G R E S H A M

C O L L E G E

THE PATTERN OF TINY FEET:

THE MATHEMATICS OF ANIMAL MOVEMENT

A lecture by

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Gresham Lecture

The Pattern of Tiny Feet

Ian Stewart

A centipede was happy quite,
Until a frog in fun
Said, 'Pray, which leg comes after which?'
This raised her mind to such a pitch,
She lay distracted in a ditch
Considering how to run.

Mrs. Edmund Craster

Nature is nothing if not rhythmic, and its rhythms are many and varied. Our hearts and lungs follow rhythmic cycles whose timing is adapted to our body's needs. Many of nature's rhythms are like the heartbeat: they take care of themselves, running 'in background'. Others are like breathing: there is a simple 'default' pattern that operates as long as nothing unusual is happening, but there is also a more sophisticated control mechanism that can kick in when necessary and adapt those rhythms to immediate needs. Controllable rhythms of this kind are particularly common — and particularly interesting — in locomotion. In legged animals the default patterns of motion that occur when conscious control is not operating are called gaits.

Until the development of high-speed photography it was virtually impossible to find out exactly how an animal's legs move as it runs or gallops: the motion is too fast for the human eye to unravel. Legend has it that the photographic technique grew out of a bet on a horse. In the 1870s Leland Stanford, former governor of California, bet $25,000 that at some times a trotting horse is completely off the ground. To settle the issue a photographer, who was born Edward Muggeridge but adopted the name Eadweard Muybridge, photographed the different phases of the gait of the horse. To do so he placed a line of cameras with tripwires for the horse to trot past. Stanford, it is said, won his bet. Whatever the truth of the legend, we do know that Muybridge went on to pioneer the scientific study of gaits. He also adapted a mechanical device known as the zoetrope to display them as 'moving pictures', a road that in short order led to Hollywood. So Muybridge founded both a science and an art.

This lecture is about gait analysis, a branch of mathematical biology that grew up around the questions 'how do animals move?' and 'why do they move like that?'. The organising principle behind such biological cycles is the mathematical concept of an oscillator — a unit whose natural dynamic causes it to repeat the same cycle of behaviour over and over again. Biology hooks together huge 'circuits' of oscillators, which interact with each other to create complex patterns of behaviour. Such 'coupled oscillator networks' underlie many of the rhythms of life.

Why do systems oscillate at all? The answer is that this is the simplest thing you can do if you don't want, or are not allowed, to remain still. Why does a caged tiger pace up and down? Its motion results from a combination of two constraints. First, it feels restless and does not wish to sit still. Second, it is confined within the cage and cannot simply disappear over the nearest hill. The simplest thing you can do when you have to move but can't escape altogether is to oscillate. Of course there is nothing that forces the oscillation to repeat a regular rhythm; the tiger is free to follow an irregular path round the cage. But the simplest option — and therefore the one that is most likely to arise both in mathematics and in nature — is to find some series of motions that works, and repeat it over and over again. And that is what we mean by a periodic oscillation.

Many oscillations arise out of steady states. As conditions change, a system that has a steady state may lose it and begin to wobble periodically. In 1942 the German mathematician Eberhard Hopf found a general mathematical condition that guarantees such behaviour: in his honour this scenario is known as Hopf bifurcation. A more evocative, but less formal, name is 'wobble catastrophe'. The workings of a clarinet, for example, depend upon the wobble catastrophe: as the clarinettist blows air across the instrument's reed, the reed ceases to remain steady and begin to vibrate. This vibration is transmitted to the air, and the vibrating air is what we hear as music.

Two biologically distinct but mathematically similar types of oscillator are involved in locomotion. The most obvious oscillators are the animal's limbs, which can be thought of as mechanical systems, linked assemblies of bones, pivoting at joints, pulled this way and that by contracting muscles. The main oscillators that concern us here, however, are to be found in the creature's nervous system, the neural circuitry that generates the rhythmic electrical signals that stimulate and control the limbs' activity. Biologists call such a circuit a CPG, which stands for 'central pattern generator'. Correspondingly, a student of mine took to referring to a limb by the acronym LEG, allegedly for 'locomotive excitation generator'. Animals have two four, six, eight or more LEGs, but we know very little directly about the CPGs that control them, for reason I shall shortly explain. A lot of what we do know has been arrived at by working backwards or forwards from mathematical models.

Some animals possess only one gait, only one rhythmic 'default' pattern for moving their limbs. The elephant, for example, can only walk. When it wants to move faster, it 'ambles' — but an amble is just a fast walk, and the patterns of leg movement are the same. Other animals possess many different gaits; the most familiar is the horse. At low speeds horses walk; at higher speeds they trot; and at top speed they gallop. Some insert yet another type of motion, the canter, between trot and gallop. The differences are fundamental: a trot isn't just a fast walk, but a different kind of movement altogether.

In 1965 the zoologist M.Hildebrand noticed that most gaits possess a degree of symmetry. For example when an animal bounds, both front legs move together and both back legs move together, so the bound gait preserves the animal's bilateral symmetry. Other symmetries are more subtle: for example the left half of a camel may follows the same sequence of movements as the right half, but half a period *out of phase* — that is, after a time delay equal to half the period. So the pace gait has its own characteristic symmetry: 'reflect left and right and shift phase by half a period'. You use exactly this type of symmetry-breaking to move yourself around: despite your bilateral symmetry, you don't move both legs simultaneously! There's an obvious advantage to bipeds in not doing so: if they move both legs at once they fall over.

The seven commonest quadrupedal gaits are the trot, pace, bound, walk, rotary gallop, transverse gallop, and canter. In the trot, the legs are in effect linked in diagonal pairs. First the front left and back right hit the ground together; then the front right and back left. In the bound everything is linked left-right, so that first the front legs hit the ground together, then the back legs. The pace similarly links the movements in the front-back direction: first the two left legs hit the ground, then the two right. The walk involves a more complex but equally rhythmic pattern: front left, back right, front right, back left, then repeat. In the rotary gallop, the front legs hit the ground almost together, but with the right (say) very slightly later than the left; then the back legs hit the ground almost together, but this time with the left very slightly later than the right. The transverse gallop is similar, but the sequence is reversed for the rear legs. The canter is even more curious: first front left, then back right, then the other two legs simultaneously. There is also a rarer gait, the pronk, in which all four legs move simultaneously. (*For pictures of these gaits, see the end of these notes.*)

The pronk is uncommon outside of cartoons but is sometimes seen in young deer. The pace is observed in camels, the bound in dogs; cheetahs use the rotary gallop to travel at top speed. Horses are very versatile, and use the walk, trot, transverse gallop, and canter, depending upon circumstances. Other animals also use several gaits, and like the horse they switch between them.

This ability to switch comes from the dynamics of GPGs. The basic idea behind CPG models is that the rhythms and phase relations of animal gaits are determined by the natural oscillation patterns of relatively simple neural circuits. What might such a circuit look like? Trying to locate a specific piece of neural circuitry in an animal's body is like searching for a needle in a haystack: to map out the nervous system of all but the simplest of animals is well beyond the capabilities of today's science. So we have to sneak up on the problem of CPG design in a less direct manner.

One approach is to work out the simplest type of circuit that might produce all the distinct but related symmetry-patterns of gaits. At first sight this looks like a tall order, and we might be forgiven if we tried to concoct some elaborate structure with switches that effected the change from one gait to another, like a car gearbox. But the theory of the wobble catastrophe tells us there's a simpler and more natural way. It turns out the symmetry patterns observed in gaits are strongly reminiscent of those found in symmetric networks of oscillators. Such networks naturally possess an entire repertoire of oscillation pattern, classified by a general mechanism known as *symmetry breaking*. The networks can switch between them in a natural manner: you don't need a complicated 'gearbox'.

For example, a network representing the CPG of a biped requires only two identical oscillators, one for each leg. The mathematics shows that if two identical oscillators are coupled together — connected so that the state of each affects that of the other — then there are precisely two typical oscillation patterns. One is the *in-phase* pattern, in which both oscillators behave identically. The other is the *out-of-phase* pattern in which both oscillators behave identically except for a half-period phase difference. Suppose that this signal from the CPG is used to drive the muscles that control a biped's LEGs, by assigning one set of muscles to each oscillator. Then the resulting gaits inherit the same two patterns. For the in-phase oscillation of the network, both legs move together: the animal performs a two-legged hopping motion, like a kangaroo. In contrast, the out-of-phase motion of the CPG produces a gait resembling the human walk. These two gaits are the ones most commonly observed in bipeds. (They can of course do other things, for example hopping on one leg, but in that case they effectively turn themselves into one-legged animals.)

What about quadrupeds? The simplest model is now a system of four coupled oscillators — one for each LEG. Now the mathematics predicts a greater variety of patterns — and nearly all of them correspond to observed gaits. The most symmetric gait, the pronk, corresponds to all four oscillators being synchronised — that is, to unbroken symmetry. The next most symmetric — the bound, pace, and trot — correspond to grouping the oscillators as two out-of-phase pairs: front/back, left/right, or diagonally. The walk is a circulating figure-eight pattern and again occurs naturally in the mathematics. The two kinds of gallop are more subtle. The rotary gallop is a mixture of pace and bound, and the transverse gallop is a mixture of bound and trot. The canter is even more subtle and not as well understood.

The theory extends readily to six-legged creatures such as insects. For example, the typical gait of a cockroach, and indeed of most insects, is the tripod, in which the middle leg on one side moves in phase with the front and back on the other, and then the other three legs move together, half a period out of phase with the first set. This is one of the natural patterns for six oscillators connected in a ring.

Myriapods (centipedes and millipedes) produce rippling patterns of leg-movements. These can be understood as travelling waves in large networks with polygonal symmetry, corresponding to (mathematically!) gluing the creatures' front ends to their rears to keep the wave travelling. The movement of fish, lizards, worms, and snakes can be described in similar ways. Even some types of protozoon — microscopic single-celled creatures — propel themselves along by rotating a helical tail, or flagellum, just like the mechanical device known as an Archimedean screw.

The symmetry-breaking theory also explains how animals can change gait without having a gearbox: a single network of oscillators can adopt different patterns under different conditions. The possible transitions between gaits are also organised by symmetry. The faster the animal moves, the less symmetry its gait has: more speed breaks more symmetry. But an explanation of *why* they change gait requires more detailed information on physiology. In 1981 D.F.Hoyt and R.C.Taylor discovered that when horses are permitted to select their own speeds, depending on terrain, they choose whichever gait minimises their oxygen consumption.

The big message here is that nature's rhythms are often linked to symmetry, and that the patterns that occur can be classified mathematically by invoking the general principles of symmetry-breaking. Of course this doesn't answer every interesting question about the natural world — but it does provide a unifying framework, and it often suggests interesting new questions. In particular, it both poses and answers the question 'why these patterns but not others?' The lesser message is that mathematics can illuminate many aspects of nature that we do not normally think of as being mathematical. This is a message that goes back to the Englishman D'Arcy Thompson, whose classic but maverick book *On Growth and Form* set out an enormous variety of more or less plausible evidence for the role of mathematics in the generation of biological form and behaviour. In an age when most biologists seem to think that the only interesting thing about an animal is its DNA sequence, it is a message that needs to be repeated, loudly and often.

FURTHER READING

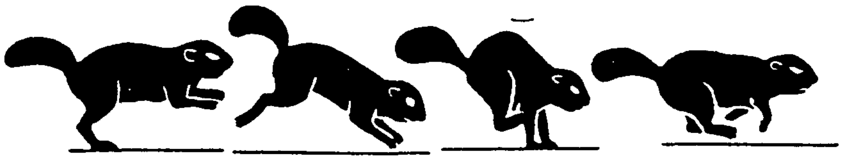
R.McNeil Alexander and G.Goldspink, *Mechanics and Energetics of Animal Locomotion*, Chapman and Hall, London 1977.

P.Gambaryan, *How Mammals Run: Anatomical Adaptations*, Wiley, New York 1974.

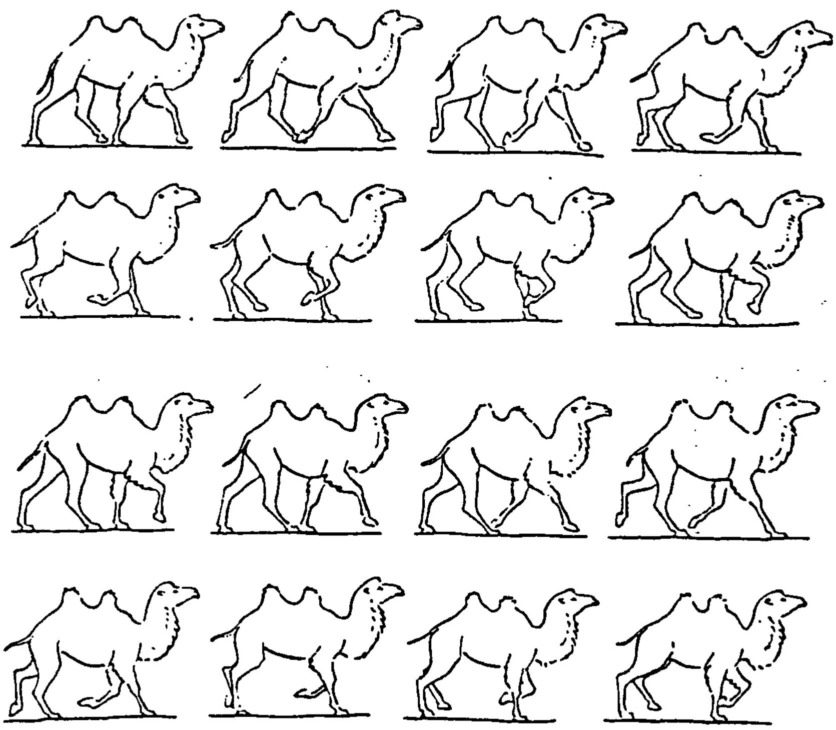
Ian Stewart and Martin Golubitsky, *Fearful Symmetry: is God a Geometer?*, Penguin Books, Harmondsworth 1992.

D'Arcy Thompson, *On Growth and Form* (2 vols.), Cambridge University Press, Cambridge 1972.

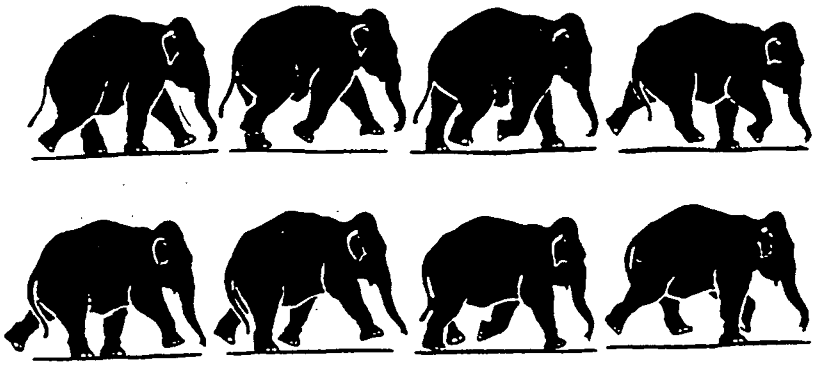
FIGURES



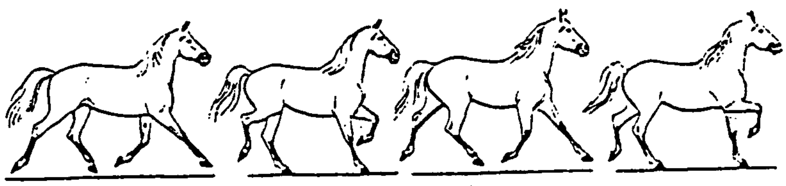
The bound of the long-tailed Siberian souslik retains bilateral symmetry



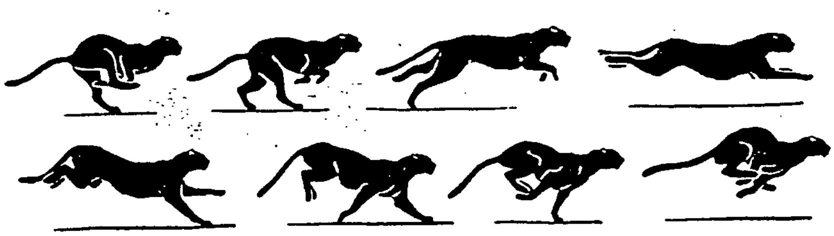
The pace of the camel breaks bilateral symmetry



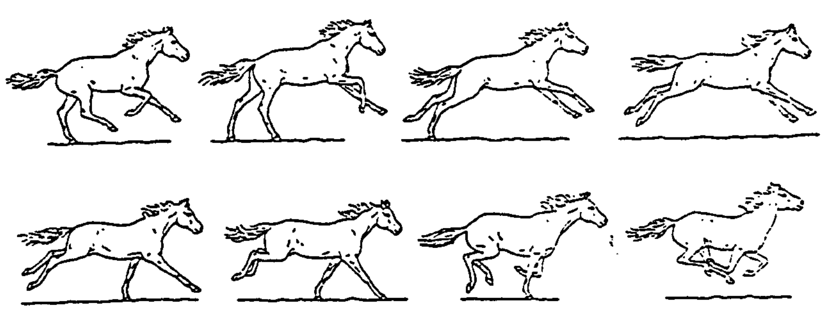
The amble of the elephant



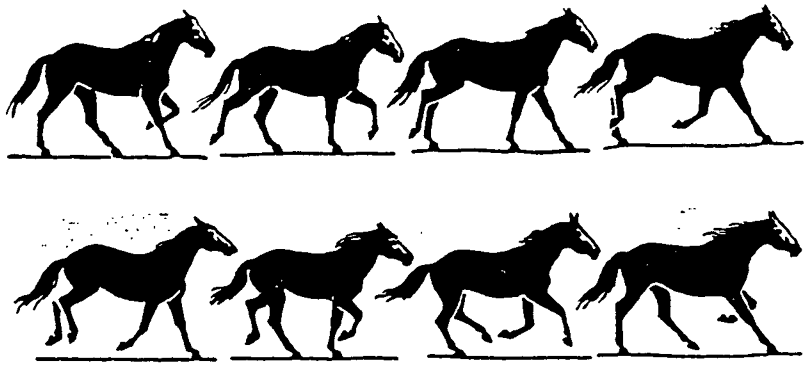
The trot of a horse



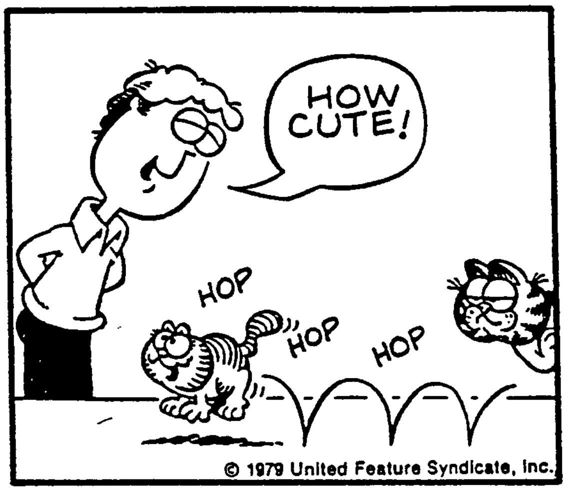
The transverse gallop of a cheetah



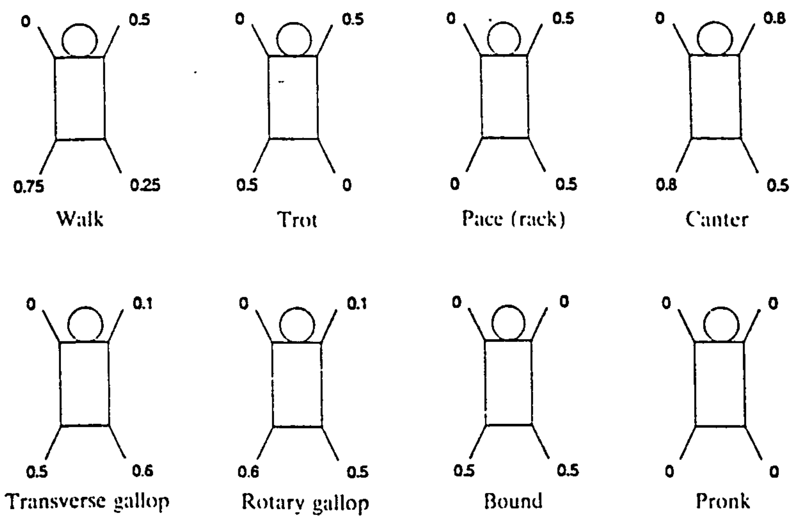
The rotary gallop of a horse



The canter of a horse



A feline pronk



Phase relationships in gaits.

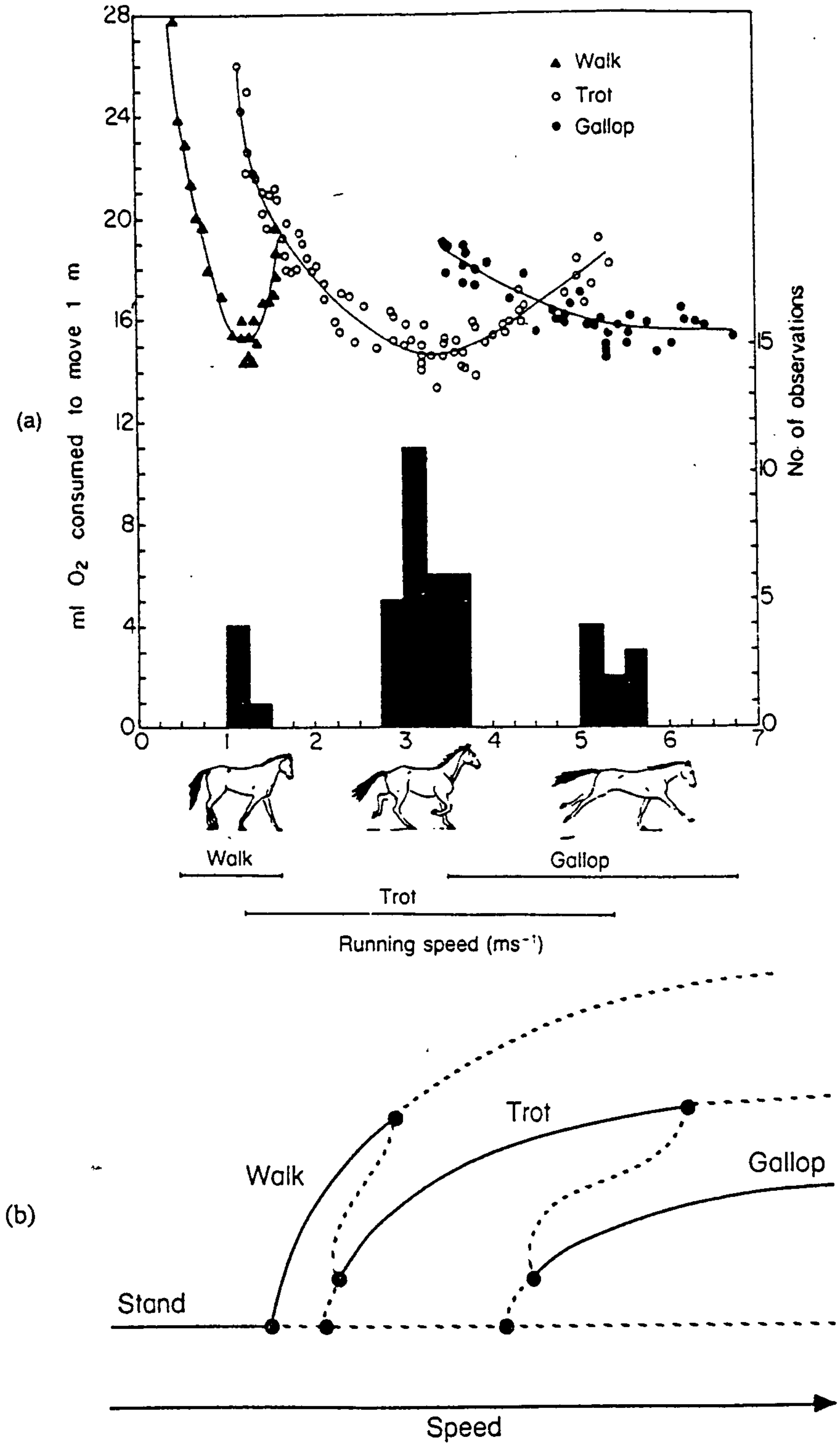


Figure 8.18 (a) Oxygen consumption (vertical axis) of horses for various gaits and speeds (horizontal axis). (b) Interpretation as a bifurcation diagram, same horizontal scale