

Fractals and search paths in mammals

Jordi Bascompte^{1,*} and Carles Vilà^{2,**}

¹Departament d'Ecologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain; ²Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apto 1056, 41080 Sevilla, Spain

Keywords: Fractal dimension, wolves, tracking, patterns of movement

Abstract

The fractal index by Katz and George (1985) for the characterization of planar curves is applied to wolf search paths recorded by radio-telemetry. All the sets of paths studied show spatial patterns whose complexity is between a straight line and a true random walk. Females' fractal dimensions show significant changes throughout the year, depending on the state of their life cycle (normal, breeding and wandering). There are also differences between males and females, but not between adults and non-adults. The results are discussed with regard to wolf food-search strategies.

1. Introduction

In nature there is a wide range of self-organized spatial structures in multiple hierarchical levels. In many situations, such structures are the counterpart of a gain in entropy because of their dissipative origin. The resulting geometry is not the classical Euclidean one, but corresponds to what we call *Fractals*. Mandelbrot (1977) introduced this term to describe systems which (i) do not have an integer dimension but a fractional one, and (ii) have the property of self-similarity when observed at different levels of the hierarchy. In other words, the detail is similar to the whole; there is no defined main scale. In recent years, the geometry of fractals has been applied to a surprising set of phenomena ranging from electrochemical deposition (Mach *et al.* 1994) to the architecture of physiological systems such as the bronchial tree (Shlesinger and West 1991) or the Hiss-Purkinje conduction (Goldberger *et al.* 1985), the growth of bacterial colonies (Fujikawa and Matsushita 1989; Matsushita and Fujikawa 1990), taxonomy

(Burlando 1990, 1993), and clusters of stars (Mandelbrot 1983).

Among others, the ecological sciences have benefited from this new approach, which provides a new way to answer multiple questions about structure and scale in ecological systems (see the detailed review by Sugihara and May 1990). For example, there are significant differences in the community structural pattern (characterized by the landscape fractal dimension) between large and small spatial scales for deciduous forest patches (Krummel *et al.* 1987) and for coral reefs (Bradbury *et al.* 1984). Such a result suggests that there are different mechanisms operating at different scales. So, new ideas on the study of landscapes are provided by the fractal approach. A constant fractal dimension over a range of scales defines a domain in which some patterns and processes are operating at different levels. On the other hand, such critical size beyond which a further increase in area represents a shift in the dimension or degree of complexity, may demarcate a boundary between two different hierarchical levels in which

*Current address: Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

**Current address: Department of Biology, University of California, Los Angeles, 621 Circle Drive South, Los Angeles, CA 90024, USA

different patterns and processes are operating (Krummel *et al.* 1987; Bradbury *et al.* 1984).

Thus, fractals allow us to incorporate a multi-scale perspective in our study of landscape ecology and, in particular, to use information about microlandscape in the hope that such information may embody the essence of landscape ecology, traditionally studied at human-scale (Wiens and Milne 1989). Of course, the complexity of the landscape will affect the movement patterns of animals, as shown for tenebrionid beetles by Wiens and Milne (1989). More interestingly, the patterns of movement themselves can be studied from a fractal perspective, and their dimensionality may be subjected to evolutionary considerations as it may be related to food searching strategies, determining the probability of a trophical encounter (Sugihara and May 1990).

The movements of animals, as well as their home ranges, have important implications for the optimization of food search patterns, energy investment, habitat selection, territorial and social behaviour, etc. The study of both aspects for a given species or population has traditionally been carried out within a Euclidean framework. For studies of home ranges, several parametric and non-parametric methods have been widely used (for example the harmonic mean and the minimum convex polygon methods; White and Garrott 1990). Loehle (1990) has developed a different, more realistic approach to the study of home ranges from the perspective of fractals.

In contrast, the analysis of movement patterns is far less common because of both (i) the difficulty of obtaining complete records of the displacement of an animal, and (ii) the difficulty that such analysis represents. The basis for these analyses has been computer simulations (Pyke 1983; Bovet and Benhamon 1988) or the tracking of invertebrates (Pyke 1978; Wiens and Milne 1989; Kareiva and Shigesada 1983) or small vertebrates (Cody 1971; Pyke 1981).

In this paper we consider an index for characterizing the complexity of planar curves – their degree of space-filling – proposed by Katz and George (1985). This index is interesting because (i) it is intuitive and easily computed, and (ii) it permits statistical comparisons. We apply it to the study of the variation throughout the year of the

daily movement patterns of several Iberian wolves (*Canis lupus signatus*) monitored by radio-telemetry.

2. A fractal measure for spatial paths

Some of the complex patterns characteristic of biological phenomena are of the form of planar curves composed of connected line segments. What follows is a technique to classify such patterns by means of a numerical quantity, the fractal dimension, which was applied by Katz and George (1985) to classify the growth paths of cells. This index is proportional to the degree of convolution (or inversely proportional to the degree of straightness) of the planar curves.

As these planar curves become more irregular (tend to fill more space in the plane), their fractal dimension is higher, despite the fact that all curves, topologically, are one-dimensional. This fractal dimension (D) relates the total length of the curve (L) with the maximum total area (A) that such a curve could fill, in the following way

$$L^{1/D} = k A^{1/2}, \quad (1)$$

where k is a constant. Developing the last expression and taking into account some decisions about the nature of the data and the significance of the different parameters involved (see Katz and George 1985 for details), the fractal dimension can be estimated as:

$$D = \frac{\log(n)}{\log(n) + \log(d/L)}, \quad (2)$$

where n is the number of steps, L is the sum of the length of each segment (the total length) and d is the planar diameter, that can be estimated as the greatest distance between two points in the curve.

It is easily seen that when the path is a straight line, $L = d$ holds, and, consequently, $D = 1$. This corresponds to a straight path. When the curve tends to fill the space, the dimension would approach two. This happens when the path is a random walk. This is shown for expression (2) by

Katz and George (1985), and it can also be justified from different approximations as, for example, by considering modified Brownian diffusion processes. For such generating processes, with no serial correlation between the displacements in successive time intervals, it is easily demonstrated that $D = 2$ (Sugihara and May 1990). The more convoluted the patterns, the higher the fractal dimension. One interesting property of expression (2) is that it can characterize constrained paths, *i.e.*, search paths that are constrained in a limited area. In such a case, the path tends to cross itself many times, and D , according to expression (2), can be a value greater than two (Katz and George 1985). With data obtained by radio-telemetry, such as those considered here, one would expect to find such a situation when studying the foraging path of a herbivore feeding on a small vegetation patch.

There are different ways to quantify fractal dimensions, which are more or less useful depending on the nature of the data. A very general method is box counting, which has been used in several environmental studies (Sugihara and May 1990; Loehle 1990). Loehle (1990) provides a general and useful algorithm to estimate fractal dimensions using box counting. However, for the particular type of data studied here, search paths in mammals, we prefer to use expression (2) for several reasons. In the first place, we aim to present a method that can be used by field ecologists working with telemetry data. Expression (2) is very intuitive, easy to apply, and related to the degree of directionality of the path. It can classify a path as a straight, random or constrained one. Secondly, sample sizes used in this study lie below the minimum value necessary to obtain a good estimate of fractal dimension by box counting using the Loehle (1990)'s algorithm (each fractal dimension is calculated for the positions of the animals every half-hour, which imply that the number of different points is less than 48, and Loehle finds that a sample size of 48 is still inadequate). Finally, the most interesting advantage of using expression (2) is that parametrical statistical analysis (based on the normal distribution of the variable studied) can be directly applied. This is justified because the fractal dimensions of a population of computer generated random walks fit a

lognormal distribution (Katz and George 1985). Consequently, the logarithm of the fractal dimensions would fit a Gaussian distribution.

Thus, we can test whether a collection of paths or a particular one is a random walk. In a similar way, we can compare the fractal dimensions of different populations, testing for significant differences in the degree of complexity of the search paths using Student's *t* test or analysis of variance (ANOVA).

Katz and George (1985) provide a table showing the mean fractal dimension, mean of the logarithms and standard deviation of logs, for a number of simulated random walks with different numbers of steps or line segments. It also gives the confidence limits to assess whether an individual search path or a population lies inside the interval, and is thus an example of a random walk. To assess the chances that populations of search paths are random walks, we compute the mean and the standard deviation of the logs of the fractal dimension and the mean of the number of steps (n). Then we look for the corresponding value of the log of the fractal dimension for random walks of the same number of steps in the table provided by Katz and George (1985). Both values are compared by using the *t*-test. To compare different populations of search paths, the mean of the logs of the dimensions of each population is compared using the *t*-test. In this case it is important that the average number of steps in both populations be the same, given the dependence between D and n . However, while this dependence is high for very low n -values ($n = 4$), after a given n -size the differences are very slow, as studied by Katz and George (1985) for random walks. In particular $D(n=19) - D(n=99) = 0.03$.

To summarize, expression (2) is an easy measure of the straightness of a planar curve which allows us to infer and test different hypotheses about the degree of complexity shown, by using simple statistical analysis. It is certainly evident that measure (2) varies with the number of steps n and, so, it must be related to such value. Other approximations to calculate the fractal dimension, as for example box counting, also show this dependence with data size, a problem termed the dilution effect and the time-fill effect by Gautes-

tad and Mysterud (1994). However, this is not a problem in our case, because all of the statistical tests carried out to ascertain whether a given path or a population of paths are random walks take into account n . That is to say, confidence limits and average fractal dimension for a random walk are provided for each n -value in Katz and George (1985)'s Table. This has the advantage that it is possible to use small data sets, which is very useful for the nature of data studied in this paper. The only restrictions are the usual statistical ones: the larger the data set, the higher the test's potentiality.

In the next section we apply expression (2) to characterize the patterns of movement of wolves, and to illustrate the kind of biological information one can infer from such an index.

3. Search paths in wolves

During the course of a research on wolf ecology and behaviour in the Zamora and León provinces (northwestern Spain) from 1988 to mid-1991, six wolves were captured: two adult females (F1, F2), one young female (f3), two adult males (M1, M2) and one young male (m3) (for details see Vilà 1993). The young individuals were trapped at the age of four months; the adults were from three to six years. The wolves were captured using foothold traps and were equipped with radiotransmitters fitted in collars. After releasing the wolves, the transmitters allowed the location to be determined at any time of the day, and thus provided valuable information on the animals' movement, home range, activity patterns, habitat selection, life cycles, and other behavioural and ecological aspects.

The study area was about 4,000 km² and included many small villages, with an average of 20 to 30 inhabitants/km². The relief is smoothly hilly, with altitudes ranging from 700 to 2,000 m. The valleys are mostly covered by agricultural fields, many of which have recently been abandoned as the result of a decrease in rural populations during the present century. The hills are largely covered by several Mediterranean shrub associations, with some pine (*Pinus* spp.) plantations and oak (*Quercus* spp.) forests.

In this paper we study the search paths recorded during preselected days in which the position occupied by one of the wolves was determined by triangulation (Mech 1983) every half-hour during an entire day (in two of the search paths, however, the locations were recorded at hourly intervals). We estimate the minimum distance traveled by the wolf during the day as the sum of the distance between consecutive points (parameter L in equation 2). Although this is an underestimation, we consider that the resulting value is close enough to the real distance travelled by the wolf to let us deduce some general movement patterns. In this way, the total length travelled by the wolves was estimated to vary from 0 to 43 km in one day, the mean distance being 12 km for the adult females and 14 km for the adult males (Vilà 1993). Most displacements took place during the night and at dusk. As the females were monitored for a longer period, they provide most of the search paths considered in this study (total, N=75): 31 for F1, 25 for F2, 11 for f3, 2 for M1, 4 for M2 and 2 for m3. We have excluded search paths for which the locations corresponding to four hours or more were lost (the animal was missing or technical problems forced the end of the tracking session). Days with lost tracking periods shorter than four hours were also excluded from computation when the lost locations occurred during the period of activity time or the animal's behaviour suggested that a significant part of the displacements were unknown. Finally, we also excluded those days in which the total movements or the planar diameter was small (less than 1.5–2 km). Under these circumstances, the triangulation error (in our case usually around ± 300 m, see Mech 1983) could play an important role for the interpretation of the search paths. Days with little or no movement were rather common in breeding females during the first two months after birth.

In Figure 1 we show two examples of such search paths. As can be observed, they are more complex than straight lines. We attempt to quantify their degree of complexity. In some instances it has been estimated as the mean directionality (Batschelet 1981), but this only considers the changes of direction between successive straight displacements, and all the information in relation to the length of the displacement in each direction

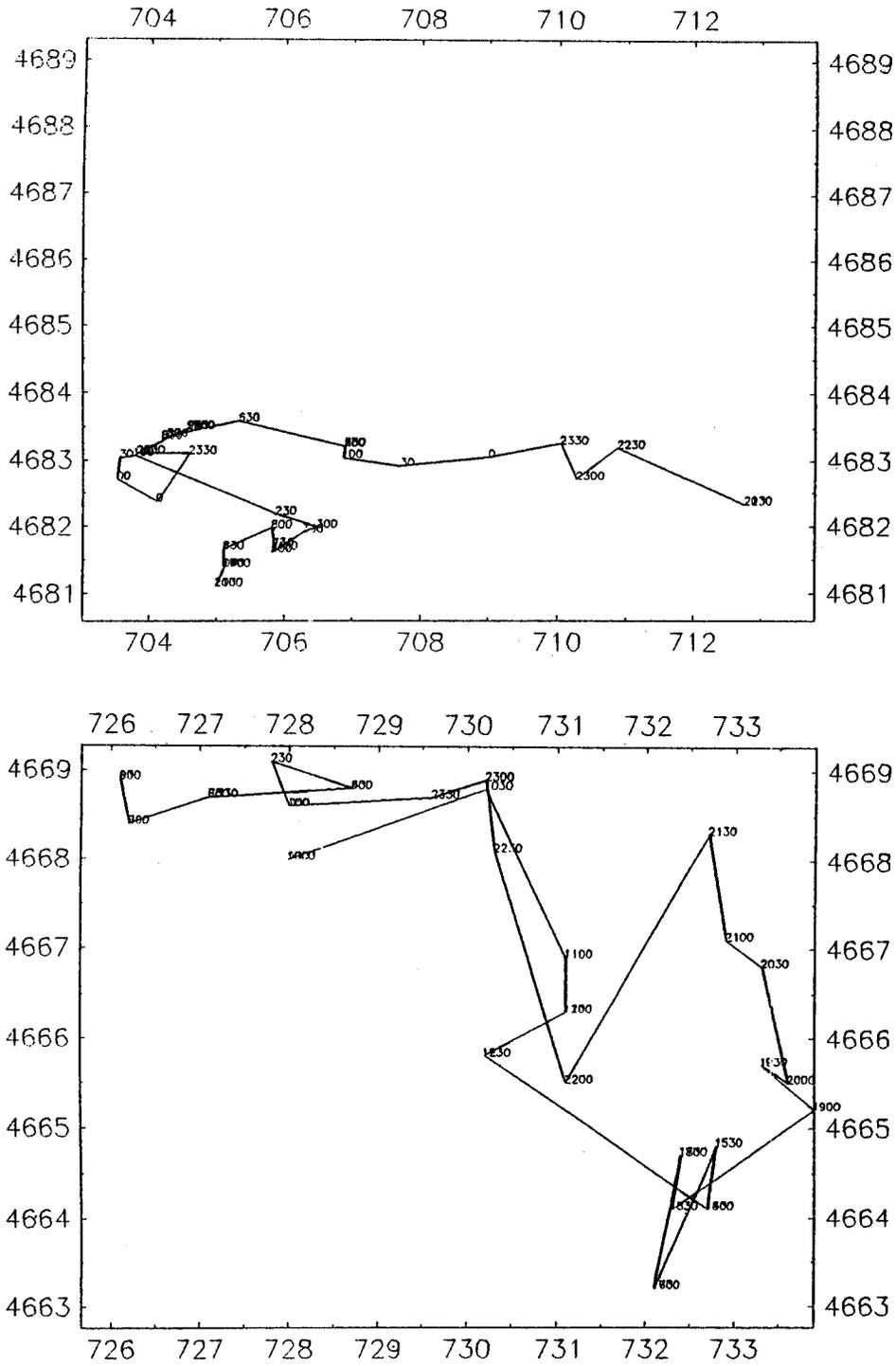


Fig. 1. Two adult females' search paths with fractal dimensions, according to expressing (2), 1.27 (top) and 1.47 (bottom).

is lost. Here we apply Katz and George's (1985) index (expression 2) in order to characterize the search paths of the wolves. For each individual we have estimated the fractal dimension of each 24-hr tracking.

During their development and throughout the year, the wolves pass through different periods of their life cycles. For this study we will consider two periods for the adults: a) when they are breeding and the cubs are less than four months old and remain around the den or "rendezvous site" (Joslin 1967) almost all the time, and b) the rest of the year. As one of the adult females (F1) lost its group and wandered alone for more than one year without seeming to have a well-defined home range, we will consider a third group of search paths including its displacements. We will consider separately the search paths for f3 and m3 until the first spring and thereafter. At that time, they started moving outside their habitual home ranges for periods lasting several days, and they were progressively more independent from their parents (Vilà 1993).

4. Results

Figure 2 shows the distribution of the fractal dimensions of the daily search paths studied here, the average fractal dimension (\pm S.D.) being $D = 1.497 \pm 0.275$, $N = 75$. On the other hand, as noted above, the fractal dimension of a random walk approaches two. In particular, for the average number of steps in the daily patterns studied here ($\bar{n} = 12.13$), the mean of 501 computer-generated random walks give a value $D = 1.83$ (see Katz and George, 1985's Table I). The difference is significant ($t = 48.73$, $df = 74$, $p < 0.001$). The same conclusion is reached for each one of the subsets studied in the present paper: males ($t = 18.50$, $df = 7$, $p < 0.001$), females ($t = 44.6$, $df = 66$, $p < 0.001$), adults ($t = 43.88$, $df = 64$, $p < 0.001$) and non-adults ($t = 18.97$, $df = 9$, $p < 0.001$). All fractal dimensions are lower than that expected from random walks, and so, wolf search paths are straighter (for methodological procedures see Katz and George 1985). Note that N is the number of daily patterns for which we have calculated the fractal dimension, and n is the number of steps in

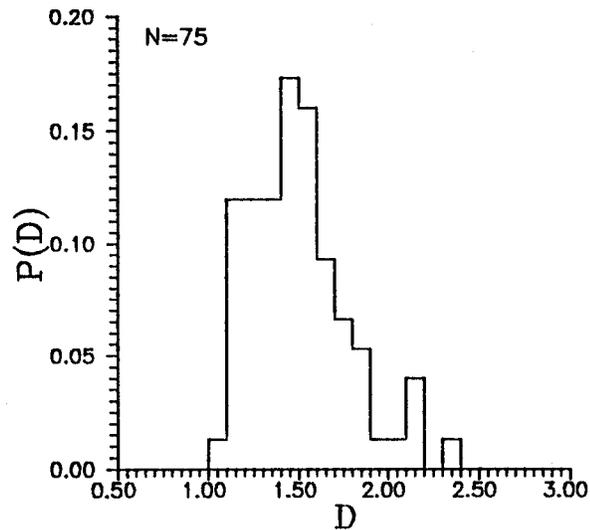


Fig. 2. Probability (P) distribution of the fractal dimensions (D) for all the wolf search paths studied in this paper.

each one of these daily patterns. The former value is taken into account when testing for statistical differences, while the latter value is used to find the tabulated value with which we have to compare our dimension.

4.1. Effect of life stage on females' search paths

After noting that both adult females (F1 and F2) showed the same general patterns through the year, we have grouped both subsets of data. In this subsection we looked for any difference in the fractal dimension of the search paths related to the life stage of the females (normal, $D = 1.473 \pm 0.252$, $N = 31$; breeding, $D = 1.726 \pm 0.292$, $N = 9$; wandering, $D = 1.284 \pm 0.164$, $N = 16$). There are significant differences between these three stages (ANOVA, $F = 10.39$, $df = 2.53$, $p < 0.001$). The differences are significant in all pair comparisons ($p < 0.05$).

This result suggests that the fractal dimension of the search paths changes throughout the year in the adult females. There is a maximum fractal dimension when the female has young cubs. In such a case, females can only explore a reduced area in order to return to the same point, the den where the pups wait. During this period of life, all

the females' travels were very short (see Vilà 1993).

On the other hand, the wandering female shows the lowest fractal dimension. Her daily displacements were not constrained to a defined area and she was continuously moving to new places. In fact, this female travelled over an area much larger than usual, exceeding 1,000 km².

4.2. Effect of life stage on males' search paths

The same comparison reached in the preceding subsection is now made for the adult males. In this case we compare the fractal dimension of reproducing males with that for non-reproducing males. There are no significant differences ($t = 0.52$, $df = 4$, $p = 0.63$) between the movement patterns of reproducing males ($D = 1.619 \pm 0.119$, $N = 3$) versus non-reproducing ones ($D = 1.691 \pm 0.193$, $N = 3$). This result, although it must be tempered by the low number of available data, suggests that males show no statistical differences in their search paths throughout the year.

4.3. Effect of the sex on wolves' search paths

In relation to the effect of sex in the movement patterns, there are no statistical differences between males and females if we consider young and adult animals together ($t = 0.950$, $df = 73$, $p = 0.345$). If we eliminate the young animals from the comparison, there are still no significant differences at the $\epsilon = 0.05$ level, although they are close to significant ($t = 1.85$, $df = 60$, $p = 0.068$). If from the female group we eliminate all the animals that are breeding, the differences between adult males and females are significant ($t = 2.49$, $df = 51$, $p < 0.05$). The fractal dimension in males' search paths ($D = 1.655 \pm 0.148$, $N = 6$) is higher than that of females ($D = 1.409 \pm 0.242$, $N = 47$). Thus, it seems that there are different strategies of space utilization, possibly linked with hunting, scent marking, or exploration, resulting in more space filling movements in males than in females.

4.4. Effect of age on wolves' search paths

There are no statistical differences between adult ($D = 1.478 \pm 0.270$, $N = 62$) and non-adult ($D = 1.586 \pm 0.293$, $N = 13$) animals ($t = 1.334$, $df = 73$, $p = 0.1864$). This result is maintained even in the case in which we exclude females with cubs from the comparison, although in this case the t -value is near the critical significance level ($t = 1.902$, $df = 64$, $p = 0.0617$). On the other hand, the same conclusion is reached when comparing from f3 the search paths before and after the first spring, in which she became subadult, making excursions away from her parental territory ($t = 0.714$, $df = 9$, $p = 0.493$). This lack of difference can be associated with the fact that, in wolves, dispersion is not a sudden phenomenon but a gradual one, with young individuals alternating progressively shorter stays in their parents territories with wandering abroad (Van Ballenberghe 1983).

5. Summary and discussion

In this paper we have applied a fractal index to characterize animal movements. The method is easy to apply and it allows statistical comparisons among different subsets of data. We have exemplified it by applying this framework to the study of wolf search path data. We have looked for differences in the degree of complexity in wolf search paths according to sex, life stage and age. All the data from this study show fractal dimensions whose complexity is between a straight line and a true random walk. There is a high degree of patchiness in wolf habitats in Spain, and food is not uniformly distributed. In fact, wolf prey are distributed in space in a non-uniform way, and recent theoretical work show that the effect of predation alone is sufficient to trigger and maintain this spatial distribution (Lewis and Murray 1993). This is in agreement with the observation that non-linear biological interactions generate an unexpected range of spatiotemporal patterns in spatially explicit models (Basompte and Solé 1995). The diet of wolves in Spain is mainly comprised of medium-sized prey (see for example Salvador and Abad 1987; Cuesta *et al.* 1991). These prey are sparse but, due to their relative large daily move-

ments and patchy distribution, they are easy to locate by a carnivore like the wolf, with a well-developed sense of smell and an extensive home range. As a consequence, wolves do not need to travel in a more convoluted way, and more of their displacements will be between feeding grounds. The results are rather straight search paths.

Our data show that there are significant differences in the search paths of females depending on whether they are breeding or not, or if they are wandering. When the females had young cubs their movility was highly restricted. They had to return daily to the spot where the cubs were waiting to be fed. With the cubs younger than a few weeks the females hardly moved at all. When the cubs were several weeks old the movements of their mother increased, but the global movility was still reduced (see Vilà 1993), conditioning the general shape of the search paths. During the rest of the year the movements were much less convoluted: it was not necessary to restrict the movements around one place. For the female that lost her territory and wandered along a great extension for several months this trend was exaggerated. Her movements were not restricted at all and she moved widely, occupying new areas continuously. As a result, the fractal dimension of her search paths is lower than that for the other adult female and the time when she had a stable territory, that is, her movements were more straight than usual.

Males, on the other hand, did not show such differences during the year. They were not subjected to the same restrictions than females, or at least they were not as much subjected as females were, and they could keep their search behaviour more constant all the year. Nevertheless, there were some differences between the search paths for males and females (after excluding breeding females). The males' paths were more convoluted. Both sexes seemed to have different strategies in their use of space. This may suggest a more intensive patrolling of the territory in males that may result from the fact that they travel longer distances daily although the home ranges are not larger (Vilà 1993), or may be also related to scent marking behaviour or hunting.

The fractal index used in this study shows to be suitable for the analysis and interpretation of search paths in a wide range of animals. We use

it with wolf movements as deduced from radio-telemetry data, but it can be applied to any kind of multiple locations for a single animal (recaptures, snow tracking, or visual observation). The main advantages of this method are that the fractal dimension is very easy to estimate and interpret, and can be used for statistical comparisons. The way in which this index is defined allows its use with rather short data sets and even then can keep its validity for statistical comparisons if the number of steps used in the calculations are taken into account. All these properties are even more useful when we are dealing with endangered or scarce species, or when the data are especially hard to get (highly mobile animals, difficult to capture, difficult to track). Under both circumstances (both applicable to the wolf in Spain) it is difficult to get sample sizes big enough as to use other methods to estimate the fractal dimension of search paths.

6. Acknowledgements

We wish to thank Steven A. Frank, Miguel A. Rodríguez, Alberto García and Francisco Rodríguez-Trelles for comments and suggestions, and Ricard V. Solé for his constant encouragement and advice during the last four years. The assistance with the field work of Vicente Urias, Antonio Kuntz, Jorge Reija, and Chema Valdillo was essential for the record of data. Kelly Maldonado and Jennifer Leonard corrected the English version. Both authors are supported by a postdoctoral grant from the Spanish Ministry of Education and Science.

References

- Bascompte, J. and R.V. Solé. 1995. Rethinking complexity: modelling spatiotemporal dynamics in ecology. *Trends Ecol. Evol.* 10: 361–366.
- Batschelet, E. 1981. *Circular statistics in biology*. Academic Press, London.
- Bradbury, R.H., R.E. Reicheet and D.G. Green. 1984. Fractals in ecology: methods and interpretation. *Mar. Ecol. Prog. Ser.* 14: 295–296.
- Bovet, P. and S. Benhamou. 1988. Spatial analysis of animal's movements using a correlated random walk model. *J. Theor. Biol.* 131: 419–433.

- Burlando, B. 1990. The fractal dimension of taxonomic systems. *J. Theor. Biol.* 146: 99–114.
- Burlando, B. 1993. The fractal geometry of evolution. *J. Theor. Biol.* 163: 161–172.
- Cody, M.L. 1971. Finch flocks in the Mohave Desert. *Theor. Popul. Biol.* 2: 142–158.
- Cuesta, L., F. Bárcena, F. Palacios and S. Reig. 1991. The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera 1907). A new analysis of stomach's data. *Mammalia* 55: 239–254.
- Fujikawa, H. and M. Matsushita. 1989. Fractal growth of *Bacillus subtilis* on agar plates. *J. Phys. Soc. Jpn.* 58: 3875–3878.
- Gaustestad, A.O. and I. Mysterud. Fractal analysis of population ranges: methodological problems and challenges. *Oikos* 69: 154–157.
- Goldberger, A.L., V. Bhargava, B.J. West and A.J. Mandell. 1985. On a mechanism of cardiac electrical stability. The fractal hypothesis. *Biophys. J.* 48: 525–528.
- Joslin, P.W.B. 1967. Movements and home sites of timber wolves in Algonquin Park. *Am. J. Zool.* 7: 279–288.
- Kareiva, P.M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* 56: 234–238.
- Katz, M.J. and E. George. 1985. Fractals and the analysis of growth paths. *Bull. Math. Biol.* 47: 273–286.
- Krummel, J.R., R.H. Gardner, G. Sugihara, R.V. O'Neil and P.R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* 48: 321–324.
- Lewis, M.A. and J.D. Murray. 1993. Modelling territoriality and wolf-deer interactions. *Nature* 366: 738–740.
- Loehle, C. 1990. Home range: a fractal approach. *Landsc. Ecol.* 5: 39–52.
- Mach, J., F. Mas and F. Sagués. 1994. Laplacian multifractality of growth probability distribution in electrodeposition. *Europhys. Lett.* 25: 271–276.
- Mandelbrot, B.B. 1977. *Fractals: form, chance, and dimension*. Freeman, San Francisco.
- Mandelbrot, B.B. 1983. *The fractal geometry of nature*. Freeman, San Francisco.
- Mandelbrot, B.B. 1984. Fractals in physics: Squig clusters, diffusions, fractal measures, and the unicity of fractal dimensionality. *J. Stat. Phys.* 34: 895–930.
- Matsushita, M. and M. Fujikawa. 1990. Diffusion-limited growth in bacterial colony formation. *Physica A* 168: 498–506.
- Mech, L.D. 1983. *Handbook of animal radio-tracking*. University of Minnesota Press, Minneapolis.
- Pyke, G.H. 1978. Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor. Pop. Biol.* 13: 72–98.
- Pyke, G.H. 1981. Optimal foraging in hummingbirds: rule of movement between inflorescences. *Anim. Behav.* 29: 882–896.
- Pyke, G.H. 1983. Animal movements: an optimal foraging approach. *In The Ecology of Animal Movement*. Edited by I.R. Swingland and P.J. Greenwood. Clarendon Press, Oxford.
- Salvador, A. and P.L. Abad. 1987. Food habits of a wolf population (*Canis lupus*) in León Province, Spain. *Mammalia* 51: 45–52.
- Shlesinger, M.F. and B.J. West. 1991. Complex fractal dimension of the bronchial tree. *Phys. Rev. Lett.* 67: 2106–2108.
- Sugihara, G. and R.M. May. 1990. Applications of fractals in ecology. *Trends Ecol. Evol.* 5: 79–86.
- Van Ballenberghe, V. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. *J. Mamm.* 64: 168–171.
- Vilà, C. 1993. Aspectos morfológicos y ecológicos del lobo ibérico *Canis lupus* L. Ph.D. thesis. University of Barcelona.
- White, G.C. and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego.
- Wiens, J.A. and B.T. Milne. 1989. Scaling of “landscapes” in landscape ecology, or, landscape ecology from a beetle's perspective. *Landsc. Ecol.* 3: 87–96.