STUDYING ANIMAL MOVEMENT

A lecture for the Physics in Life-Sciences course illustrating why we study animal movement, the methods that are used and giving examples of some animals that have been studied.

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Lecture Notes can be found at: `http://www.ed.ac.uk/~wis/`

Introduction

You have heard (or will hear) a lot about the physics of animal movement. What I will try to show in this lecture in the more practical side of the study of animal movement. This will take the form of a section on WHY we study animal movement; a section on HOW we study it; and finally a section showing some examples of WHAT we study. My particular interest is locomotion in terrestrial vertebrates – especially primates – so I apologise to those of you who would rather learn about what goes on in other phyla; in the aquatic or aerial environment; or the internal movements that go on inside animal bodies. The latter aspect I really will not cover at all so I should probably retitle the lecture straight away to "Studying animal locomotion with special emphasis on large terrestrial vertebrates". We would need a complete lecture course to cover the whole of animal movement and that is not what I am here to do.

Why study animal locomotion?

"Why" is always an interesting question when applied to any scientific endeavour. The 'why' question can be argued on a number of levels. Tinbergen [13] suggests 4 'why's' in biology and some nice examples are given in Krebs and Davies [5]. Consider the question, "Why do starlings (*Sturnus vulgaris*) sing in the spring?". There are 4 answers depending on the interpretation of why.

1. The answer can be given in terms of the **survival value** or **function** which in this case is that starlings sing to attract mates.

2. The answer can be in terms of **causation**. In this case in terms of physiology because increasing day length has altered hormone levels which have triggered the singing behaviour and anatomically because of air flowing through the syrinx causes membrane vibrations.

3. In terms of **development**: starlings sing because they have learned the songs of their neighbours.

4. Finally in terms of **evolutionary history**. This answer would involve an analysis of how we suppose that bird song has become more complex through evolutionary time due to sexual selection whereby certain songs are more successful at attracting females and how singing prowess might be an honest advertisement of male fitness.

1 and 4 can be described as "Ultimate" causes (some distance from the result), 2 and 3 are "Proximate" (cause and effect are closer).

Of course all these different why's are not independent. There is an evolutionary component to all of them, and evolution can only function in the context of anatomy and physiology. However they are sufficiently distinct that they are all correct and none are better answers than the others.

When we study locomotion we are interested in all these different levels. In terms of function, animals move around their environments for a variety of reasons: to acquire food; to search for mates; to avoid predators. The causation is the brain which sends electrical impulses down nerve fibres which trigger the contractile machinery in the muscles to move the limbs in a coordinated fashion which propels the animal (well in vertebrates anyway – and I did say this lecture would mostly concentrate on vertebrates). In terms of development many animals are unable to walk at birth and have to learn the appropriate movement patterns as they grow up. Locomotion is also highly size dependent so the movement patterns also need to change as an animal grows. Other movements, such as the appropriate foraging techniques and, in some animals, tool manufacture and use need to be learnt in a social context. In terms of evolutionary history, locomotion can be selected for energetic efficiency; for performance; or most likely some combination of the two. It is also highly constrained by the machinery on offer. Wheels are pretty rare in the natural world and muscle, whilst excellent in terms of efficiency is not so good in terms of power to weight ratio.

FIGURE 1. Power output relative to mass [14]

ENGINE	OUTPUT, WATTS/KG	OUTPUT, HP/LB
18th-century steam pump	10	0.005
Cilia	30	0.02
Skeletal muscle	200	0.12
Electric motor	200	0.12
Automobile engine	400	0.24
Motorcycle engine	1,000	0.6
Aircraft engine, piston	1,500	0.9
Aircraft engine, turbine	6,000	3.6

In practical terms this means that biologists studying locomotion are (amongst others) ecologists, biomechanists (I prefer the term biomechanics), physiologists and functional anatomists.

How do we study locomotion?

There are a whole host of ways of studying locomotion and I am only going to give a few examples here. This will be grouped by the use that the data is being put to.

Behavioural monitoring

Locomotion is primarily a behaviour so many of the general behavioural monitoring techniques can be applied to the study of locomotion. So an ecologists interested in time and energy budgets will record locomotor behaviour as one of the classes of activity that an animal performs. At the simplest level this will involve noting down what locomotion activity an animal is doing at regular intervals throughout the observation period.

FIGURE 2. Simple behavioural monitoring and sources of error [6]

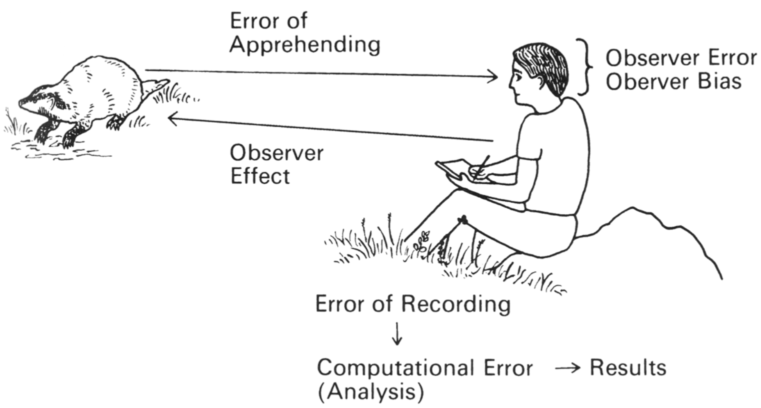
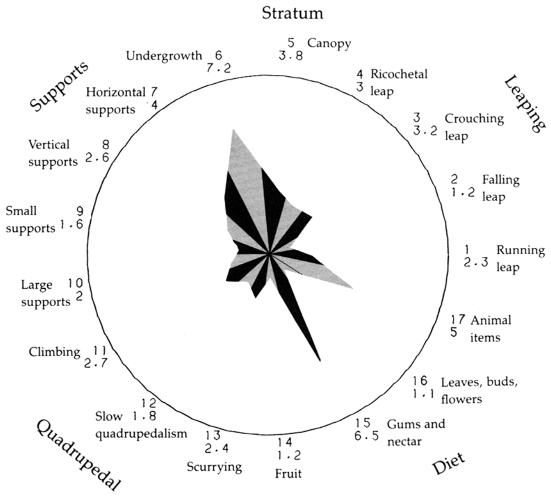


FIGURE 3. Senegal bushbaby (*Galago senegalensis*) [2]

This information will eventually enable us to build up an ethogram of the behaviour of a particular animal. This is an indication of the amount of time an animal spends doing various behaviours of interest. For an arboreal primate this will include information of the supports that the animal prefers to move along, the height in the forest that it was seen, and the types of locomotion that were observed.

FIGURE 4. Polar plot of the activity profile of the Senegal bushbaby (*Galago senegalensis*) [10]



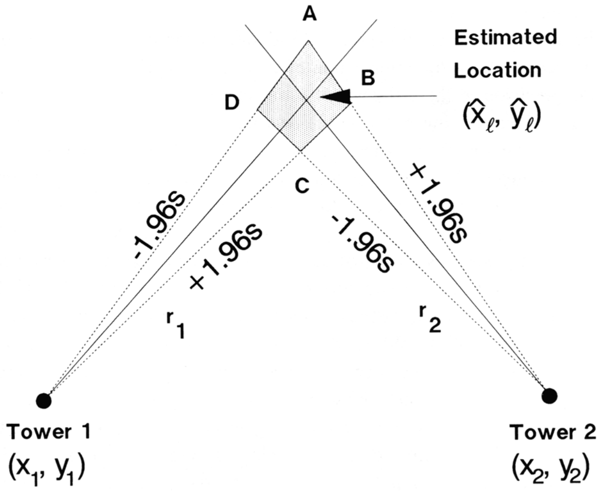
To increase the amount of information, the observer can estimate the quantitative nature of the movement: slow quadrupedalism; fast quadrupedalism; 2 metre leap etc. Often we are interested in how far an animal moves in a given period and this can be done by mapping the animal's position at regular intervals. Spatial position can be measured in a rather more sophisticated by various types of radio tracking. Triangulation using two or more directional receivers can be used to define the position or for very large scale studies (migration of marine mammals for example), the animal can be fitted with a data logging system connected to a GPS[1] satellite receiver. Flocking of birds or the population dynamics of marine algae can be picked up directly from satellite images.

FIGURE 5. **Radio collared coyote (*Canis latrans*) [6]**

FIGURE 6. **Mobile radio-tracking tower [15]**

1. Global positioning system.

FIGURE 7. Estimation of location by triangulation [15]



We also use radio collars to measure other parameters that directly reflect the locomotor state of the animal. Acceleration is a useful measure with apparatus varying from a mercury switch that pulses the transmitter signal on and off as the animal moves to integrated circuits (the sort used to trigger car air-bags or measure the acceleration experienced by pilots) that directly measure acceleration which can be used to calculate leap distances and the duration of strenuous bursts of activity.

FIGURE 8. Accelerometer collar on a mongoose lemur (*Eulemur mongoz*)

One of the more direct approaches that was used to measure maximum speeds of various savannah ungulates was to chase them around with a landrover and see how fast you had to drive to overtake the subjects.

Motion analysis

Those of us interested in biomechanics and functional anatomy often use motion analysis to look at the details of what is going on. In its simplest form this involves filming the animal in question and looking at the individual frames of film to see how the animal moves from frame to frame. This technique was pioneered in the late 19th century by Eadward Muybridge who used a number of fixed cameras which were triggered by trip wires that were activated when the subject broke them. He was the first person to solve the problem of what galloping horses looked like in mid-stride (something that had troubled artists wanting to paint galloping horses for the previous few centuries).

FIGURE 9. Drawing Horses [7]

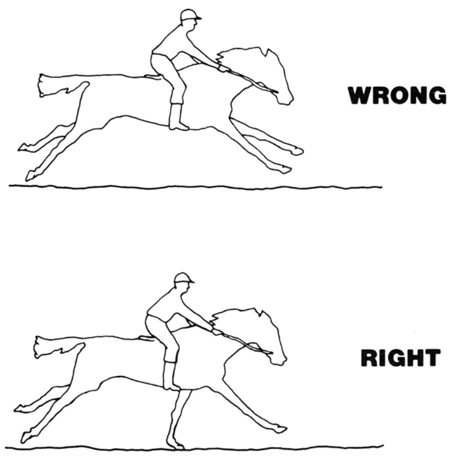
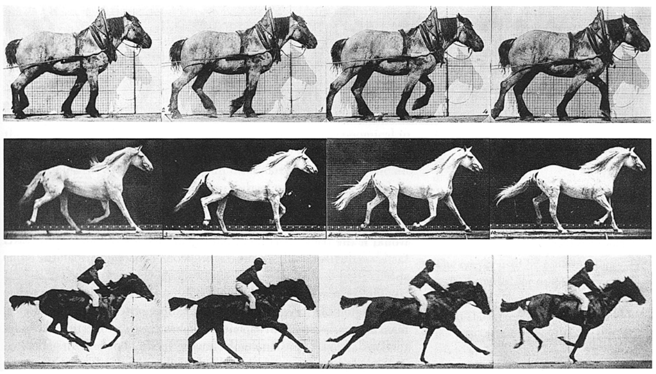


FIGURE 10. Eadward Muybridge's horses [2]



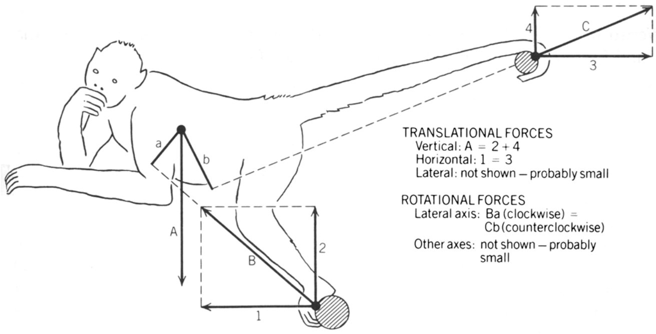
Modern studies have looked at much faster animal movements such as the flapping wings of a humming bird or a lacewing. The humming bird diagram is a single high-speed photograph, but the lacewing picture has been taken using a triple flash. By knowing the time between flashes we can calculate a number of important parameters such as the wingbeat frequency and the velocity of the animal.

FIGURE 11. **Antillean crested Hummingbird (*Orthorhynchus cristatus*) [2]**

FIGURE 12. **Triple flash photograph of a lacewing (*Chrysopa carnea*) [2]**

Using high-speed video equipment we can sample movements up to several thousand times a second and if you have enough patience you can look through the still images and measure the animal's position, frame by frame. Once you have position data you can differentiate with respect to time to find velocities and again to find accelerations. If you then apply Newton's Laws of motion you can calculate the forces that are involved and hence the forces that need to be generated by the animal and the stresses that the skeleton needs to accommodate.

FIGURE 13. Free-body diagram of a spider monkey (*Ateles* sp.) [4]



We can directly measure other parameters associated with movement. Muscle activation can be monitored by electrodes attached to the skin of the animal (or needles inserted into the muscle body). Stresses can be measure by strain gauges attached to the bones and tendons of interest. X-ray films can be taken which allow you to see the movements of the bones inside the animal rather than just the externally visible movement.

FIGURE 14. Electromyographic recordings from a brown lemur (*Eulemur fulvus*) [3]

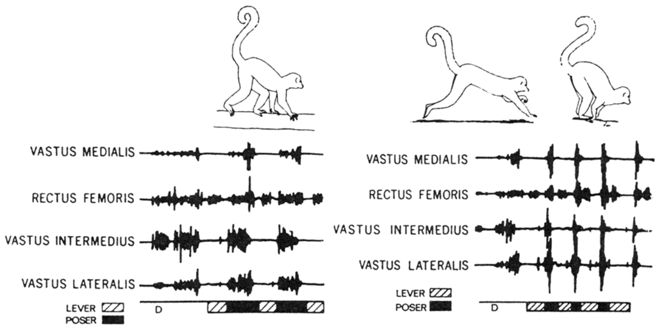


FIGURE 15. Rosette strain gauge [8]

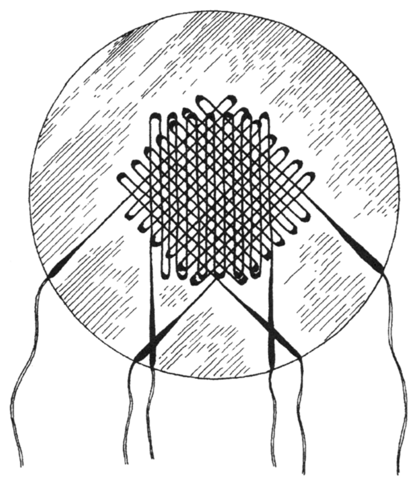
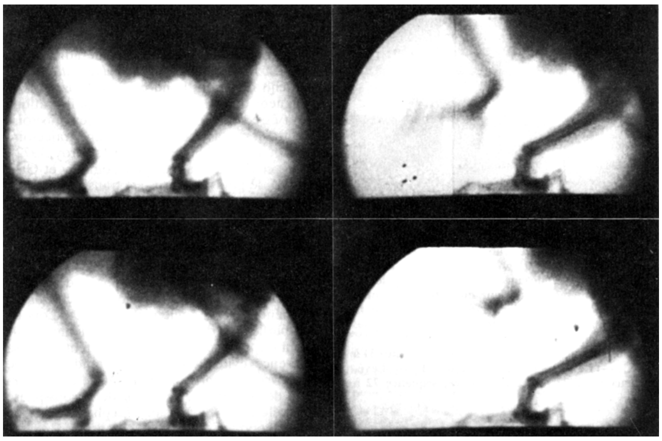


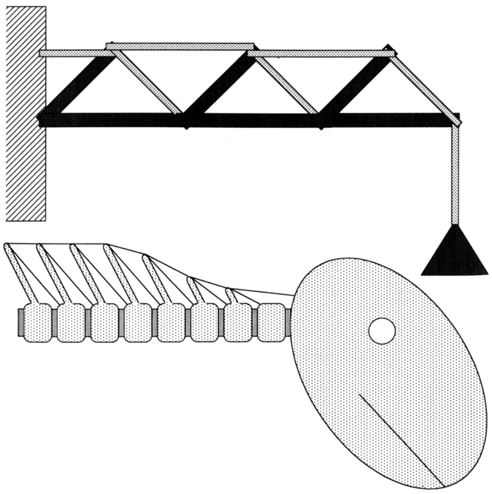
FIGURE 16. X-ray film of an asymmetric leap of Allen's bushbaby (*Galago alleni*) [3]



Functional anatomy

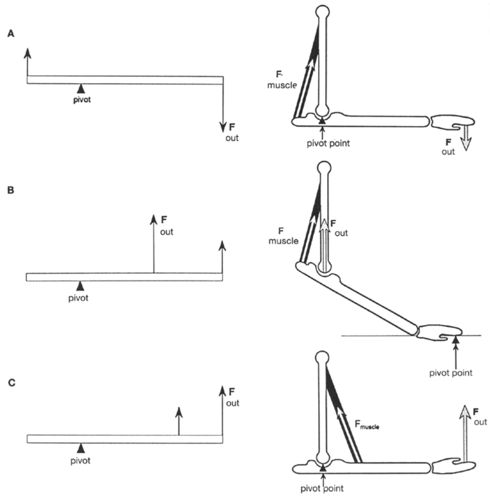
In order to understand movement you need to know the mechanics of the underlying structure. This takes us into the realms of functional anatomy. People have been dissecting animals for centuries – millennia in fact. Bony skeletons can tell us a lot about the mechanical engineering underlying a structure since the physical principles are exactly the same. Trusses are a way of minimising the weight of a structure by separating the compressive and tensile elements of the beam. Figure 17 shows how this is used in the necks of quadrupedal mammals.

FIGURE 17. Protruding trusses [14]



Similarly joints and muscles can be treated as lever systems with the joint restricting the movement at the joint and the muscles applying forces (Figure 18). The actions of muscles can be measured *in situ* using Electromyographic as illustrated in Figure 14.

FIGURE 18. **Lever analysis of forces acting at joints [12]**



Functional anatomy is often essential when trying to find out how an animal moves the way it does. Jumping spiders use hydraulic pressure to extend their hind legs. Kinkajous have specialised ankle morphology that allow the animal to rotate its foot through 180° so that it hang by its claws with its head downwards.

FIGURE 19. **Leaping jumping spider (*Sitticus pubescens*) [11]**

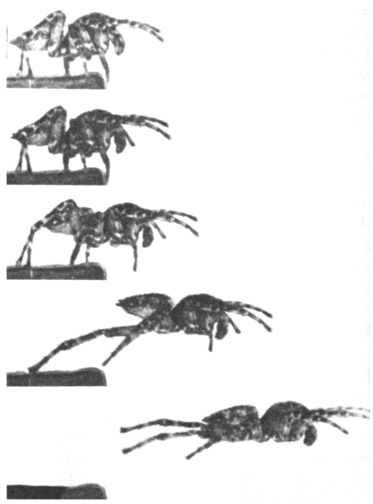


FIGURE 20. **Kinkajou (*Potos flavus*) hanging by its hind feet [2]**

Modelling

Many modern studies of animal movement use some sort of modelling technique. This includes simple predictions of movement from forces acting about joints to full-blown 3D computer simulations. It is particularly useful for studying movements that cannot be observed. If you are interested in how dinosaurs move then you can base your model on how large terrestrial mammals move and extrapolate to the dinosaur you are interested in. You can even feed in information from fossilised footprints to produce a more accurate (or perhaps I should say a more believable) estimate.

FIGURE 21. **How a *Triceratops* might have galloped based on a white rhinoceros (*Ceratotherium simum*) [1]**

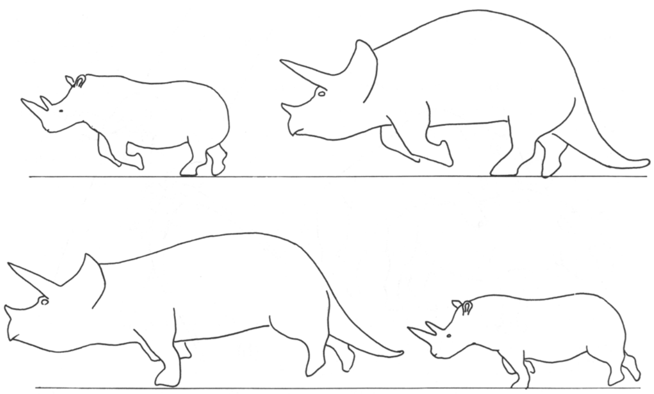
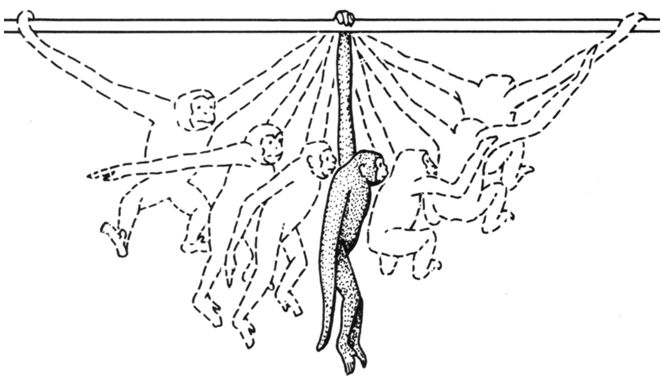


FIGURE 22. Estimated speeds of dinosaurs[2] [1]

	ESTIMATED LEG LENGTH	ESTIMATED SPEED		GAIT
	Meters	*Meters Per Second*	*Miles Per Hour*	
data from Davenport Ranch (fig. 3.4)				
large theropod	2.0	2.2	(4.9)	walk
small theropod	1.0	3.6	(8.1)	run
large sauropod	3.0	1.0	(2.2)	walk
small sauropod	1.5	1.1	(2.5)	walk
data from Winton (fig. 3.1)				
large theropod	2.6	2.0	(4.5)	walk
small theropods	0.13–0.22	3.0–3.5	(6.7–7.8)	run
ornithopods	0.14–1.6	4.3–4.8	(9.6–10.7)	run

Some ongoing work I am involved in concerns the specialised locomotor form of gibbons which is called brachiation. I am trying to find out whether this form of locomotion is particularly suited to arboreal animals of a particular body size since gibbons live sympatrically with other primates that do not use this form of locomotion.

FIGURE 23. Illustration of a siamang (*Hylobates syndactylus*) brachiating [9]

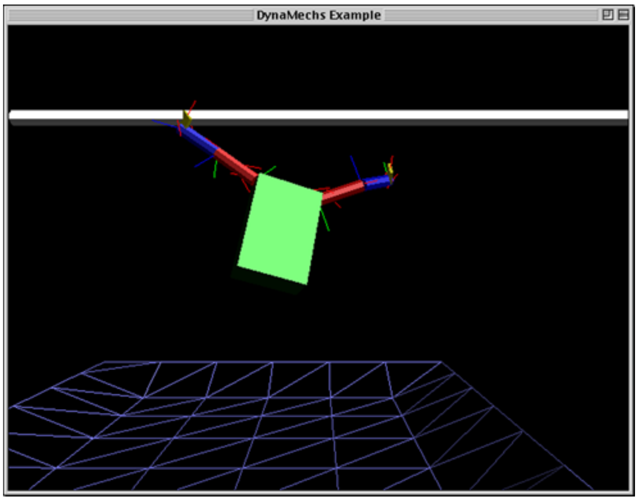


This is ongoing work but we are using a multi-way approach including video motion analysis of captive gibbons at Edinburgh Zoo, human motion analysis of people pretending to be gibbons (only for the more athletic) and computer simulation.

2. Human top speed is approximately 10 ms^{-1}; racehorses 16 ms^{-1}; greyhound 17 ms^{-1}. Any other speeds you hear quoted for animals are largely apocryphal. There is no good evidence for faster speeds in terrestrial mammals: top speed is actually a very difficult parameter to measure.

FIGURE 24. Video footage of a siamang (*Hylobates syndactylus*) at Edinburgh Zoo

FIGURE 25. Computer simulation of a gibbon brachiating



Summary

In conclusion, the study of animal movement is alive and well. I have tried to give you a flavour of what sort of things go on. There is also plenty of work on invertebrates and on the various internal moving parts of the body (heart, lungs, guts, jaws etc.). All of it follows the same laws of physics as everything else does although the level of complexity can be very much higher than we are currently able to deal with. Whoever said that aerodynamics had proved that bumblebees could not fly was clearly potty! They obviously can and now we have a better understanding of fluid dynamics we know something about how they manage it. However do not expect to see a flapping aeroplane anytime soon.

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