial animals, for example with a study employing radio tracking with a spatial error of 50 m. In fact, organisms face heterogeneity at several scales in both marine and terrestrial ecosystems, and tracking techniques (such as radio tracking, Argos or GPS) are shared by these ecosystems to study animal movements in response to environmental heterogeneity. The simulations presented here show that FPT analysis can be applied using these tracking techniques.

RECOMMENDATIONS WHEN ASSESSING SEARCH EFFORT USING FPT ANALYSIS

Growing technological developments for wild-animal tracking provide important information about habitat use, which can be applied to conservation problems in both terrestrial and marine ecosystems (for example the migration of the white-napped crane, Higuchi *et al.* 1996; or the definition of at-sea protected areas for albatrosses, BirdLife International 2004). In the latter example, Kernel estimation was used on Argos data sets to quantify habitat utilization at sea, which is based on location density only (Worton 1989). Undoubtedly this approach is of great conservation value, but it could lead to overestimation of the importance of areas very close to breeding colonies (Wood *et al.* 2000). By considering fully the behaviour of the animal, FPT analysis can solve this problem and allow important foraging areas to be defined at several spatial scales (see example for black-browed albatross in Fig. 5) in relation to environment and fisheries (Pinaud & Weimerskirch 2005, 2007).

Despite the increasing availability of spatial data on animal movement, a quantitative understanding of factors affecting animal movements and distribution is still limited, especially in relation to providing predictive models in response to changing environments (Jonsen *et al.* 2003). The development of analytical approaches such as FPT will help to fill this gap. Changes in patterns of movement at biologically relevant scales can indicate appropriate spatial scale(s) for conservation

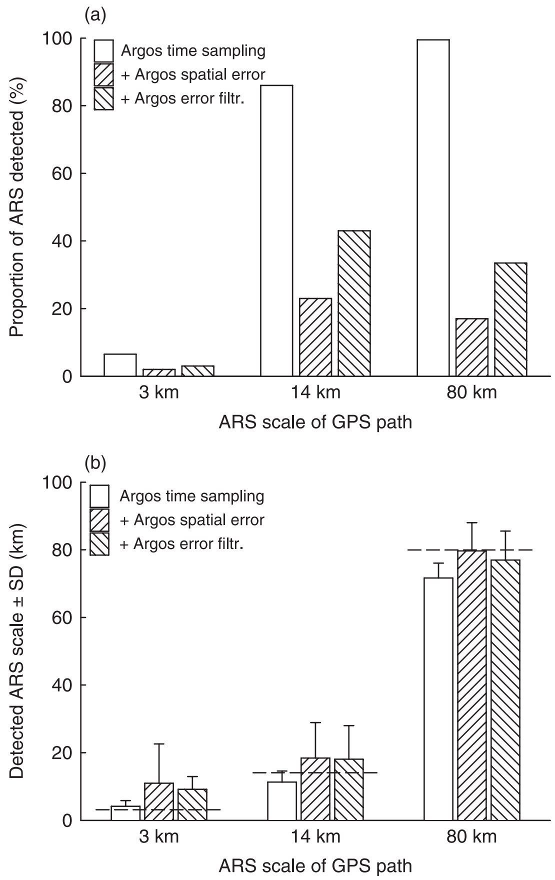

Fig. 6. Results of first-passage time (FPT) analysis of the black-browed albatross GPS path [with initial area-restricted search (ARS) at scales of 3, 14 and 80 km], where Argos noise is simulated with different components: white bars, time-sampling rate; left-hatched, time-sampling rate and spatial error; right-hatched, time-sampling rate and spatial error with a velocity filtering. (a) Proportion of ARS events detected by FPT analysis at different simulation steps; (b) detected ARS scales at different simulation steps. In (b), horizontal, hatched lines indicate true ARS scales detected from the GPS path.

guidelines (Nams, Mowat & Panian 2006). In fact, it is possible to relate and map variations in FPT as a function of habitat variables to identify pertinent factors affecting movement decisions and habitat use (Frair *et al.* 2005; Pinaud & Weimerskirch 2005, 2007).

This study provides several recommendations for successful application of FPT analysis to data sets originating from different tracking methods. First, the intensity of ARS behaviour affects the probability of its detection, with small scales/duration events relative to the tracking system error less detectable. Using Argos, a very good estimation is reached with 13 locations describing the ARS behaviour. This sample can be reduced to seven locations after application of velocity filtering (reduction of spatial error). Second, the resolution of FPT is dependent on the spatial resolution of the system, with an equation given in Fig. 3. When the location accuracy is not constant (for example with Argos), the FPT resolution is dependent on the larger error in location (in this example, class B). This effect implies that an ARS event occurring at a smaller scale than the larger location error can be detected by FPT analysis, but will be overestimated: its observed value will be close to the larger location error. Third, the frequency at which locations are obtained affects the detection of fine-scale ARS events; more regular fixes are better. Argos (the most widely used individual tracking system) enables detection of scale-dependent movements at scales >20 km in a heterogeneous structure (patches of different sizes), and I recommend the application of velocity filtering (following, for example, McConnell *et al.* 1992).

Depending on the latitude of the study (satellite passes are more frequent around the poles, providing more locations per day) and characteristics of platform terminal transmitters (PTT, influencing location accuracy), some limitations affect the detection and quantification of ARS behaviour by FPT analysis. In the case of very infrequent satellite passes, some fitting techniques such as curvilinear interpolations of tracking data (Tremblay *et al.* 2006) could improve this estimation. Many tracking studies use PTTs integrating a duty cycle timer (succession of 'on' and 'off' periods of various durations in order to save power, resulting in a bimodal distribution of time intervals between successive locations). This can limit ARS detection by FPT analysis, and the resolution will be given by the longest interval between consecutive locations (the duration of 'off' mode). To isolate this problem, I recommend running FPT in two stages. The first step is to run FPT analysis on the whole path in order to detect large-scale ARS. To obtain similar time intervals between consecutive locations along the path, some locations in the 'on' mode session can be randomly removed. The second step is to run FPT analysis on each 'on' mode session in order to detect small scale events. This two-step procedure was the same as that used by Fauchald & Tveraa (2003) to detect small, nested scale ARS within intensively searched areas at large scale.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Parameters used to simulate Argos noise according to each Argos location class.

Appendix S2. Analysis of the GPS path of a black-browed albatross.

Appendix S3. Example of an Argos path simulated at different steps from a GPS path.

Appendix S4. Two examples of simulated paths, showing effective area-restricted search in both kinds of patch.

Appendix S5. First-passage time as a function of time elapsed since departure, for a simulated path.

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