

Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird

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Foraging animals are expected to adjust their path according to the hierarchical spatial distribution of food resources and environmental factors. Studying such behaviour requires methods that allow for the detection of changes in pathways' characteristics across scales, i.e. a definition of scale boundaries and techniques to continuously monitor the precise movement of the animal over a sufficiently long period. We used a recently developed application of fractals, the changes in fractal dimension within a path and applied it to foraging trips over scales ranging across five orders of magnitude (10 m to 1000 km), using locations of wandering albatrosses (*Diomedea exulans*) recorded at 1 s intervals with a miniaturized global positioning system. Remarkably, all animals consistently showed the same pattern: the use of three scale-dependent nested domains where they adjust tortuosity to different environmental and behavioural constraints. At a small scale (*ca.* 100 m) they use a zigzag movement as they continuously adjust for optimal use of wind; at a medium scale (1–10 km), the movement shows changes in tortuosity consistent with food-searching behaviour; and at a large scale (greater than 10 km) the movement corresponds to commuting between patches and is probably influenced by large-scale weather systems. Our results demonstrate the possibility of identifying the hierarchical spatial scales at which long-ranging animals adjust their foraging behaviour, even in featureless environments such as oceans, and hence how to relate their movement patterns to environmental factors using an objective mathematical approach.

Keywords: search behaviour; albatross; fractals; foraging paths; Indian Ocean

1. INTRODUCTION

Animals live in an environment that is patchy and hierarchical, and the manner in which individuals search for spatially dispersed resources is crucial to their success in exploiting them (Pyke 1984; Bell 1991). The effects of heterogeneity in resource distribution on individual foraging processes are of recent interest to ecologists, as well as the effects of ecological scale on animal perception and decision making (Kotliar & Wiens 1990; Lima & Zollner 1996; Fauchald 1999). The tortuosity of foraging paths, for instance, represents animal reactions to landscape heterogeneity in which animals translate environmental stimuli into movements (Crist *et al.* 1992; With 1994). Our understanding of these relationships and processes has heavily relied on studies of small organisms for which monitoring of movement and manipulation of micro-landscapes was feasible (e.g. Crist *et al.* 1992; With 1994), but the fine monitoring of foraging paths of larger animals has recently developed (e.g. Gross *et al.* 1995; Bergman *et al.* 2000; Johnson *et al.* 2002; Marell *et al.* 2002; Fauchald & Tveraa 2003).

Long-ranging animals are also confronted with changing constraints potentially associated with behavioural changes at various scales, and further, their long foraging or migratory trips, often across biomes and/or climatic regions, integrate a wider range of constraints (Bergman *et al.* 2000; Johnson *et al.* 2002). Understanding how an organism perceives and uses its environment at various scales from information about its movement is not an easy

task, because measuring the fine-grained movement of wide-ranging animals in their natural habitat is difficult and because the use of arbitrary measurement scales, such as those defined by geographical features, may bias the perception of animal response (Sugihara & May 1990; Russell *et al.* 1992; Johnson *et al.* 2002).

The use of satellite tracking data has allowed the study of long distance movements (Jouventin & Weimerskirch 1990; Bergman *et al.* 2000), but the number of points recorded per day does not allow for the integration of fine-grained movement and decisions. Today, global positioning system (GPS) tracking methods provide the data for such investigations (Steiner *et al.* 2000; Weimerskirch *et al.* 2002). Most studies of vertebrate ecology have modelled foraging movements at a specific scale (e.g. Gross *et al.* 1995; Marell *et al.* 2002), and a few have recently attempted to assess the variability of movement at different scales (Bergman *et al.* 2000; Johnson *et al.* 2002; Fauchald & Tveraa 2003). However, little has been done to investigate the movement rules and search patterns in hierarchical patch landscapes (Johnson *et al.* 2002; Fauchald & Tveraa 2003), mainly owing to the difficulties in measuring changes in movement patterns at different scales (Nams & Bourgeois 2003). Over the past decade, mathematical approaches have helped in exploring the possible strategies used by animals to travel in heterogeneous landscapes and search for spatially dispersed resources (Viswanathan *et al.* 1996, 1999). However, accurate enough data are insufficient for drawing firm conclusions on long-ranging animals. Among the mathematical tools, fractal geometry has been increasingly used in ecology (Sugihara & May 1990) and has proved useful in investigating landscape perception in animals (Crist *et al.* 1992; With 1994). A change in fractal D within a

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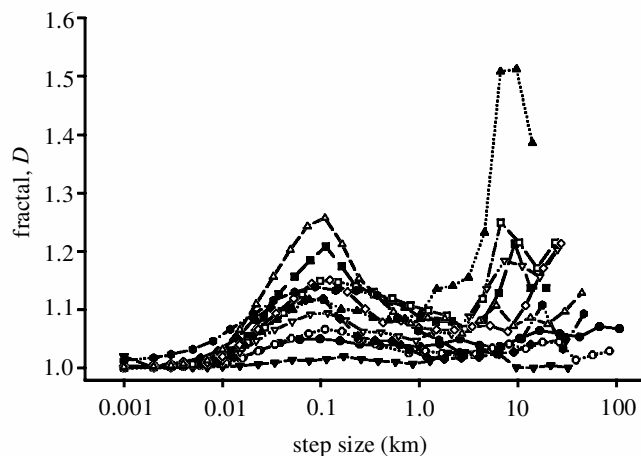


Figure 1. Analyses of the fractal dimensions of the 11 flights. All birds exhibited at least one major change in fractal dimension at a divider size of *ca.* 100 m and the five longest flights strongly suggest a second transition at a divider size of *ca.* 10 km. These transitions define three spatial domains that are hierarchically organized: *ca.* 100 m, 1–10 km and more than 10 km. Each symbol represents an individual albatross.

pathway itself carries information on changes in behaviour across scales (Nams 1996; Nams & Bourgeois 2003), hence providing insights on the searching behaviour of animals in complex hierarchical landscapes. Here, we use the unique opportunity given by the combination of a very recent technological development (miniaturized GPS) and a particular application of fractals to examine whether a long-range foraging animal, the wandering albatross (*Diomedea exulans*), differs in search behaviour and movement patterns at various scales of its foraging trip, and to identify the boundaries between scales (Russell *et al.* 1992).

2. MATERIAL AND METHODS

(a) Data recording

Birds were fitted with GPS devices weighing 105 g over January–March 2001 and in January 2002 at the Crozet Islands, southern Indian Ocean. All the birds equipped were experienced birds, i.e. adults with previous records of successful reproduction (all more than 15 years of age). Loggers are described in Steiner *et al.* (2000) and further details on the deployment in Weimerskirch *et al.* (2002). The recording interval in these GPS devices can be programmed, and we chose a recording interval of 1 s. We used 11 bird tracks (nine males and two females) of sufficient duration (at least 5 h of recording at sea) to allow a fractal analysis. Four tracks corresponded to the incubation period and seven tracks corresponded to the brooding period. As no significant difference in fractal dimensions were found between each period, we pooled all birds in the subsequent analyses. We subsequently tested for a range of intervals from our dataset, and we found that in such fast-moving animals, the rate of location recording must be very high to allow for the detection of fine-grained constraints: the first transition shown in figure 1 disappeared for recording intervals that were higher or equal to 3 s. This emphasized the need for the development of these technologies to unravel processes in animals that can move fast and take decisions at both very small and large spatio-temporal scales.

(b) Data analysis

Fractal measures refine the spatial or temporal complexity and heterogeneity of resource characteristics into a single quantified value (Leduc *et al.* 1994). The fractal dimension (D) measures the tortuosity of lines, and is the continuous analogue of discrete geometric dimensions (Milne 1991): the fractal D for movements lies between 1 (straight line) and 2 (maximum tortuosity that covers a plane entirely). Traditionally the fractal D is measured by the divider method (Dicke & Burrough 1988), i.e. by walking a pair of dividers of a given size along the path. One way to minimize the problem of edge effects in the divider method is to measure the length of the path by randomly starting from any point along the path, working the divider in both directions, which is called the fractal mean D and was developed by V. Nams (available at <http://www.nzac.nzac.ca/envsci/staff/vnams/fractal.htm>). We used this method to calculate the fractal dimension of the bird trajectories (hereafter called fractal D). This is repeated while increasing the size of dividers, and then the $\log(\text{path length})$ is plotted on $\log(\text{divider size})$. If the \log – \log plot is linear, then the tortuosity of the movement path is the same for all spatial scales. The overall fractal dimension of a trajectory is, therefore, based on the assumption that the movement patterns are scale independent, so if D does change with scale (i.e. the \log – \log plot is nonlinear), then it implies that movement patterns are not scale independent and that the overall D value is meaningless (Turchin 1996). For instance, an animal moving with a correlated random walk will show a \log – \log plot that is curved downwards (Turchin 1996). It would then be useful to calculate D for a different spatial scale. One way of doing this is by sliding a window along the x -axis of the \log – \log path length and using regression to measure the slope; plotting the fractal dimension for each sliding window also allows the detection of the major changes in the D values with the scales (Nams 1996). These changes define ‘transitions’ between ‘domains’ for which the fractal dimension is scale independent (Wiens 1989). The observed ‘transitions’ were centred around one value, but the peak gradually increases and then decreases. We defined the limits of the transition as the first significant break in the slope of relationship between the path length and divider size (more information available from <http://www.nzac.nzac.ca/envsci/staff/vnams/fractal.htm>). We define the fractal dimension of each ‘domain’ as D_1 , D_2 and D_3 (as defined by our approach). To calculate the mean fractal dimension for each ‘domain’, we used the transformation developed by Nams & Bourgeois (2003): the fractal dimension was normalized using $\log_{10}(D - 0.998)$, and then the mean, s.d. and CV could be calculated, and the values back-transformed. The calculation of D_3 was, in fact, not performed, owing to the small number of points obtained per individuals at that scale. The ‘transition’ was clear enough, but the limited autonomy of the GPS devices could not allow for a sample size that was sufficient for calculating a reliable fractal dimension.

The test of the influence of wind direction on fractal dimension normally requires circular statistics, but because our wind directions were spread continuously within the same 180° section (220°–340°), standard regression analysis could be used to detect any trends (Batschelet 1981).

3. RESULTS

The 11 wandering albatrosses equipped with miniaturized GPS devices were tracked along trips varying between 149 and 1110 km in length. Despite the variability in

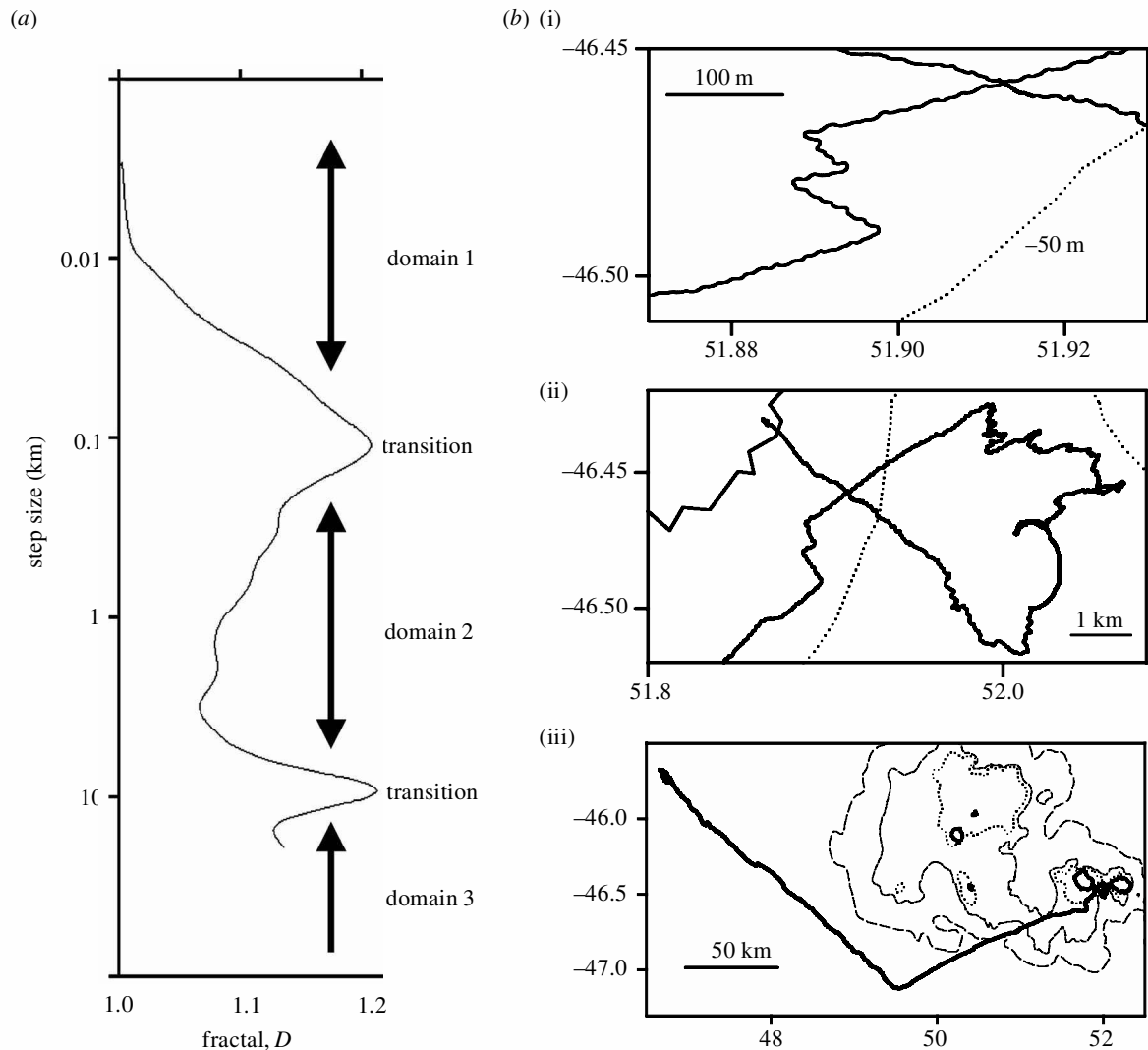


Figure 2. The trajectory of bird B0402 exemplifies the hierarchical scales of movement patterns in different parts of the journey as defined by fractal analysis. (a) For this bird, the relationship between the fractal dimension, as in figure 1, is presented. The two peaks, called transitions, define three domains of movements that are illustrated by the boxes immediately opposite in (b). (i) At a fine-grain level, all lines are in fact composed of zigzag movements; (ii) the path is more tortuous at 1 km grain scale than at the large grain scale shown in (iii).

foraging range, all birds consistently exhibited a marked change in fractal dimension (D) at a divider size of *ca.* 100 m, and a second change at 10 km that was perceivable only on long journeys (figure 1). These 'transitions' define three nested 'domains': a small scale domain at *ca.* 100 m, an intermediate one between 1 and 10 km, and a large one that was more than 10 km (figure 2). Interestingly, all flights exhibited the same pattern irrespective of the overall wind conditions, which varied between flights (wind strength from 15 to 30 knots ($1 \text{ knot} = 0.5144 \text{ m s}^{-1}$) and overall wind direction from 225° to 350°).

The value of the fractal dimension of the small domain (less than 100 m), D_1 , was not related to the wind strength ($F_{1,9} = 0.45$, $p = 0.52$) or overall wind direction ($F_{1,9} = 0.15$, $p = 0.71$). The average value of the fractal D for this domain was $D_1 = 1.01$ (C.I. 95%: 1.001–1.018). The average fractal D for the intermediate domain (1–10 km), $D_2 = 1.08$ (C.I. 95%: 1.015–1.350), was higher than in the first domain (Wilcoxon paired test: $Z = -2.93$, $p = 0.003$). The fractal D_2 was related to the distance travelled by a bird at the continental shelf edge ($F_{1,9} = 15.49$,

$p = 0.003$, $r^2 = 0.63$, figure 3), but there was no relationship between the fractal D of the small domain, D_1 , and the continental shelf edge ($F_{1,9} = 0.10$, $p = 0.76$). D_2 was not related to the wind strength ($F_{1,9} = 0.09$, $p = 0.77$) or the overall wind direction ($F_{1,9} = 0.32$, $p = 0.58$).

4. DISCUSSION

The marked changes in the fractal D , 'transitions', indicate that the patterns of movement of the animal change across scales, hence that the size range of an animal may be divided into regions, 'domains', where each of the different aspects of the animal's biology are important. In the wandering albatross the two observed transitions thus define three domains in which the movement of the animal varies qualitatively, and corresponds to different activities and/or constraints (figure 2). This method thus provides an objective way to define the scale at which constraints or behavioural decision operate. From our results we can interpret the small domain (less than 100 m) as corresponding to short-term and small-scale adjustment

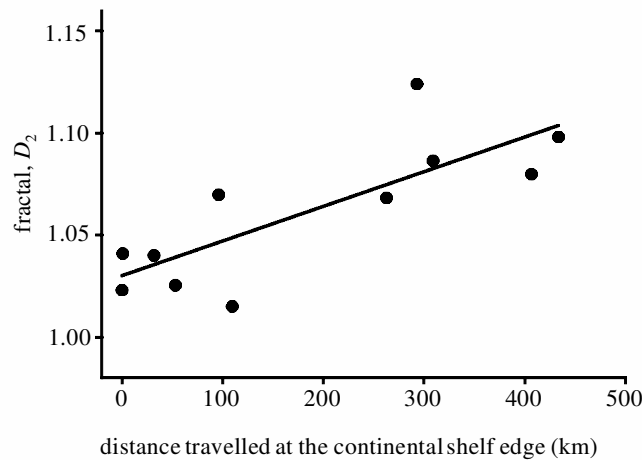


Figure 3. The fractal dimension D_2 of the intermediate domain increases with the number of kilometres spent by a bird along the continental shelf edge, a favourable feeding area: $D_2 = 0.0002$ (distance) + 1.0301, $F_{1,9} = 15.49$, $p = 0.003$, $r^2 = 0.63$. There was no relation between the fractal D of the small domain and the continental shelf edge ($F_{1,9} = 0.10$, $p = 0.76$) which is consistent with the fact that this is the scale of flight pattern adjustment for displacement, regardless of the motivation for the displacement.

to local wind conditions through continuous zigzag movement. The average value of D_1 is very close to 1, i.e. indicating a straight line, which can be explained by the fact that the zigzag movement is a succession of very straight lines aimed at moving efficiently on a small scale. This movement appeared to be independent from the overall wind conditions; a similar conclusion can be drawn for the medium domain D_2 . It is, however, probable that the measure of wind strength on smaller scales than those we had access to may show that the wind characteristics were influential. In fact, this zigzag movement can be related to the specificity of the flight pattern of albatrosses, the dynamic soaring flight (Alerstam *et al.* 1993), which increases their wind use efficiency and optimizes their flight performance. This is supported by the fact that the CV of D is small (CV = 8%) and hence all birds behave in similar ways.

The medium domain (between 100 m and 10 km) probably corresponds to the scale at which the birds adjust their movement to search for food, and would, therefore, correspond to clearly identified food-rich areas that are restricted in space, such as up-welling zones, continental shelf edges or eddies in oceanic waters where patches of food are concentrated (Hunt & Schneider 1987). This is the scale at which we expect to see an increasing tortuosity of bird trajectories, as they intensively search favourable feeding areas (Kareiva & Odell 1987). Accordingly, the average fractal D_2 is higher than in the first domain, and also shows a higher variability in its values (CV = 23%), which could reflect the fact that not all birds find good foraging patches. The hypothesis that this medium domain is linked to the foraging patch is also supported by the fact that D_2 is related to the distance travelled by a bird at the continental shelf edge—an oceanographic feature known for being a prime feeding area (Weimerskirch *et al.* 2002). Although higher than D_1 , D_2 is not very high, implying that the tortuosity of the pathway when searching for food is not extreme. The albatrosses increase their

search effort in favourable areas, but do not show any intensive foraging efforts in a restricted patch. Even in food-rich areas, the main food items (large squids) are not concentrated but rather randomly distributed and are slow moving compared with albatrosses, hence the birds should follow a Lévy flight searching rule rather than a pure random walk following Brownian motion (Bartumeus *et al.* 2002) and the fractal dimension is not expected to be very high (Viswanathan *et al.* 1996). Interestingly, the trajectories of the albatrosses very rarely showed multiple crossing points, as if the searching behaviour would minimize the risk of inspecting the same spot twice which would fit with the fact that one prey equals one patch for the albatross, hence the patch is instantly depleted, i.e. ‘destructive patch foraging’ (Viswanathan *et al.* 1996, 2000). This also contributes to the straightness of the paths and hence the low fractal D value. Previous results using ARGOS suggested that albatrosses may have more tortuous movements than shown in this study (Weimerskirch *et al.* 1997), but this was probably because of the limited accuracy of the location using satellite telemetry (Hays *et al.* 2001).

The second peak, and hence the third domain (more than 10 km) only appears in the longest flights (more than 400 km, $n = 5$). Although it is not as clearly defined as the other two other domains in our analysis, this domain would correspond to a better known aspect of the bird-foraging ecology—albatrosses, like most sea birds, cover several thousands of kilometres during their foraging trips using flyways that provide favourable surface wind conditions to minimize the costs of long-foraging flights (Furness & Bryant 1996; Weimerskirch *et al.* 2000). The third domain would then correspond to long-term and large-scale adjustments influenced by the overall direction of winds within large-scale weather systems, and related to long distance jumps in a relatively well-defined route to commute between the colony and patches, or between patches.

Some studies of vertebrate ecology have modelled foraging movements on a specific scale, and a few have recently attempted to assess the variability of movement over different scales (e.g. Bergman *et al.* 2000; Johnson *et al.* 2002; Fauchald & Tveraa 2003). Different solutions fitted different scales and different species as follows:

- (i) a correlated random walk only predicted part of the movement of large arctic ungulates (Bergman *et al.* 2000; Marell *et al.* 2002); and
- (ii) short-term and short-distance simple ‘rules of thumb’ decision-making also fitted the observed behaviour of ungulates in heterogeneous landscapes (Gross *et al.* 1995).

Our results are thus among the few to document hierarchical changes in movement patterns of a large foraging predator across a wide range of scales (Johnson *et al.* 2002). The change in the movement rate can also be used to demonstrate the existence of scale-dependent changes in behaviour (Johnson *et al.* 2002), but with our approach we show how to objectively define the spatial scales at which constraints change within one foraging trip (see Fauchald & Tveraa (2003) for a different method). As with most mathematical approaches in ecology, the use of

fractals has its own methodological limits (e.g. Turchin 1996, and see § 2), but we feel that by developing the original idea of Nams & Bourgeois (2003) we provide a complementary approach to that developed using Lévy flight models (Viswanathan *et al.* 1996, 1999). The latter convincingly used Lévy flight models to predict qualitatively the displacement rules of bumble-bees, ungulates and albatrosses (Viswanathan *et al.* 1999). However, their approach also relied on the definition of two domains where the displacement rules are not the same (below and above r), and the estimation of r is a major constraint. The use of fractals may partly solve this problem through the estimation of domains, and may then allow for the definition of more accurate decision rules.

Our results also clearly suggest that not only can prey distribution be spatially organized, but climatic features such as wind may also constrain foragers at different scales. Hence, the movements of long-ranging predators are likely to reflect behavioural adjustment to both prey distribution and climatic conditions at various scales, as well as intrinsic mode of locomotion. The constraints of climatic or environmental factors on the scale-dependent change in movement shape are likely to occur in many other animals that are large-scale foragers using various modes of locomotion (e.g. currents or tidal movements for marine animals, topography for terrestrial animals). The size of the domain where food searching occurs (1–10 km) is likely to be related to the type of prey that wandering albatrosses are foraging (mainly squids) and to differ between taxonomic groups. Some studies have shown scale-dependent aggregation of foraging marine predators at the population level in relation to prey distribution (Mehlum *et al.* 1999; Fauchald *et al.* 2000). Our results, using individual behaviour, show similar hierarchies, but we suggest that they reflect both the irregular distribution of prey and the heterogeneity of scales at which environmental variables constrain the bird movement. Other groups may respond at different scales because their prey and environmental constraints are distributed differently. In a marine context, the hierarchical spatial aggregation of preys and the spatial hierarchy of climatic feature create a complex heterogeneous environment that translates into hierarchical spatial movements rules by birds, and probably other large top marine predators (see Sims & Quayle 1998). As the biology of upper trophic level predators is often considered to help understanding of the functioning of the marine environment (Boyd & Murray 2001), the use of GPS and fractal analysis to define ecological and behavioural domains could also help the understanding of the scale at which heterogeneity occurs in an environment with few spatial indicators.

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