Editorial note. We are trying to introduce a "new look" to the BHS Bulletin, and one of our plans is to commission articles by well-known zoologists summarising recent advances in their area of expertise, as they relate to herpetology. We are particularly pleased that Professor McNeill Alexander of Leeds University agreed to write the first of these. We hope that this masterly summary of "Locomotion of Reptiles" will be of interest to a wide range of readers. *Roger Meek and Roger Avery, Co-Editors.*

Locomotion of Reptiles

R. McNEILL ALEXANDER

Institute for Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK.

r.m.alexander@leeds.ac.uk

ABSTRACT – Reptiles run, crawl, climb, jump, glide and swim. Exceptional species run on the surface of water or "swim" through dry sand. This paper is a short summary of current knowledge of all these modes of reptilian locomotion. Most of the examples refer to lizards or snakes, but chelonians and crocodilians are discussed briefly. Extinct reptiles are omitted. References are given to scientific papers that provide more detailed information.

INTRODUCTION

This review is an attempt to explain briefly the many different modes of locomotion that reptiles use. Some of the information it gives has been known for many years, but many of the details have been established only in the present century, as the dates of many of the papers in the References indicate. Readers who want more technical detail may find it in Alexander (2003) or (especially for more recent advances) in the papers referred to in the text.

Running

Lizards running quadrupedally generally move diagonally opposite feet simultaneously; the left fore foot with the right hind, and the right fore with the left hind. Figure 1 represents a single step in which the right fore and left hind feet remain stationary on the ground while the left fore and right hind move forward. At the same time the bend in the body is reversed. The feet are moved forward partly by movements of the shoulder, hip and other leg joints; and partly by the bending of the back. Figure 1 emphasises the role of the back. Running is powered partly by the leg muscles and partly by the back muscles.

Lizards stand and run with their feet well out to either side of the body. Consequently, bigger forces are needed in their leg muscles than if the legs functioned like pillars, with the feet under the body and the leg joints much straighter, as in elephants. The bigger an animal is, the harder it is for them to support the weight of the body in a lizard-like stance. Imagine two reptiles of exactly the same shape, one twice as long as the other. It would be twice as long, twice as wide and twice as high, so eight times as heavy. Its muscles, however, would have only four times the cross-sectional area, so could exert only four times as much force. If the larger animal were made progressively bigger, it would eventually reach a point at which its leg muscles could no longer support it. Large dinosaurs could not have stood like lizards, and accordingly stood like elephants. Fossil footprints show that they placed their feet under the body, not out to the side.

Muscles can deliver more power when they are warm than when they are cold. Reptiles are perceived as "cold blooded", so you might expect them to be rather sluggish. Their body temperatures fall at night, but (in favourable climates) can be raised rapidly in the morning by basking in the sun. In one study, the body temperatures of the lizard *Amphibolurus* (= *Pogona*) in its natural habitat in Australia were found to be about 25°C when they emerged in the mornings, but rose rapidly in the sun to about 37°C, the body temperature of a typical mammal (Bradshaw & Main, 1968). We should not be surprised that warm lizards can sprint at about the same maximum speeds as mammals

Figure 1. A diagram of a lizard taking a step, showing how bending the body contributes to the length of the step.

of equal mass; for example, Bonine & Garland (1999) recorded a 16 gram *Cnemidophorus* (= *Aspidiscelis*) sprinting at 6 metres per second, which is faster than most measurements of maximum sprint speeds for mammals of similar mass. Lizards also compare well with mammals for economy of energy in running; the extra energy needed to run unit distance, over and above resting energy consumption, is about the same for lizards as for mammals of equal mass (Figure 7 in Full & Tu, 1991).

Many lizards rise up on their hind legs when they run fast. This seems to be an inevitable consequence of high acceleration. If a motorcyclist accelerates violently, he or she does a wheelie; the front wheel rises off the ground. The principle is the same for lizards, and is particularly effective for them because their long tails bring the centre of mass of the body well back, close to the hind legs. The effect ends when the animal stops accelerating (Clemente et al., 2008).

Muscles that can contract fast use more energy than those that can contract only slowly. Tortoises can withdraw into their carapaces, so do not have to run away from predators. Nor do they have to pursue prey. They have no need to run, and have evolved remarkably slow, remarkably economical muscles. They walk very slowly and wobble a lot, pitching and rolling as they go; their muscles are too slow either to keep the body constantly in equilibrium, or to correct a wobble quickly. They minimise the problem by using a different gait from other reptiles, moving diagonally opposite feet a little out of phase with each other (Jayes & Alexander, 1980).

Crocodiles use several gaits. They slither down slopes such as river banks on their bellies. In addition to more-or-less lizard-like walking, with their feet on either side of the body, they use a "high walk" with their legs straighter and their feet closer under the body. Their fastest gait is the "gallop", which is more like the bounding gait of rabbits than the gallops of horses and dogs. Speeds up to about 5 metres per second have been measured (Webb & Gans, 1982).

Crawling without legs

Figure 2 shows three crawling techniques used by snakes. In serpentine crawling (a) the snake passes waves of bending backwards along its body. If the snake is weaving its way between stones, tussocks of grass and other obstacles, these will tend to prevent the snake's body from sliding sideways, and each point on the body will move forward along the path that more anterior parts have already travelled. The waves will stay where they are while the body moves forward. Fixed obstacles such as stones are not, however, essential for crawling. The ventral surfaces of snakes have different coefficients of friction for sliding in different directions; low for sliding forward along the body axis, higher for backward axial sliding, and higher still for sliding at right angles to the body axis. Thus a segment of the body can slide more easily forward along the body axis, than laterally. Also, crawling snakes raise the curved parts of the body slightly off the ground. These circumstances enable snakes to crawl on flat surfaces with a moderate degree of roughness, but not on highly polished surfaces (Hu et al., 2009).

Thus lateral bending of the back is important both in the serpentine locomotion of snakes and in the running of lizards. In both cases the body is thrown into more-or-less sinusoidal waves, but there is a very significant difference: snakes use waves that travel backwards along the body, but in lizards the bends are always at the same points on the body. Serpentine locomotion depends on travelling waves and lizard running on standing waves. Legless lizards, however, use travelling waves to crawl like snakes.

Figure 2(b) shows sidewinding, a crawling technique used (for example) by rattlesnakes that works well even on loose sand. As in serpentine crawling, waves of bending form at the front end of the body and travel backwards along the body. Only the stippled parts of the body are on the ground. Each part of the body is stationary while on the ground, but is periodically lifted to a new

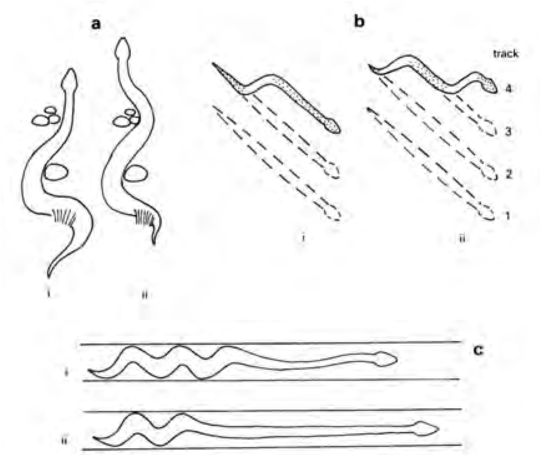

Figure 2. Diagrams of snakes crawling. (a) Serpentine locomotion; (b) sidewinding and (c) concertina locomotion. From R. McN. Alexander (1982) *Locomotion of Animals*, Blackie, Glasgow.

position. This action leaves a series of straight, parallel tracks in the sand. Sidewinding seems to be the most economical of energy of the three crawling techniques illustrated in Figure 2 (Secor et al., 1992).

Figure 2(c) shows concertina locomotion, which is effective in crevices. At any moment, short sections of the body are folded, tightly jammed against the sides of the crevice. The anterior fold of each group opens, pushing the parts of the body in front of it forwards. At the same time, new folds are added to the back of the group, drawing more posterior parts of the body forward.

Boas sometimes travel by rectilinear locomotion which, unlike the other techniques, does not involve bending of the body. Waves of rib movement move backwards along the body, shuffling the snake along.

No snake travels fast. The black racer (*Coluber constrictor*) has a reputation for speed, but its maximum sprinting speed has been recorded as only 1.5 metres per second (Bonine & Garland, 1999).

Climbing

Concertina locomotion enables snakes to climb vertical rock crevices and grooves in the trunks of trees. The folds of the body press strongly against the walls of a crevice, to secure a frictional grip to prevent falling. In addition, the ventral scales may be raised so as to increase the frictional resistance against downward sliding (Marvi & Hu, 2012). A form of concertina locomotion is also used to crawl along slender branches. The folds of the body zigzag across the upper surface of the branch, and occasionally wrap right round it (Astley & Jayne, 2007). To bridge gaps between branches, a large proportion of the length of the body may have to be extended as a cantilever, and large forces may be needed in muscles to prevent it from sagging. Small snakes can bridge the widest gaps relative to body length (Jayne & Riley, 2012).

Lizards on slender branches cannot adopt the sprawling posture used on broad substrates, but must keep their feet under the body to grip the branch. Chameleons, which spend much of their time on slender branches, keep their feet constantly under the body, not out to the side. On broad supports that they cannot grasp, Malagasy dwarf chameleons (*Brookesia*) steady themselves by resting the tail on the substrate (Boistel et al., 2010).

Geckos have strongly adhesive feet that enable them to climb smooth vertical walls. They adhere by means of van der Waals forces (forces of intermolecular attraction) that depend on very close contact with the substrate. The close contact required is obtained by having the soles of the feet covered by a carpet-like pile of setae so fine that they can be seen only by electron microscopy. Though the feet adhere so strongly, the lizard can easily detach them from the wall that is being climbed, by peeling them off like medical adhesive plasters (Autumn et al., 2000).

Jumping

Some lizards make quite impressive jumps. For a satisfactory landing, the body must be at an appropriate angle to the horizontal at the end of the jump. Lizards use tail movements to achieve this (Libby et al., 2012). This depends on the Principle of Conservation of Angular Momentum, the principle that enables divers to initiate manoeuvres such as somersaults in mid-air. Rotation of the lizard's tail or the diver's limbs in one direction, makes the body rotate in the opposite direction. Lizards whose tails had been removed did not make satisfactory landings when they jumped. If a climbing gecko falls, it uses mid-air tail movements to ensure that it lands right way up (Jusufi et al., 2008).

Arboreal lizards may jump between flexible branches. It might be imagined that the elasticity of the take-off branch might make longer jumps possible, by functioning like a springboard. This is not the case because branches do not generally recoil quickly enough to assist the lizard's takeoff. Lizards can jump further from rigid supports, than from compliant branches (Gilman et al., 2012).

Gliding

Lizards of the genus *Draco* live in forests in India and SE Asia. They travel from tree to tree by gliding, using flaps of skin supported by extensions of their ribs as wings. These are spread while the lizard is gliding; but folded like fans, against the sides of the body, while it is climbing a tree. *Draco* also have smaller wing-like structures on either side of the throat. A glide starts with a steep dive, in which the lizard gathers speed, then flattens out a bit as increasing speed enables the wings to generate more aerodynamic lift. Finally, the lizard may veer upward again to reduce its speed before landing. McGuire & Dudley (2005) induced *Draco* of various species to glide between two poles 9.3 metres apart. In the best of many trials, the angle of descent from the take-off point on one pole to the landing point on the other was 15°. This performance is poor, compared with birds; for example, the minimum equilibrium glide angle of common swifts is 5° (calculated from the maximum lift-drag ratio given by Henningsson & Hedenström, 2011). This comparison is admittedly not a fair one, and may be misleading, as the angle given for swifts referred to equilibrium gliding, not a glide between perches. The ability of *Draco* to land on a target perch shows that it has good control of its glide.

Amazingly, snakes of the genus *Chrysopelea* also glide from tree to tree or tree to ground, in S and SE Asia. As the snake takes off, it flattens its body and performs high-amplitude lateral undulations. After an initial steep dive the angle of descent decreases. The minimum recorded glide angle in the later part of a glide is 13° (Socha, 2011).

Swimming

Snakes swim like eels (but with their snouts above the water), and crocodiles also swim by undulating their bodies. Marine turtles have legs modified as flippers, and swim by flapping them much as a flying bird flaps its wings. This seems to be more efficient, than if the flippers were used like oars. Some turtles can swim quite fast, for example a young *Chelonia mydas* with a carapace only 11cm long swam at a maximum speed of 1.4 metres per second (Davenport et al., 1984).

Running on water

Tropical American lizards of the genus *Basiliscus* can run short distances on their hind legs, on the surface of water. They slap their large feet down on the water at high velocity. This supports them by a combination of three effects. First, the initial slap accelerates a substantial mass of water downwards and so gives rise to an upward reaction on the body. Secondly, upward hydrodynamic drag acts on the foot as it moves down into the water. And thirdly, the foot makes a temporary air-filled hole in the water, which is not re-filled until the foot is withdrawn. While the foot is in the hole, its upper surface is exposed only to atmospheric pressure, while its lower surface is exposed in addition to hydrostatic pressure (Glasheen & McMahon, 1996).

"Swimming" through sand

Scincus scincus, a desert lizard, buries itself and "swims" in dry sand. While it is submerged in the sand, it is of course hidden from view. Baumgartner et al. (2008) used nuclear magnetic resonance imaging to study *Scincus* moving through desert sand. They observed waves of bending travelling backwards along the body, accompanied by leg movements like those of running lizards. They suggested that the lizard's movements caused decompaction of the sand around it, making the sand behave like a viscous liquid. This would help to explain the lizard's ability to travel quite fast through the sand, at up to 0.3 metres per second. In another investigation, Maladen et al., (2009) used X-ray imaging to film Scincus "swimming" through fake sand made of glass particles. They found that the lizards' legs were folded flat against their sides while waves of bending travelled backwards along the body. I am unable to explain why one group found that leg movements were used while the other found that they were not.

REFERENCES

Alexander, R. Mc Neil. (2003). *Principles of Animal Locomotion*. Princeton University Press, Princeton.

Astley, H.C. & Jayne, B.C. (2007). Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (*Elaphe guttata*). *J. Exp. Biol.* 210: 3862-3872.

Autumn, K., Liang, Y.A., Hsieh, S.T., Zesch, W., Chan, W.P., Kenny T.W., Fearing, R. & Full, R.J. (2000). Adhesive force of a single gecko foot hair. *Nature* 405: 681-685.

Baumgartner, W., Fidler, F., Weth, A., Habbeke, M., Jacob, P., Butenweg, C. & Bohme, W. (2008). Investigating the locomotion of the sandfish in desert sand using NMR imaging. *PLoS ONE* 3 (10) e3309. doi: 10.1371/journal.pone.0003309.

Boistel, R., Herrel, A., Daghfous, G., Liboural, P., Boller, E., Tafforeau, P. & Bels, V. (2010). Assisted walking in Malagasy dwarf chamaeleons. *Biology Letters* 6: 740-743.

Bonine, K.E. & Garland, T. (1999). Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J. Zool.* 248: 255-265.

Bradshaw, S.D. & Main, A.R. (1968). Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *J. Zool.* 154: 193-221.

Clemente, C.J., Withers, P.C., *T*hompson, G. & Lloyd, D. (2008). Why go bipedal? Locomotion and morphology in Australian agamid lizards. *J. Exp. Biol.* 211: 2058-2065.

Davenport, J., Munks, S.A. & Oxford, P.J. (1984). A comparison of the swimming of marine and freshwater turtles. *Proc. Roy. Soc. B* 220: 447-475.

Full, R.J. & Tu, M.S. (1991) Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *J. Exp. Biol.* 156: 215-231.

Gilman, C.A., Bartlett, M.D., Gillis, G.B. & Irschick, J. (2012) Total recoil: perch compliance alters jumping performance and kinematics, in green anole lizards (*Anolis carolinensis*). *J. Exp. Biol.* 215: 220-226.

Glasheen, J.W. & McMahon, T.A. (1996). A hydrodynamic model of locomotion in the basilisk lizard. *Nature* 380: 340-342.

Henningsson, P. & Hedenström, A. (2011). Aerodynamics of gliding flight in common swifts. *J. Exp. Biol.* 214: 382-393.

Hu, D.L., Nirody, J., Scott, T. & Shelley, M.J. (2009). The mechanics of slithering locomotion. *Proc. Nat. Acad. Sci.* 106: 10081-10085.

Jayes, A. S. & Alexander, R. McN. (1980). The gaits of chelonians: walking techniques for very low speeds. *J. Zool.* 191: 353-378.

Jayne, B.C. & Riley, M.A. (2012). Scaling of the axial morphology and gap-bridging ability of the brown tree snake (*Boiga irregularis*). *J. Exp. Biol.* 210: 1148-1160.

Jusufi , A., Goldman, D.I., Revzen, S. & Full, R.J. (2008). Active tails enhance arboreal acrobatics in geckos. *Proc. Nat. Acad. Sci.* 105: 4215-4219.

Libby, T., Moore T.H., Chang-Su, E., Li, D., Cohen, D.J., Jusufi, A. & Full, R.J. (2012). Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature* 481: 181-184.

Maladen, R.D., Ding, Y., Li, C. & Goldman, D.I. (2009). Undulatory swimming in sand: subsurface locomotion of the sandfish lizard. *Science* 325: 314-318.

Marvi, H. & Hu, D.L. (2012). Friction enhancement in concertina locomotion of snakes. *J. R. Soc. Interface* in press.

McGuire, J.A. & Dudley, R. (2005). The cost of living large: comparative gliding performance in flying lizards (*Agamidae Draco*). *Am. Nat.* 166: 93-106.

Secor, S.M., Jayne, B.C. & Bennett, A.F. (1992). Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes. J. Exp. Biol.* 163: 1-14.

Socha, J.J. (2011). Gliding flight in *Chrysopelea*: turning a snake into a wing. *Integr. Comp. Biol.* 51: 969-982.

Webb, G.J. W. & Gans, C. (1982). Galloping in *Crocodylus johnstoni,* a reflection of terrestrial activity? *Rec. Austr. Mus.* 34: 607-618.