

Scale-free dynamics in the movement patterns of jackals

R. P. D. Atkinson, C. J. Rhodes, D. W. Macdonald and R. M. Anderson

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Using conventional radio-tracking techniques employed by field ecologists, evidence for scale-free (fractal) behaviour in the foraging trajectories of a species of African jackal is presented. It is believed that the particular form of foraging strategy observed here is a response by the jackal to its need to locate resources in an unpredictable environment. The methods used in this study are completely general and can be applied to other radio-tracked species, thus beginning a systematic investigation of foraging strategies in mammals.

R. P. D. Atkinson and D. W. Macdonald, *Wildlife Conservation Research Unit, Dept of Zoology, Univ. of Oxford, Oxford OX1 3PS, UK.* – C. J. Rhodes and R. M. Anderson, *Wellcome Trust Centre for the Epidemiology of Infectious Disease, Dept of Zoology, Univ. of Oxford, Oxford OX1 3PS, UK.*

The literature on spatial memory (Macdonald 1976, Roberts 1979, 1981, Vander Wall 1982, Kamil and Balda 1985) and navigation in animals (Tolman 1948, Menzel 1973, Peters 1978, Gould 1986, Chapuis et al. 1987, Gallistel 1993) suggests following orderly paths is within the capabilities of a wide variety of species. Canids are well-equipped to detect and follow specific scent trails (Neuhaus 1953, Kaimus 1955, Becker et al. 1957, Moulton et al. 1960, Albone 1984, Hepper 1988, Thorne 1995), to re-trace paths (Peters and Mech 1975, Macdonald 1979a, b, Bowen and McTaggart Cowan 1980), to orient an individual (Eisenberg and Kleiman 1972, Walther 1978, Wells and Bekoff 1981), and to otherwise increase foraging success (Henry 1977, Harrington 1981, 1982). It is therefore highly feasible that a foraging jackal can track the resources within its home range, perhaps using prior knowledge of locations and a navigational strategy based on the “principle of least effort” (Zipf 1949). Indeed, there is evidence that canids can and do follow predictable routes (red foxes, *Vulpes vulpes*, Doncaster and Macdonald 1997; Blandford’s foxes, *Vulpes cana*, Geffen and Macdonald 1993).

This examination of foraging in side-striped jackals (*Canis adustus*) was initiated by observations of apparent disorder in nightly foraging trajectories and of lack

of between-night repetition in order of use of specific sites. These observations immediately suggested that jackals were foraging for unpredictably available resources. Daytime checks of sites visited overnight were rarely illuminating, prompting a mathematical approach to the problem specifically distinguishing Lévy flight (a class of random walk with fractal characteristics) from Brownian random walk foraging strategy. We immediately reject other descriptions of search patterns (highly systematic, straight walk) (Bell 1991) as clearly not fitting the foraging trajectories of our jackals.

We present evidence for scale-free patterns in the foraging trajectories of side-striped jackals, a widely distributed African canid. By analysing the results of detailed radio-tracking studies conducted in Zimbabwe, we show that the night-time movement patterns adopted by the jackals exhibit long range correlations with no characteristic time scale (Lévy 1947, Schlesinger et al. 1993, Stanley et al. 1994, Peng et al. 1995, Stanley et al. 1996, Viswanathan et al. 1996). Further, by demonstrating the non-integer dimension of the sets of points visited by the jackals we suggest that Lévy statistics provide a suitable means of characterising the observed jackal movements, offering the

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strong possibility that jackals' movement patterns might be fractal (i.e. self-similar at a range of scales) (Mandelbrot 1982). Such fractal patterns with temporal or spatial self-similarity are also termed scale-free or scale invariant patterns. Following the suggestion of Viswanathan et al. (1996) we propose that this scale-free pattern is a response by the jackal to its need to locate resources in a complex and unpredictable environment and may, in fact, be a widespread behaviour in land animals which search for resources in similar circumstances. Finally, we discuss the relevance of our findings to current issues in epidemiology, animal management and conservation.

Data collection

Between October 1993 and October 1994 four resident, territory-holding adult female and three adult male side-striped jackals were radio-tracked from a single four-wheel drive vehicle using hand-held directional aerials on 150 square kilometres of commercial farmland centred 40 kilometres southwest of Harare. One adult male black-backed jackal (*Canis mesomelas*) was also tracked. A radio-fix was taken every ten minutes, the jackals' positions were located on a grid overlying a map of the study site, and the x and y co-ordinates of this position recorded. Jackals were located to within 100m of their true position with a tested accuracy of > 90%. Each jackal was tracked for eight hours per night for three nights and for twelve hours on one night, after which a four night tracking session was started on the next jackal. The typical diet of these animals is small mammals (= 5 kg) and fruit (Atkinson et al. in press).

Of the jackals whose data is presented in this paper, F4, F6, F9 and M6 were known to be mates of other radio-tracked jackals, but it is likely that the remaining study jackals (F2, M8, M9 and M10) were also paired with unknown animals. Although no concrete evidence was acquired, it is likely that all study jackals were rearing young over the period September to November. However, this study makes no assumptions about or attempts to explore the effects of age, sex, pup rearing, territoriality or return tendency on movements, concentrating instead on identifying general patterns.

Analysis of jackal foraging trajectories

Having rejected obviously incorrect descriptions of jackals' movements, we next discriminated between possible random walk models: the gaussian (or Brownian) and the Lévy flight. Evidence to support such discrimination comes from the presence or absence of scale invariance in the data and the shapes of the

underlying probability distributions for the variables under consideration. We show that application of gaussian random walk models is inappropriate for this investigation, although it has been adopted for other species in a variety of taxa (e.g. *Amoeba proteus*, Sayers et al. 1979; bacteria, Berg 1983; green rice leafhoppers *Nephotettix cincticeps*, Andow and Kiritani 1984; ants, Adler and Gordon 1992).

Lévy flights are movements in two-dimensional space which are not described by the normal probability distribution. Rather than a normal distribution with finite variance (i.e. tails which taper rapidly out), Lévy statistics describe distributions with longer, power law tails. Extreme fluctuations are a characteristic of this distribution. Such statistics have been found in the fluctuations of prices in the stock exchange, heartbeats and leaking taps (Casti 1997), particle motion in magnetic fields, the random walk of electrons, kinetics of macromolecules and fluid dynamics (Schlesinger et al. 1993). Although rarely looked for in living organisms, Lévy statistics have been found useful in describing the movements of amoebae *Acanthamoeba castellanii* (Schuster and Levandowsky 1996), microzooplankton (Klafter et al. 1990) and *Drosophila melanogaster* (Cole 1995). They have been detected, but not recognised as Lévy statistics, in the fractal random walks of foraging larval clownfish *Amphiprion perideraion* (Coughlin et al. 1992). However, Lévy statistics have only been used to describe the movements of unicellular organisms and invertebrates, with the exception of Viswanathan et al.'s (1996) work on albatrosses and later studies on deer (Viswanathan et al. 1999).

We first analysed the radio-tracking data to look for any evidence of long-range correlations in the movements of the jackals. Long-range correlations in the time-series data are indicative of scale invariance and hence fractal properties. Using the approach of Viswanathan et al. (1996), who studied the foraging patterns of the wandering albatross (*Diomedea exulans*) we analysed the time series of displacement frequencies i.e. the number of times per hour of the night each jackal moved position. This methodology differs slightly from that of the former study in that we defined $u(i)$ as the number of times per hour each jackal moved position, whereas Viswanathan et al. (1996) used the number of 15-s intervals per hour the birds were stationary. However, since these are complementary to each other they are equally valid approaches to use to detect long-term correlations. An example of the displacement frequency for the female jackal F4 is shown in Fig. 1. By treating each of the displacement frequencies as step increments in a random walk we constructed the running sum $y(t) = \sum_{i=1}^t u(i)$, and then analysed the root mean squared (r.m.s.) of the fluctuation of the displacement.

$$F(t)^2 = \langle (\Delta y(t))^2 \rangle - \langle \Delta y(t) \rangle^2 \quad (1)$$

where $\Delta y(t) = y(t_0 + t) - y(t_0)$.

The presence of long range correlations with no characteristic time scale is indicated by a scaling relationship $F(t) \propto t^\alpha$, where the exponent $\alpha \neq 1/2$. Any uncorrelated time series or Markov process (over sufficiently long time) would give $\alpha = 1/2$ (Stanley et al. 1994, 1996, Peng et al. 1995, Viswanathan et al. 1996).

Figure 2 shows a log-log plot of $F(t)$ against t for each of the radio-tracked jackals, and the linearity of the plots indicates that there is good evidence for scale invariance scaling relationship. The mean gradient of the eight best fit lines yields $\alpha = 1.04 \pm 0.11$ (mean \pm sd). For the seven *C. adustus*, the mean $\alpha = 1.04 \pm 0.12$.

Application of Eq. (1) which generates $\alpha \neq 1/2$ is strong evidence that gaussian models are not appropriate to analysis of the jackals' displacement frequency times series.

Although we believe this method is the strongest discriminant of gaussian versus non-gaussian behaviour, we also examined the distribution of step lengths (the distance travelled between successive 10-minute radio-fixes) for our sample of seven side-striped jackals. The distribution of step-lengths (Fig. 2) does not fit a gaussian distribution, further supporting the rejection of gaussian random walk models as inappropriate to the jackals' case (Kareiva and Shigesada 1983, Andow and Kiritani 1984, Bovet and Benhamou 1988, Marsh and Jones 1988).

To investigate the possible origin of this scale-free behaviour further, we calculated the dimension, D , of the trajectory of each of the jackals' sets of visiting points, as determined by radio-telemetry (Sugihara and May 1990, Williamson and Lawton 1991, Hastings and

Sugihara 1993, Addison 1997, Bascompte and Vila 1997). Figure 3 shows two such sets from two different female jackals over a twelve-hour night. Plots of the same animal on successive nights show no indication of orderly foraging, ruling out the possibility that jackals are visiting predictably productive sites. To calculate the dimensions of these sets we used a 'dividers' method. In this technique, the total length of the trajectory is measured using dividers of different lengths, linearly interpolating between points visited successively by jackals. For a smooth curve in the plane we expect $D = 1$, because the total length is independent of the measuring scale. For a set of points scattered uniformly in the plane we expect $D = 2$, the same as the Euclidean dimension. To test goodness of fit of our jackal data against these two models we applied the algorithm used to calculate D for 240 computer generated points scattered randomly in the plane, which simulated the number of points obtained in a four night radio-tracking session. In this case, the calculated dimension $D = 1.9$ (i.e. $\cong 2$). This demonstrates that the algorithm we have used is able to detect a uniform distribution of points in the plane using the same number of observations as we have from the tracking data. This gives us confidence that the $D \neq 2$ result from the tracking data is a real effect.

The calculated dimensions for the trajectories followed by each of the jackals over successive nights are shown in Table 1.

The mean foraging trajectory dimension, D , for the eight jackals = 1.53 ± 0.22 . Since D for our study jackals lies clearly between 1 and 2, this gives strong evidence for scale-free dynamics in the foraging be-

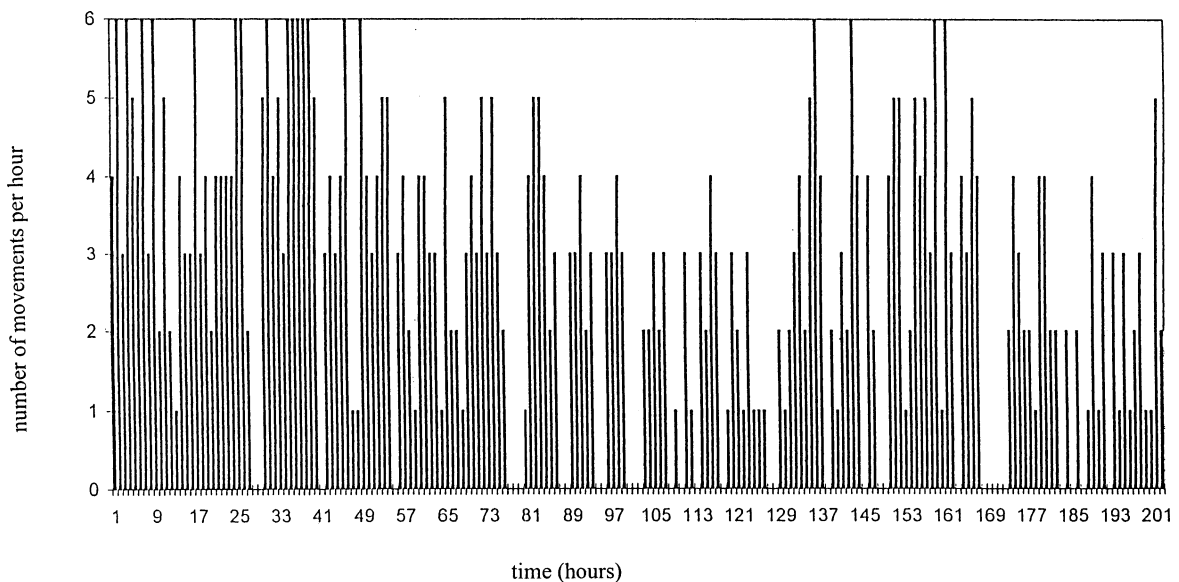


Fig. 1. The displacement frequency times series for female jackal F4, on which 1181 radio fixes over 200 hours were taken. The displacement frequency is the number of times in each hour when F4 changed position on each 10-minute radio-fix. Hence the number varies between 0 and 6.

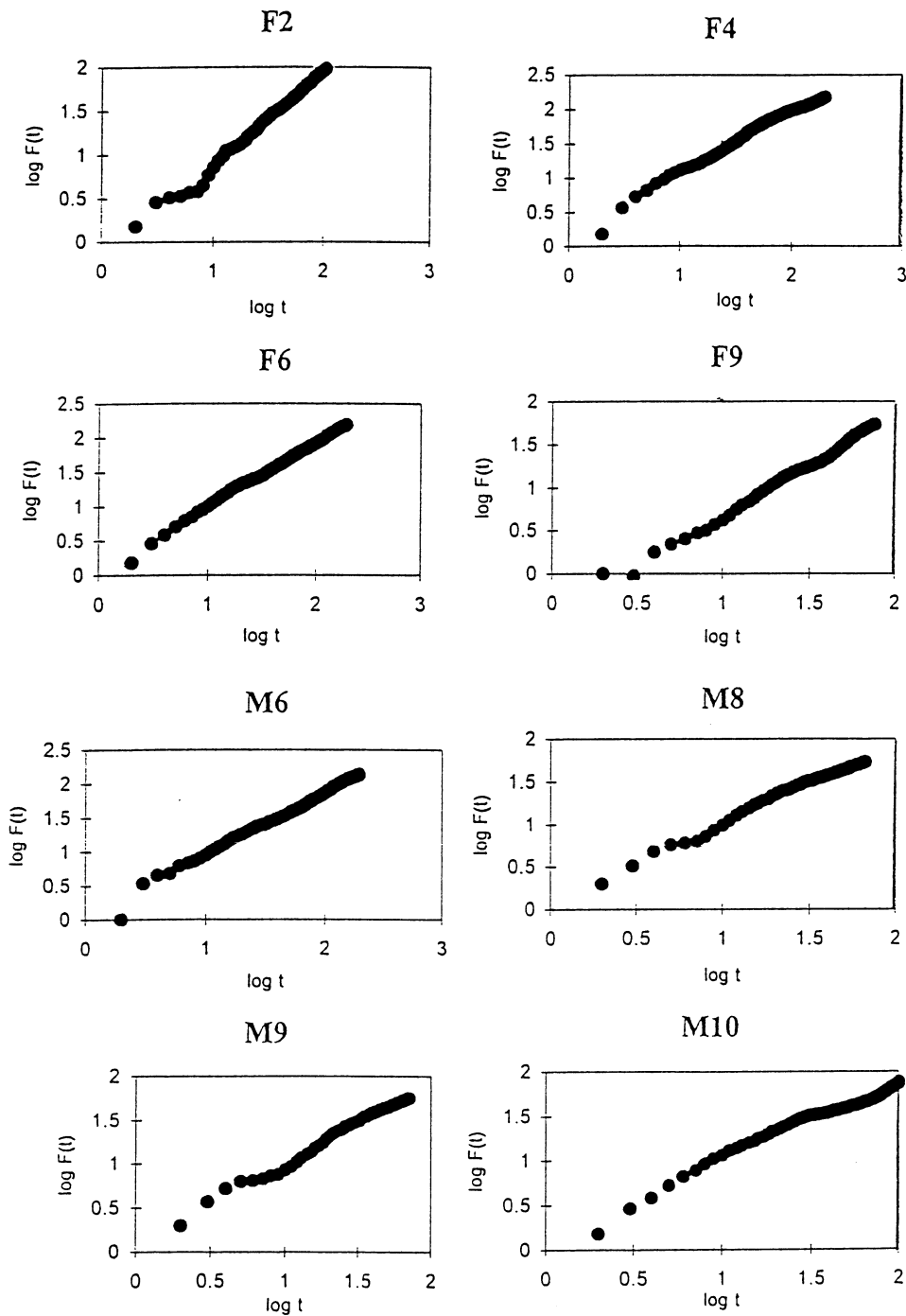


Fig. 2. The r.m.s. of the fluctuation of the displacement of the random walk constructed from the displacement frequency time series, for each of the radio-tracked jackals. Because $\alpha \neq 1/2$ this strongly indicates the presence of long range correlations with no characteristic time scale in the movements of the jackals during foraging. The calculated best fit lines are not shown.

haviour of jackals. From Table 1, there seems to be no significant difference between the dimensions calculated for male or female jackals. Additionally, there is limited evidence, based on the tracking of one male black-backed jackal, that the foraging strategies of side-

striped and black-backed jackals under particular circumstances are broadly similar. For the seven *C. adustus*, the mean dimension $D = 1.55 \pm 0.23$.

The complexity of the search paths illustrated in Fig. 3 and the presence of occasional long-distance step

lengths point to the possibility that Lévy statistics underlie the strategy which jackals use to explore the space they inhabit. The value of D calculated above is consistent with this proposition and it is known that the points visited by a Lévy flight form a fractal (Klafter et al. 1996). Lévy flights can be generated from a sequence of individual steps with an underlying power law distribution. The exponent of the distribution of step lengths, μ , is related to the dimension D by the relation $D = \mu - 1$. As stated above, the step lengths cannot be described by a gaussian distribution and performing a Lévy analysis we found that for the seven *C. adustus* $\mu = 2.02 \pm 0.30$. Hence the values of D and μ , arrived at by independent calculations, are broadly consistent with the proposition that Lévy statistics underlie the foraging strategy of jackals.

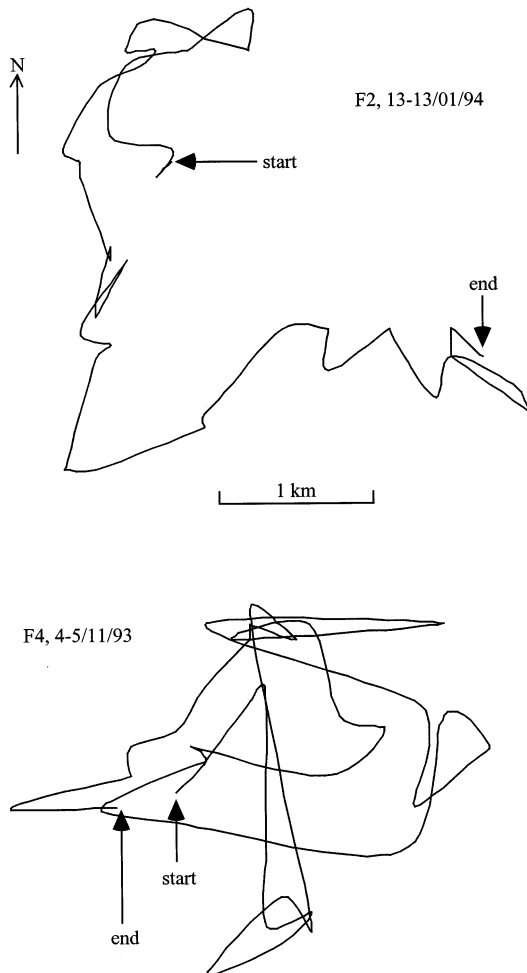


Fig. 3. The movement patterns of two female jackals (F2 and F4) over a 12 hour tracking session. The paths are constructed by joining the sampling points (x-y co-ordinates) of the time sequence of locations. The radio tracking co-ordinate system locates the position of a jackal to within a box with 100 metre sides.

Table 1. Calculated dimension of the foraging trajectories for the 4 female and 4 male jackals in the radio-tracking study. The algorithm used to calculate D was applied to 240 points scattered randomly in the plane, which simulated the number of points obtained in 5 successive 8-hour tracking session. In this case, the calculated dimension $D = 1.9$ (i.e. ≈ 2).

Animal code	Species	Dimension, D
F2	<i>C. adustus</i>	1.83
F4	<i>C. adustus</i>	1.65
F6	<i>C. adustus</i>	1.32
F9	<i>C. adustus</i>	1.80
M6	<i>C. adustus</i>	1.49
M8	<i>C. adustus</i>	1.23
M9	<i>C. mesomelas</i>	1.38
M10	<i>C. adustus</i>	1.55

Conclusion

The current study suggests strongly that Lévy flights exist in the foraging patterns of jackals. The power law distribution of displacement frequencies fits the model described by a Lévy random walk, rather than a Lévy flight, but the displacement frequency is an easily-measured surrogate for the physical path taken by jackals, and the displacement values themselves echo the moves actually made by the jackal in two dimensional space-which is the Lévy flight itself.

We have shown that the foraging behaviour of the side-striped jackal, investigated by standard radio-tracking techniques, can be characterised by a Lévy flight. This result extends to terrestrial carnivores a pattern of behaviour hitherto observed only in the search patterns of deer (Viswanathan et al. 1999), wandering albatrosses in the South Atlantic (Viswanathan et al. 1996) and a number of uni-cellular organisms (Klafter et al. 1990) and invertebrates (Dicke and Burroughs 1988). Similarly, we propose that this particular strategy is well suited to locating food resources in a complex and unpredictable environment, and scale-invariant search paths may well be a response to fractally distributed resources in the landscape. Where individuals compete for resources, there may be selection pressure in favour of Lévy flights and against normal random (Brownian) movements, because Lévy flights are quicker to find new areas to exploit. Jackals compete against other jackals and other foraging species, so the Lévy flight will permit the rapid assessing of new areas by this swarm of foragers. Whether the Lévy pattern is the optimum search strategy, though, is an intriguing open question. As both side-striped and black-backed jackals exhibit Lévy foraging behaviour it is possible that it is a widespread response amongst similar animals with similar demands.

Our study also raises the possibility that realistic patterns of animal movement can be incorporated into spatial models of disease spread (Macdonald 1980, Ball 1985, Smith and Harris 1991, Rhodes et al. 1998). The sprinkling of outbreaks of jackal (and fox) rabies ahead

of main fronts, which is so characteristic of the disease, could conceivably be due to the virus 'freeing' the infected animal to make longer tracks across country. Even if infected, due to the power law nature of the step lengths, extremely long steps are still less likely than shorter ones, and this may explain why the majority of rabid dogs, for example, do not make such journeys (Haig 1977). Furthermore, the consequences of Lévy ranging behaviour extend to animal management and conservation. If Lévy foraging is a response to temporally and spatially unpredictable resources, then human activities which increase the proportion of such landscapes with an animal's territory could have dramatic effects on its movements.

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