

# Automatic Monitoring of Primate Locomotor Behaviour Using Accelerometers

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## Key Words

Accelerometry • Red-ruffed lemur • Primate locomotion • Leaping behaviour

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## Abstract

Accelerometry data were transmitted by a radio collar attached to a hand-reared red-ruffed lemur housed in a large indoor/outdoor enclosure at Chester Zoo. An observer simultaneously recorded locomotor behaviour using a manually operated event recorder. Both data streams were recorded directly to hard disk to ensure accurate synchrony. Leaps were modelled using a  $y = x^2 - x^3$  formulation for the take-off acceleration, to link peak acceleration to leap distance. Cyclic locomotor modes were analysed using power spectra and the modal frequency used to estimate stride periodicity. Comparison of the dual data shows that leaping behaviour can be recorded reliably, and acceleration magnitude provides accurate predictions of the distance travelled. Cyclic activities were less well characterised, but calibration should permit travel distance estimations equalling or bettering those from conventional techniques.

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## Introduction

Primates as an order is remarkable, not only for its range of body size (well in excess of 50–200,000 g) but for its locomotor diversity: apart from powered flight and burrowing, there are few modes of locomotion which are not frequently performed by at least one primate species. Moreover, for any primatologists to whom captive care and conservation are important issues (we hope, all), it is important to recognise that locomotor behaviour is an indicator for primate welfare – too little, too much or inappropriate locomotion can all be indicators of poor welfare conditions [Poole and Schwibbe, 1993], and an adequate locomotor repertoire is essential

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for captive animals that are to be reintroduced into their natural environment – animals with inadequate locomotor skills cope badly with the extra pressures of free-ranging life [Box, 1991].

Since body mass and mass distribution will inevitably have a marked effect on the costs of raising the body against the force of gravity and on the costs of accelerating body segments, respectively, we can expect that primates will be particularly strongly selected for efficiency of movement [Oxnard et al., 1990], whether to minimise energetic costs or to enhance performance, especially when the latter is ecologically crucial. Locomotor adaptation is therefore one of the most striking aspects of the diversity of primates. Thus, the functional anatomy of the primate locomotor system is appropriately addressed from the biomechanical perspective, and questions of locomotor adaptation cannot be fully answered without this perspective. To be worthwhile, any study of the locomotor system will require a quantitative assessment of what a species performs, how often and, sooner or later, the scale of external forces involved in such performances. These external forces will affect both the loads which must be sustained by the musculoskeletal system and the internal muscle forces which must be exerted, and, hence, the metabolic or physiological energy costs of motion and posture, in a given environment.

Locomotor specialisation has major implications for an animal's functional anatomy [Swartz, 1993], and the interaction of inherited body form and environment will thus determine the expression of locomotor adaptation which will be observed at any given time and place. The latter is the proper subject of field studies of locomotion. Field studies of locomotion may count the frequency of given locomotor performances such as leaping, climbing or quadrupedal walking, or they may measure the period over which they are performed or the distance over which they are performed ('bout length'). Any one of these can provide useful information, and the choice is usually a pragmatic one, with the proviso that height change, which, under earth gravity, will be the most costly parameter of cyclical or non-cyclical locomotion, should always be taken into consideration; for estimates of the energy costs of locomotion, however, frequency, bout length and height change all need to be recorded (see Warren and Crompton [1998] and below).

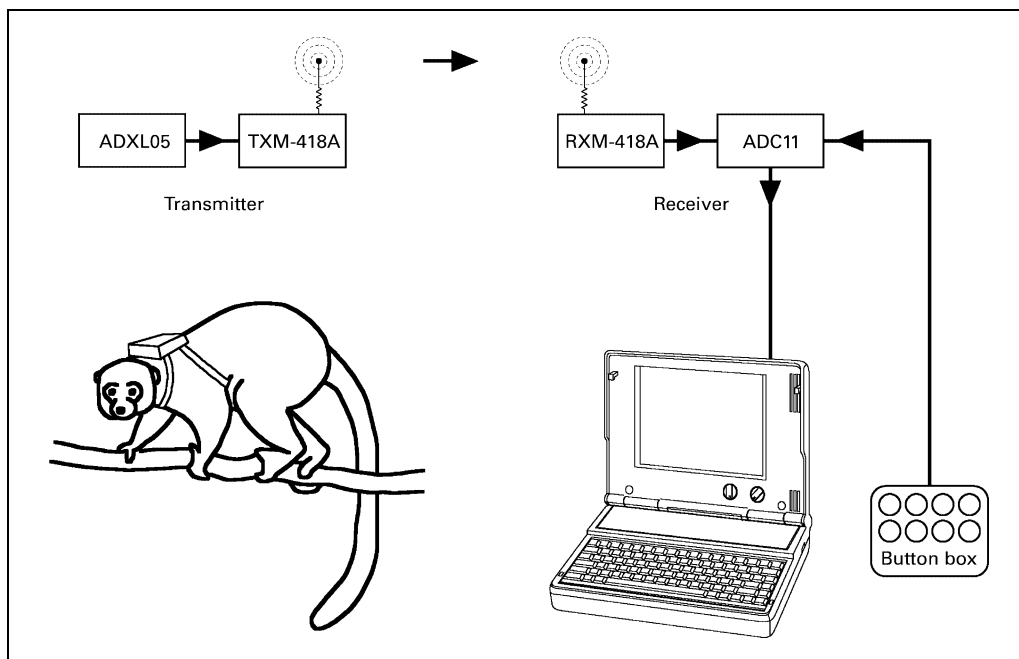
Traditionally locomotor behaviour is monitored using standard behavioural recording techniques such as check sheets to note down an animal's locomotion at any particular time [Altmann, 1974]. Whilst there have been a large number of studies using these techniques, and specifically designed to gather as much biomechanically relevant data as possible [Fleagle, 1978; Crompton, 1983], they are not without their difficulties. They are of course extremely time-consuming and physically demanding. More specifically, however, the types of data required for assessment of biomechanical variables are very difficult to quantify observationally, and some impossible. For example the observer may be able to recognise when an animal is leaping but not (accurately) how far; or he can record the occurrence of running but not the speed. In addition, changes in locomotor behaviour are often very rapid so that it can be difficult to record when such changes take place. Video-recording an animal's activity can get around some of these problems [Demes et al., 1996] – especially if some sort of scale can be included in the picture so that distance can be measured with greater accuracy (and there are systems on the market to facilitate this, such as Noldus Ethovision, Wageningen, the Netherlands). However, video systems measure instantaneous position, and these data need to be

differentiated once to produce velocity and twice to produce acceleration information, which is required for estimation of mechanical costs. This differentiation produces a large increase in the noise level within the data which causes its own set of problems [Pezzack et al., 1977; Walker, 1998]. Acceleration can be measured more accurately in the laboratory situation using force plates [Günther et al., 1991] or force poles [Demes et al., 1999], and these approaches can also provide information on peak forces, which are likely to be vitally important in determining the required strength, and hence the form, of the skeleton [Alexander, 1992] but these approaches are not readily adapted to be suitable for free-ranging animals.

Even video recording fails us when an animal is out of sight, and thus in practice it is impossible to monitor a free-ranging animal for a complete 24-hour cycle – or, over many successive days, for the 12–16 h of nocturnal or diurnal activity. Increasing evidence of cathemerality in strepsirrhines in particular suggests that less than 24-hour follows may be insufficient [Andrews and Birkinshaw, 1998]. A second, related issue is that the locomotor element of an animal's daily energy expenditure budget depends on the proportion of the total horizontal and vertical travel distance which is covered in the different locomotor modes, such as quadrupedalism or leaping [Warren and Crompton, 1998]. The metabolic costs of given performances may readily be measured, under laboratory conditions, by analysis of gas exchange (for cyclical modes of locomotion such as quadrupedal walking), or estimated, from a dynamic analysis of the mechanics of individual performances of non-cyclical activities such as leaping, given force plate or acceleration and mass distribution data, and using standard values for muscular efficiency. Field data should normally include information on the frequency of a given locomotor performance, on height change and on the mean distance travelled per bout (instance of performance), but we still require a knowledge of the total distance travelled in each activity period. This figure is difficult to obtain. Even when animals are followed through their entire active period, which is all too rare, estimates of distance travelled based on periodic position fixes (even as often as every 5 min) [Crompton and Andau, 1986, 1987] are likely to underestimate the actual distance travelled in an entire cycle. A continuous, uninterrupted record of activity is therefore highly desirable.

Radio tracking is widely used in animal behaviour studies [Kenward, 1987]. The most familiar radio tracking devices use signal strength as an indicator of the direction and distance of the subject animal. Early extensions of this include addition of a vibration switch so that the signal pulses on and off as the animal moves (and this has proved to be useful for getting rough activity patterns – for a review of techniques, see Amlaner and Macdonald [1980]) or simple thermocouple devices, which change the rate of the audible signal according to body temperature. The sophistication of radio telemetry has increased enormously over the last few decades, and it is now fairly easy to transmit quite specific data from sensors attached to the animal.

Since force is the product of mass and acceleration, acceleration is a very appropriate quantity to measure when studying locomotion. Biomechanical studies have used accelerometers to measure accelerations for a number of years [Morris, 1973]. However until recently, accelerometers have been extremely expensive and very power-hungry devices, which made them unsuitable for telemetry. The advent of air bags in cars (air bag inflation is triggered by the deceleration produced by an impact) has led to the development of cheap solid-state accelerometers which draw

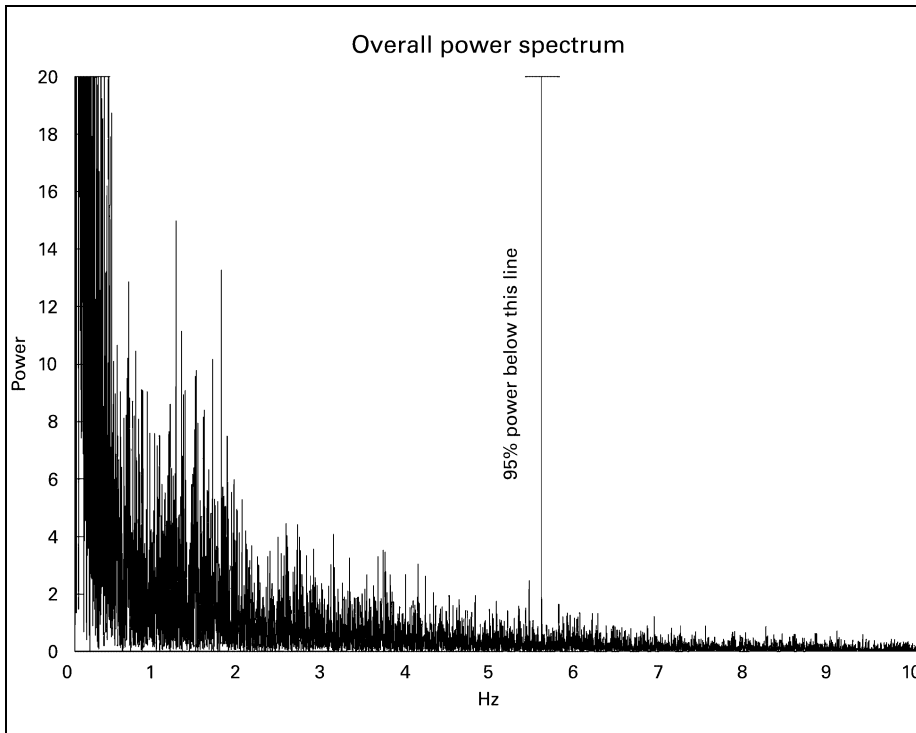


**Fig. 1.** Schematic diagram of the radio telemetry set-up.

relatively little current. This makes battery power a realistic option and has reduced the costs of producing a suitable telemetry collar to a much more affordable level. This has allowed collars to be made that either transmit acceleration data [Sellers et al., 1998] or store the data in the collar so that it can be downloaded later [Yoda et al., 1999]. Given that body mass and sufficient metric data to estimate mass distribution between segments (and hence, with minimal data on typical body posture, the position of the body centre of mass) may be readily gathered when a subject is trapped for fitting a radio collar [Crompton et al., 1996], it ought to be possible to gather the data required for calculation, using particle physics approaches, of a complete record of the mechanical costs of locomotion over the entire activity cycle under field conditions. This paper reports a trial of a radio-collar-based system for telemetered accelerometry in prosimian primates, which is intended to evaluate the types of data which may be derived from such a system and their reliability. (Such a system could also be used for monkeys or apes, but would require several orders greater robusticity and tamper tolerance.)

## Materials and Methods

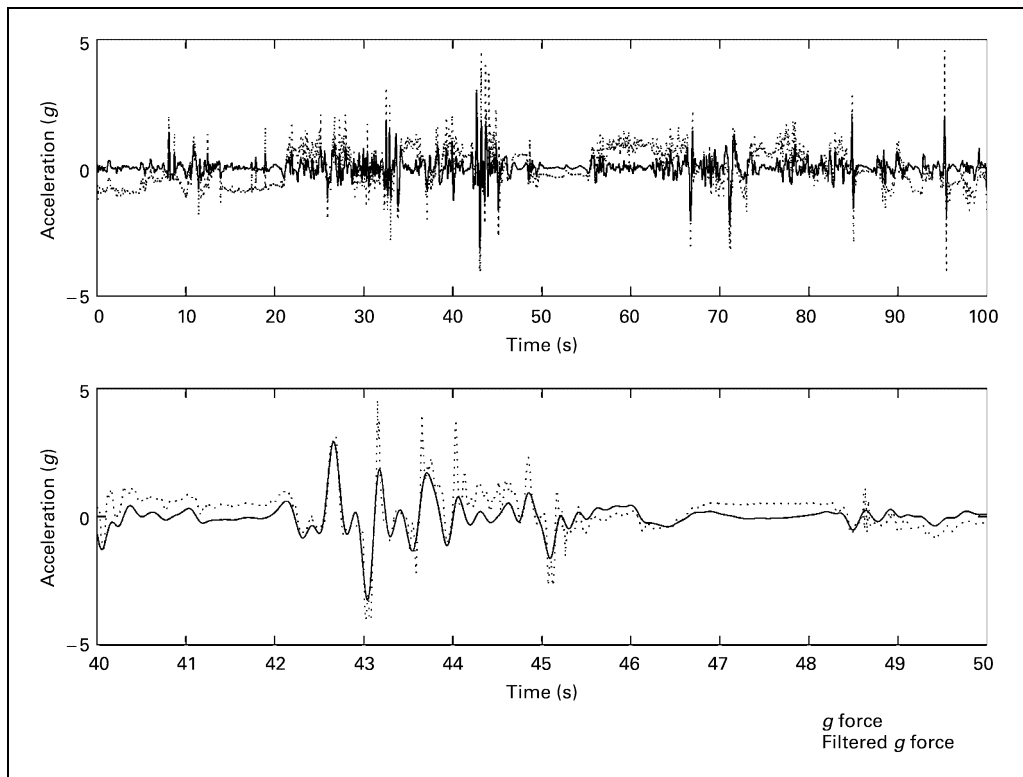
Figure 1 shows a schematic diagram of the telemetry system. The transmitter uses an Analog Devices ADXL05 solid-state accelerometer interfaced to a Radiometrix TXM-418A. The receiver consists of a Radiometrix RXM-418A and associated decoding circuitry



**Fig. 2.** Graph showing the power spectrum of the accelerometry data.

[Varley and Cotterrell, 1994]. The receiver is connected to the computer using a Pico Technologies ADC-11 analogue-to-digital converter. This is an 11-channel, 10-bit device that connects to a PC compatible laptop via the printer port. It also handles the data from the event recorder so that the data logging software can easily guarantee synchronous recording of both the behavioural and acceleration information. The collar weighs approximately 100 g, and the transmitter unit is  $90 \times 60 \times 30$  mm. The battery life is approximately 1 week, and the transmission range is 200 m although this figure can be increased by using a larger receiving aerial.

The accelerometer was attached to a hand-reared red-ruffed lemur (*Varecia variegata rubra*) using a small harness. Chester Zoo, like many zoos, has a policy of minimising keeper/animal contact, so a hand-reared animal was chosen to simplify the collaring procedure and to reduce the stress levels in the animal. Even so we were limited in the amount of time that we were permitted to attach the collar to two 4-hour sessions. The animal very quickly ignored the presence of the collar and then the animal was observed moving around its enclosure. Its locomotor behaviour was recorded by an observer using a commercial event recorder whilst the acceleration data were being logged at a rate of 100 samples per second. For this study broad locomotor categories were used: resting, climbing, slow quadrupedalism, fast quadrupedalism and leaping. This simplified the manual behavioural recording to ensure a high degree of accuracy and consistency.



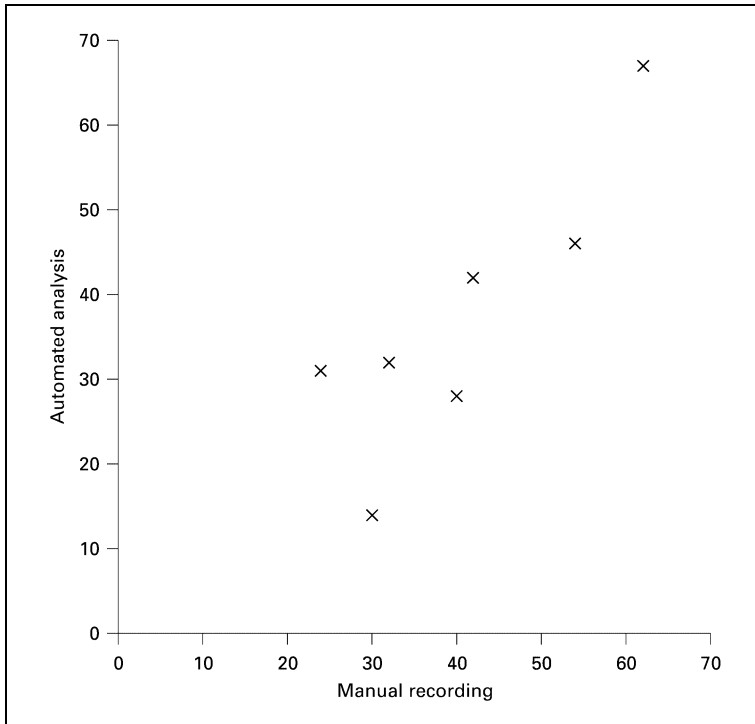
**Fig. 3.** Graphs showing the effects of filtering the raw accelerometry data. The lower graph is a close-up of the central section of the upper graph.

## Results

Like most automated logging systems this one generates large amounts of data. The sampling rate was approximately 100 samples per second which equates to 3 megabytes per hour. Our goal for this study was to produce a signal-processing regime that could take these data and produce a locomotor budget that was approximately equivalent to the one recorded by the observer. To achieve this, a number of signal-processing techniques were tried and the results compared with those observed to evaluate the technique.

The data were divided into 256 sample blocks (approx. 2.5 s). Each block was then analysed, and a particular locomotor activity was assigned to it. The analysis depends upon a number of measurements made on the acceleration waveform.

Initially the waveform needs to be cleaned up by removing the DC offset and reducing the amount of high-frequency noise: this can be readily performed using a commercial signal-processing tool kit, such as that supplied for Matlab (Matlab version 11, The Math Works Inc., Natick, Mass., USA). Figure 2 shows the power spectrum of the data and indicates that 95% of the energy is contained below about 5 Hz. Therefore the data were filtered so that frequencies lower than 0.2 Hz and

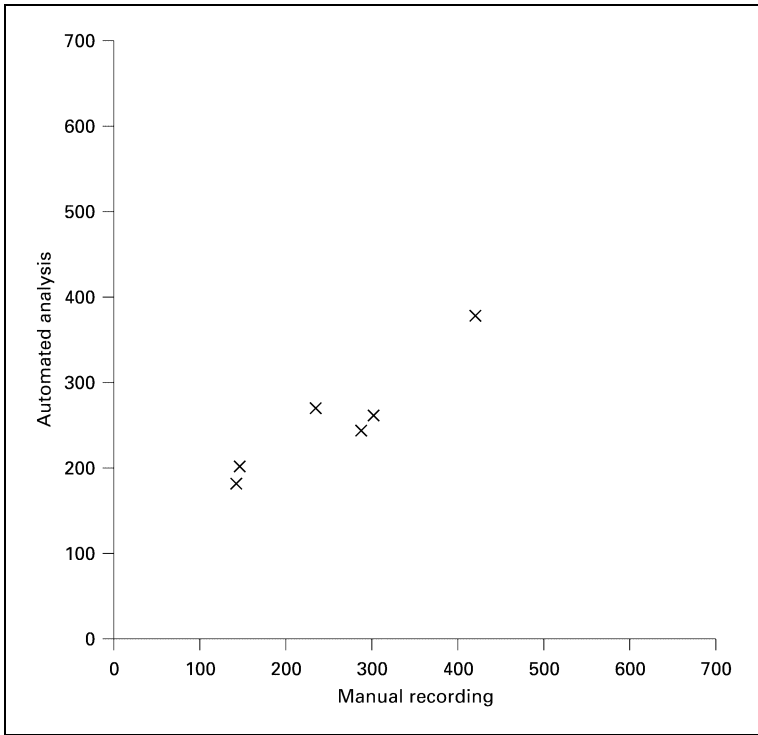


**Fig. 4.** Graph showing the number of leaps identified by the automated analysis and the number recorded by the observer. The acceleration threshold used for identification was 1.7 g, and each data point represents an approximately 30-min sample block.

higher than 5 Hz are attenuated using a digital Butterworth IIR implementation in Matlab (for the method, see Winter [1979]). This removes the DC effect of orientation (accelerometers pick up the acceleration due to gravity) and reduces the high-frequency artifacts caused by the radio collar bouncing around on the animal. The effects of filtration can be seen in figure 3.

For each block, the peak acceleration is measured. If this is greater than a threshold amount, a leap is considered to have occurred. This threshold value is chosen empirically so that the number of leaps identified automatically matches the number of leaps scored by the observer. This calibration exercise is necessary when comparison with observer data is required since the decision as to what comprises a leap as opposed to a long stride within a quadrupedal bout is somewhat arbitrary. Figure 4 shows the results of this exercise using an acceleration threshold of 1.7 g.

If the data block is not considered to contain a leap, it is tested to see whether it represents a period of cyclic locomotion. This is done by measuring the root mean squared amplitude of the waveform and seeing whether this is above a threshold value. Again an empirical value was chosen (0.2 g) so that the observer data match the accelerometry data. Figure 5 shows the results of this.



**Fig. 5.** Graph showing the length of time identified as being spent undergoing cyclic locomotion from automated analysis and as recorded by the observer. The criterion for cyclic locomotion was a root mean squared acceleration greater than 0.2 g, and each data point represents an approximately 30-min sample block.

In addition to these simple measures of locomotor activity, we can also calculate the distance travelled by these different locomotor modes. Leaping is a ballistic motion, and as such there is a well-known relationship between take-off velocity and the range of the leap. If we assume the optimal take-off angle of 45°, the relationship (for discussions of take-off angles, see Crompton et al. [1993] and Demes et al. [1996]), derived from standard ballistic equations [Norton, 1982] is as follows:

$$v_{to} = \sqrt{rg} \tag{1}$$

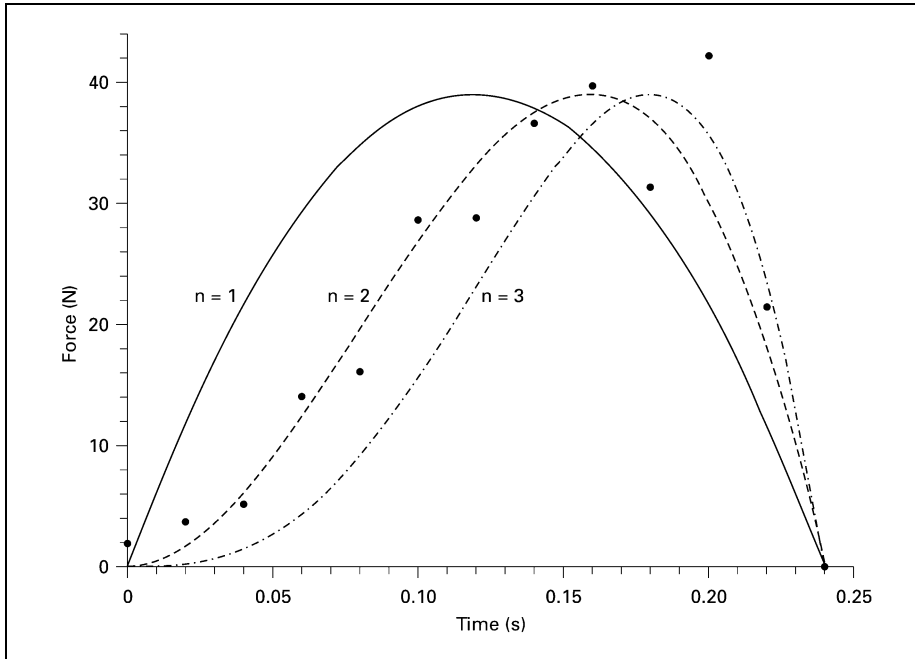
where  $v_{to}$  is the take-off velocity,  $r$  is the range of the leap and  $g$  is the acceleration due to gravity.

From Newton's laws of motion, the impulse can be equated to the change of momentum, and force can be equated to mass times acceleration so that:

$$m(v_{to} - v_0) = m \int_0^{t_{to}} a \, dt \tag{2}$$

where  $m$  is the mass of the projectile,  $v_0$  is the initial velocity,  $a$  is the acceleration and  $t_{to}$  is the take-off time.





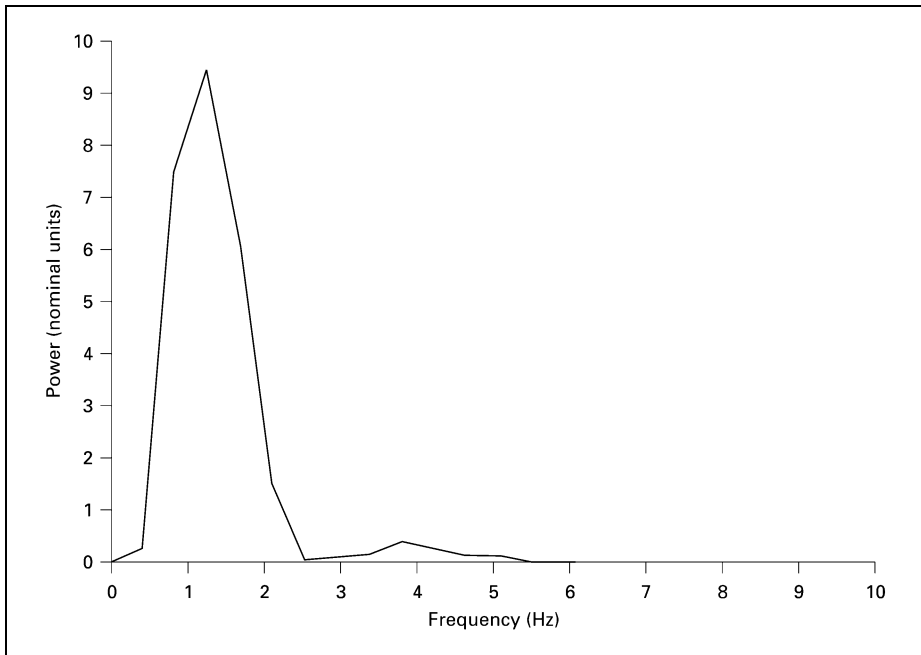
**Fig. 6.** Graph showing a set of acceleration values measured from a video sequence (for details of methods see Sellers and Crompton, 1994) of a leaping *Lemur catta* (filled dots) and a set of curves of the form  $y = x^n - x^{n+1}$  with values of  $n$  from 1 to 3.

The mass drops out of the equation, and the initial velocity for a standing leap is zero. The only thing that needs to be defined is the acceleration. By observation we have seen that during the take-off phase of a leap, the acceleration slowly increases from zero to a maximum value about two thirds of the way through and then rapidly falls off to zero [Sellers, 1992; Günther, 1989]. This shape can be approximated by a function of the form  $y = x^n - x^{n+1}$  over the range from 0 to 1, where  $n$  is a positive integer. Increasing the value of  $n$  makes the peak value occur later and increases the steepness of the function. Figure 6 shows actual leap acceleration data (for the method, see Sellers and Crompton [1994]) and a set of approximation functions with differing values of  $n$ . As can be seen, a value of  $n = 2$  gives the best fit. This equation then needs to be normalised so that its peak value is defined as  $a_{max}$  and the acceleration falls back to zero at  $t_{to}$ . The equation for the acceleration then becomes:

$$a = \frac{27}{4} a_{max} \left( \frac{t^2}{t_{to}^2} - \frac{t^3}{t_{to}^3} \right) \quad (3)$$

Combining equations 1, 2 and 3 gives:

$$\sqrt{rg} = \frac{9}{16} t_{to} a_{max} \quad (4)$$



**Fig. 7.** Graph showing the power spectrum in an interval identified as cyclic locomotion.

Another factor that controls the leap equation is the distance through which the animal accelerates during take-off. If we ignore any use of the substrate as a spring-board, this is approximately 70–80% of the fully extended length of the hindlimb in lemuroids [Sellers, 1996]. This extension distance can be calculated by integrating the acceleration equation once to give velocity ( $v$ ) and again to give distance ( $s$ ).

$$v = \frac{27}{4} a_{max} \left( \frac{1}{3} \frac{t^3}{t_{to}^2} - \frac{1}{4} \frac{t^4}{t_{to}^3} \right) + K \quad (5)$$

$$s = \frac{27}{4} a_{max} \left( \frac{1}{12} \frac{t^3}{t_{to}^2} - \frac{1}{20} \frac{t^5}{t_{to}^3} \right) + Kt + L \quad (6)$$

Since at  $t = 0$ ,  $v = 0$  and  $s = 0$ , both  $K$  and  $L$  can be shown to be zero, by solving equations 4 and 6, we get:

$$a_{max} = \frac{32}{45} \frac{rg}{s} \quad (7)$$

$$t_{to} = \frac{5}{2} \frac{s}{\sqrt{rg}} \quad (8)$$

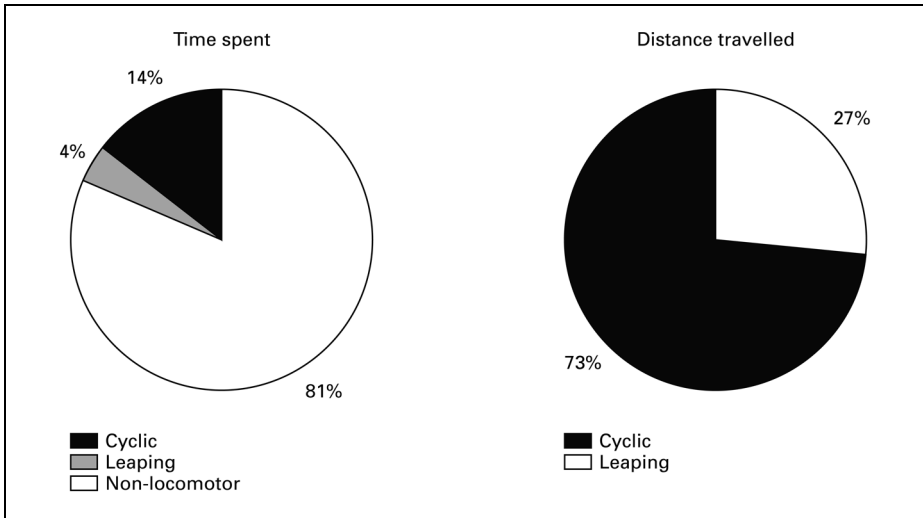
From these equations, we can relate leap distance to peak acceleration for any lemuroid with known leg length ( $s \approx 0.7 \times \text{leg length}$ ). For a red-ruffed lemur with an acceleration distance of perhaps 0.35 m this means that an acceleration of 2 g is equivalent to a leap of approximately 1 m. Therefore by measuring the peak acceleration for all identified leaps, we can work out an equivalent distance.

For intervals identified as cyclic locomotion, a Fourier transform is performed and converted into a power spectrum by squaring the values as illustrated in figure 7. The modal frequency is then chosen to represent the characteristic frequency of the interval. Arguably the median might be a better measure of central tendency but this would be influenced by high-frequency components in the interval which are mostly thought to be artefacts due to the accelerometer bouncing on the animal. In practice there was very little difference between the two values and the modal value, by identifying the largest peak in the frequency spectrum, which matched the value that would be chosen by a human performing the analysis. This value is the stride frequency in the interval and can be used to calculate the speed of the animal. Unfortunately the relationship between speed and stride frequency is not straightforward, due to changes in stride length with speed and discontinuities when gait changes: from walking to trotting and then to galloping. However a linear fit with a gradient change at the trot/gallop (walk/gallop transition in primates) copes quite well with empirically observed data [Heglund et al., 1974] although there is evidence that primates have lower than expected stride frequencies for given running speeds [Alexander and Maloiy, 1984] so that primate empirical data should be used for calibration. The most accurate solution to this problem is to measure the actual stride frequencies recorded from an animal on a treadmill at varying speeds. A similar but rather less accurate result can also be obtained from calibrated video analysis of free-moving animals. For this paper we were unable to get suitable video footage for red-ruffed lemurs so we used an empirically derived relationship ( $\text{velocity [ms}^{-1}] = 1.8 \times \text{stride frequency [Hz]} - 2.1$ ) obtained by filming free-ranging ring-tailed lemurs [Scott, 2000] for illustrative purposes.

As far as the present study goes, we may present locomotor budgets in terms of time and distance travelled in figure 8. An 'itemized' budget based on net, physiological costs is of course the ultimate goal.

## Discussion

Acceleration data clearly provide interesting information on the activity of an animal. With adequate calibration it is likely that the results can surpass those obtained by traditional observational means and the data can be analysed very rapidly to produce directly meaningful information. Perhaps its main advantage is that it allows continuous, long-term monitoring, limited only by battery life and the transmission range of the equipment. Data may thus be collected without gaps and, within the limits of the study period, we can be confident that even rare locomotor performances will be recorded. The latter is important, since it is certainly true that anatomical adaptations may be as much driven by the occasional peak locomotor stresses as by those occurring regularly. But quantities such as maximum speed and maximum leaping distance are difficult to record by traditional means [Alexander, 1992]. Acceleration data are themselves directly useful: from them we can work out



**Fig. 8.** Charts showing the proportions of time and the distance travelled that can be attributed to the major locomotor modalities.

the external forces that the animal is applying to its substrate and can estimate the bending forces experienced by its skeleton. It also allows actual travel distances and energy usage to be estimated. With calibration these estimates should be very reliable although even the results obtained with simple models should be a great deal better than nothing. The fact that the monitoring can occur for continuous, long periods avoids any biases associated with observation times and may reveal hitherto unknown activity patterns.

There are a number of caveats. Currently there are a number of behaviours that cannot be specifically identified that would affect the time budget. Vigorous shaking, grooming and foraging all potentially generate large accelerations of the torso and these will be misdiagnosed as cyclic locomotion. In addition, differing types of locomotion within the broad classes such as climbing or hopping cannot currently be identified. It is possible that some of these may be diagnosed by more specific pattern matching of the acceleration signal with the acceleration signature associated with these activities, and this is an area we are currently working on. There is also the perennial bugbear of any radio tracking exercise, i.e. that the presence of the collar itself affects the behaviour [White and Garrott, 1990; Gursky, 1998]. This is practically insoluble, and the best we can do is to minimise the weight and size of the collar and minimise the disturbance caused by capture and release.

Radio tracking technology is advancing. When this study was performed, the only affordable accelerometers were single-channel devices. There are now dual-channel devices with lower power requirements so that it would now be feasible to build a tri-axial system. Multiple-channel telemetry is also possible although there is always a trade-off between sample frequency and number of channels because of band width limitations. A better approach for such a 3-axis system might be to calculate the resultant acceleration using a microprocessor within the collar so that

only a single signal needs to be transmitted. Another improvement would be to record orientation as well as acceleration data so that all 6 degrees of freedom could be transmitted. This would certainly improve the possibility of distinguishing between different locomotor submodalities, but would increase the complexity and power requirements of the collar. Orientation can be accurately measured with gyroscopes although this is currently an expensive option. The current design has a battery life of several days but it would be useful to increase this to several weeks. Improvements in sensor technology will help here, and intelligent power-saving strategies such as switching off the accelerometers between samples should also help.

There are a number of simplifications inherent in the calculation of travel distance that could perhaps be improved. The formulation for leaping makes a number of assumptions. Firstly, it assumes that the accelerometer measures the actual acceleration of the animal. With a single accelerometer this would only be the case if the axis of the accelerometer matched the direction of travel. This is approximately true since this axis is in line with the torso; however, it will generally underestimate the acceleration. In addition, rapid change in accelerometer orientation will appear as an acceleration signal since the accelerometer picks up the acceleration due to gravity. This is the DC component of the signal and is normally filtered out, but when orientation is changing rapidly the contribution of this fixed component will alter and show up as a varying signal. Ultimately the only cure for this is to record all 6 degrees of freedom (3 acceleration axes and 3 orientation axes). The second assumption is that the acceleration curve can be modelled using the  $y = x^2 - x^3$  formulation. The choice of this function is a pragmatic necessity, since it provides a very simple relationship between peak acceleration and leap distance. It would be possible to use the actual recorded acceleration curve, but this would require the software to identify the start and end of the take-off acceleration which proved to be impossible since the alteration in orientation that occurs in leaping means that the signal is never seen to fall to zero. Again a tri-axial approach may overcome the problem. We have also assumed that the trajectory is  $45^\circ$  and that there is no height change during the leap. Both these assumptions are unlikely to be true [Crompton et al., 1993; Demes et al., 1996], and again a full 6 degrees of freedom system would be needed to record this information. In any case, the energetic cost and the skeletal strain depend on the acceleration rather than the distance travelled and height change. Currently we cannot distinguish landing and take-off except as twin acceleration peaks close together, and we cannot detect the effects of substrate compliance. With cyclic locomotion we need to be careful that the modal frequency is actually the stride frequency since certain gaits can cause double oscillations per stride. This is unlikely to be a problem with prosimians but might be with other mammals such as horses. The relationship between stride frequency and speed is problematic [Heglund et al., 1974; Alexander and Maloiy, 1984]. Gait changes do occur at characteristic speeds that have been measured for many mammals, and animals tend to have preferred speeds so this problem is not entirely intractable. Currently the best solution would be to produce empirical calibration curves for a variety of individuals covering the varying body sizes for the study animals. However this is impractical in many cases so that our approximate solution may be the only option. The acceleration data can of course be re-analysed if and when better calibration information becomes available. There would also be considerable bene-

fit in investigating the physical relationship between the recorded acceleration signal and the movement of the animal. The current approach is entirely empirical, which means that it may be necessary to calibrate each individual animal. However by combining telemetred accelerometry data with motion capture and force plate data in a laboratory setting it should be possible to model how the signal relates to locomotion much more precisely, which might ultimately allow the technique to be used with minimal calibration.

## Conclusions

Remote locomotor monitoring using accelerometers is a viable approach to providing a complete picture of the locomotor budget of a subject animal. Within its limitations, it allows us to measure the amount of time spent performing a variety of locomotor tasks, and it does provide an estimate of the distance travelled using these different locomotor modalities. Whilst a degree of healthy distrust in the absolute values measured is recommended, the information gained is extremely useful for comparative studies; and if accelerometry data can be calibrated by a period of simultaneous use of more conventional techniques, then its reliability is greatly increased [a miniature, highly flexible pressure plate is currently under development for the authors for this purpose (RSscan International, Lammerdries, Belgium), which we hope will allow external reaction forces to be measured during arboreal locomotion, for species where subject paths can be reasonably well predicted]. Future technological improvements such as tri-axial sensors and orientation measurements should make remote monitoring approaches even more attractive for field researchers.

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## References

- Alexander RMcN (1992). *Exploring Biomechanics: Animals in Motion*. New York, Scientific American Library.
- Alexander RMcN, Maloiy GMO (1984). Stride lengths and stride frequencies of primates. *Journal of Zoology* 201: 135–152.
- Altmann J (1974). Observational study of behaviour: Sampling methods. *Behaviour* 49: 227–267.
- Amlaner CJ, Macdonald DW (eds.) (1980). *A Handbook on Biotelemetry and Radio Tracking*. Oxford, Pergamon Press.
- Andrews JR, Birkinshaw CR (1998). A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates: Lemnidae), in Lokobe Forest, Madagascar. *Folia Primatologia* 69(suppl 1): 175–182.
- Box HO (1991). Training for life after release: Simian primates as examples. *Symposium of the Zoological Society of London* 62: 111–123.
- Crompton RH (1983). Age differences in locomotion of two subtropical Galaginae. *Primates* 24: 241–259.

- Crompton RH, Andau PM (1986). Locomotion and habitat utilization in free ranging *Tarsius bancanus*: A preliminary report. *Primates* 27: 337–355.
- Crompton RH, Andau PM (1987). Ranging, activity rhythms and sociality in free-ranging *Tarsius bancanus*: A preliminary report. *International Journal of Primatology* 8: 43–71.
- Crompton RH, Sellers WI, Günther MM (1993). Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. *Proceedings of the Royal Society of London B* 254: 41–45.
- Crompton RH, Li Y, Günther MM, Alexander RMcN (1996). Segment inertial properties of primates: New techniques for laboratory and field studies of locomotion. *American Journal of Physical Anthropology* 99: 547–570.
- Demes B, Fleagle J, Jungers WL (1999). Takeoff and landing forces of leaping strepsirrhine primates. *Journal of Human Evolution* 37: 279–292.
- Demes B, Jungers WL, Fleagle JG (1996). Body size and leaping kinematics in Malagasy vertical clingers and leapers. *Journal of Human Evolution* 31: 367–388.
- Fleagle JG (1978). Locomotion, posture and habitat use of two sympatric leaf monkeys in West Malaysia. In *Recent Advances in Primatology, Vol. 1: Behaviour* (Chivers DJ, Herbert J, eds.), pp 331–336. New York, Academic Press.
- Günther MM, Ishida H, Nakano Y (1991). The jump as a fast mode of locomotion in arboreal and terrestrial biotopes. *Zeitschrift für Morphologie und Anthropologie* 78: 341–372.
- Günther MM (1989). *Funktionsmorphologische Untersuchungen zum Sprungverhalten an mehreren Halbaffenarten* (Galago moholi, Galago (Otolemur) garretti, Lemur catta). PhD thesis, Freie Universität Berlin.
- Gursky S (1998). Effects of radio transmitter weight on a small nocturnal primate. *American Journal of Primatology* 46: 145–155.
- Heglund NC, Taylor CR, McMahon TA (1974). Scaling stride frequency and gait to animal size: Mice to horses. *Science* 186: 1112–1113.
- Kenward RE (1987). *Wildlife Radio Tagging*. San Diego, Academic Press.
- Morris JRW (1973). Accelerometry – A technique for the measurement of human body movements. *Journal of Biomechanics* 6: 729–736.
- Norton FGJ (1982). *Advanced Mathematics*. London, Pan.
- Oxnard CE, Crompton RH, Lieberman SS (1990). *Animal Lifestyles and Anatomies: The Case of the Prosimian Primates*. Seattle, University of Washington Press.
- Pezack JC, Norman RW, Winter DA (1977). An assessment of derivative determining techniques used for motion analysis. *Journal of Biomechanics* 10: 377–382.
- Poole TB, Schwibbe M (eds.) (1993). IPS international guidelines for the acquisition, care and breeding of nonhuman primates. *Primate Report* special issue: 1–29.
- Scott JD (2000). *Is There a Reliable Relationship between Stride Frequency and Overall Velocity in Quadrupedal Primates?* BSc dissertation, University of Edinburgh.
- Sellers WI (1992). *A Study of Leaping in Prosimian Primates*. PhD thesis, University of Liverpool.
- Sellers WI (1996). A biomechanical investigation into the absence of leaping in the locomotor repertoire of the slender loris (*Loris tardigradus*). *Folia Primatologica* 67: 1–14.
- Sellers WI, Crompton RH (1994). A system for 2- and 3-D kinematic and kinetic analysis of locomotion, and its application to analysis of the energetic efficiency of jumping in prosimians. *Zeitschrift für Morphologie und Anthropologie* 80: 99–108.
- Sellers WI, Varley JS, Waters SS (1998). Remote monitoring of locomotion using accelerometers: A pilot study. *Folia Primatologica* 69: 82–85.
- Swartz SM (1993). Biomechanics of primate limbs. In *Postcranial Adaptation in Nonhuman Primates* (Gebo DL, ed.), pp 5–42. DeKalb, Northern Illinois University Press.
- Varley JS, Cotterrell D (1994). Performance of a low cost radiotelemetry system for physiological applications. *Journal of Physiology* 479: 120.
- Walker JA (1998). Estimating velocities and accelerations of animal locomotion: A simulation experiment comparing numerical differentiation algorithms. *Journal of Experimental Biology* 201: 981–995.
- Warren RD, Crompton RH (1998). Diet, body size and the energy costs of locomotion in saltatory primates. *Folia Primatologica* 69(suppl 1): 86–100.
- White GC, Garrott RA (1990). *Analysis of Wildlife Radio-Tracking Data*. San Diego, Academic Press.
- Winter DA (1979). *Biomechanics of Human Movement*. New York, Wiley & Sons.
- Yoda K, Sato K, Niizuma Y, Kurita M, Bost CA, Le Maho Y, Naito Y (1999). Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *Journal of Experimental Biology* 202: 3121–3126.