

FUNCTIONS OF THE TAIL IN BIPEDAL LOCOMOTION OF LIZARDS, DINOSAURS AND PTEROSAURS

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This paper investigates the reported decrease in speed that follows tail-loss in those lizards with actively functional tails. The balance function of the tail may be less important to the bipedal locomotion of lizards than was previously suspected. Instead it is possible that the tail has an important role in regulating stride frequency. These findings may shed some light on peculiarities of tail structure in dromaeosaurid dinosaurs and rhamphorhynchoid pterosaurs.

□ *Reptilia, Lacertilia, Theropoda, Pterosauria, bipedal locomotion.*

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Most investigations into the role of the tail in lizard locomotion have been concerned with the effects of tail removal on speed (Pond, 1978; Ballinger *et al.*, 1979; Punzo, 1982; Daniels, 1983; Table 1). Notable exceptions include Snyder's (1949) analysis of the role of the tail in bipedal locomotion, and Ballinger's (1973) investigation of its use as an aid to balance. Except for the gecko

(*Phyllodactylus marmoratus*) used by Daniels (1983), all the lizards used in those investigations were facultative bipeds and possessed what Vitt *et al.* (1977) have termed 'actively functional' tails.

Vitt *et al.* (1977) recognised two broad categories of tail function in lizards: passively functional tails, where function is primarily predator distraction via autotomy (e.g. *Phyllodactylus*), and actively functional tails that contribute to various activities such as fighting, climbing, terrestrial locomotion and swimming. Earlier studies (cited above) revealed that lizards with actively functional tails suffered a decrease in their maximum recorded speeds (by as much as 42%) following removal of the tail. By contrast, the gecko studied by Daniels (1983) almost doubled its average running speed following tail autotomy. Snyder (1949) did not report running speeds for his animals. However, he did show that abbreviation of an animal's tail impaired its bipedal ability: removal of the posterior third of the tail resulted in the lizard being unable to complete more than three strides bipedally, and when the posterior two-thirds of the tail was removed the animal was unable to run bipedally at all. The general conclusion that has been drawn from these experiments is that the actively functional tail of a running lizard acts as an organ of balance, as well as a counterbalance mechanism that moves the animal's centre of gravity closer to the pelvis and closer to the force exerted by the hindlimb (Snyder, 1962; Ballinger *et al.*, 1979; Punzo, 1982). Because of the tail's seeming importance in locomotion, its retention

Author	Year	Tail Type	Effects of Tail Removal
Snyder	1949	AF	Impaired balance (unable to run bipedally)
Ballinger	1973	AF	Impaired balance (decreased perching ability)
Pond	1978	AF	Decrease in speed
Ballinger <i>et al.</i>	1979	AF	36% decrease in speed
Punzo	1982	AF	32% decrease in speed
Punzo	1982	AF	42% decrease in speed
Daniels	1983	PF	100% increase in speed
Daniels	1985	PF	18% increase in speed

TABLE 1: Summary of previous investigations into the role of the tail of lizard locomotion. AF = Actively functional tails; PF = Passively functional tails.

should be favoured in animals with actively functional tails (Vitt, 1983).

As part of a larger study of lizard locomotion I analysed the effects of partial tail loss on individuals of *Physignathus lesueurii*, the Eastern Water Dragon. These lizards are facultative bipeds attaining a snout-vent length up to 275mm. They have long tails which have a relatively low frequency of damage (see Vitt *et al.*, 1977 for an analysis of tail break frequencies), and where damage does occur it is usually restricted to the distal third of the tail.

METHODS

Locomotion in the water dragons was investigated by timing the animals as they ran along a specially constructed runway (Fig. 1). Each lizard performed a minimum of six trials on the runway, and during each trial two metres of smoked paper was placed on the floor of the runway to record the animal's footfalls. The smoked paper was later sprayed with acrylic lacquer to provide a permanent record, which was analysed with the aid of a Houston "Hi-Pad" digitizer.

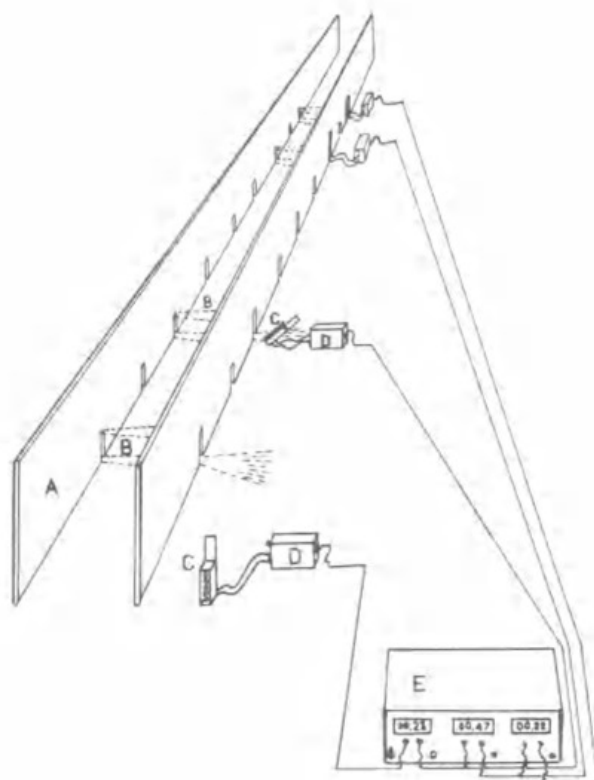


FIG. 1. Runway and timer mechanism. A = runway; B = light curtain; C = photosensitive diode array; D = electronic timer trigger; E = digital timer.

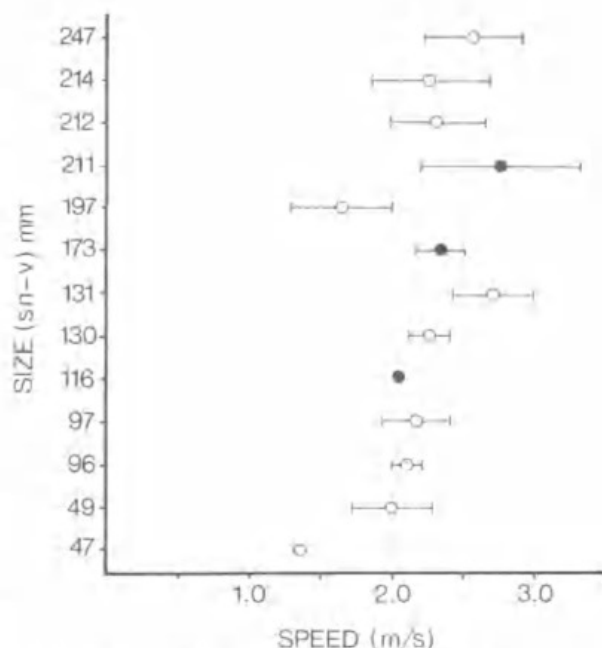


FIG. 2. Summary of locomotion data for *P. lesueurii*. The vertical axis gives the rank order of size (sn-v snout-vent length, in mm) and the horizontal axis gives the range of maximum speeds (m/s) attained by each lizard. (Closed circles denote animals with abbreviated tails).

RESULTS

The trackway results obtained for the water dragons are somewhat surprising in view of the previous studies; they provide evidence of bipedal ability in animals with as much as 40% of the tail missing. A consistent tripedal trackway was obtained from an animal that was estimated to have lost about 80% of its tail. Moreover, there was no evidence that the water dragons with damaged tails were any slower than animals with complete tails. In fact, the highest average speed recorded on the runway (3.3m/s) was achieved by a water dragon that lacked approximately 40% of its tail (Fig. 2).

DISCUSSION

Although the results shown in Fig. 2 seem to be inconsistent with those of earlier studies, the discrepancy may be explained quite simply. First, it is probable that the water dragons used in this study never achieved their maximum speeds while on the runway: most of the animals were still accelerating at the end of the trial section. Consequently it is possible that some animals might have suffered a reduction in maximum speed (as a consequence of tail loss) without it becoming

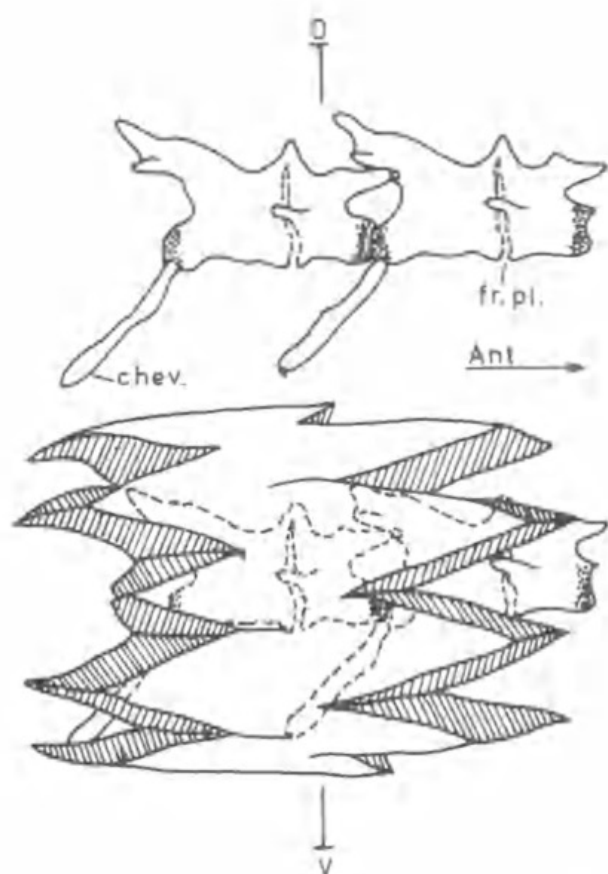


FIG. 3. Fracture planes in caudal vertebrae of autotomizing lizards and the segmental nature of caudal musculature; chev. = chevron; D = Dorsal; fr. pl. = fracture plane; V = Ventral (after Sheppard and Bellairs, 1972).

evident. Second, and perhaps more importantly, it seems that in attributing the recorded decrease in maximum speed in their animals to the fact that the centre of gravity was no longer positioned so close to the force exerted by the hindlimbs, both Punzo (1982) and Ballinger *et al.*, (1979) may have overlooked a simpler explanation. When carrying out their experiments these investigators apparently severed the animals' tails as near as possible to the vent (although this is not explicitly stated by Ballinger and co-workers in their paper). There is little doubt that tail removal in this way would affect the balance of the lizard. Here it should be remembered that the major femoral retractor muscles, the caudi-femoralis group, originate from the proximal 10 or 11 caudal vertebrae (Romer, 1922; Snyder, 1954). It seems unlikely that the tail could be removed just distal to the vent without severing some parts of this musculature, thus impairing the efficiency of

femoral retraction and impairing locomotor performance. Conversely, lizards that indulge in tail autotomy are unlikely to do so at the expense of the femoral retractor muscles. This is clear from the increase in speed of the gecko after tail autotomy and the consequent loss of a considerable fraction of body weight (Daniels, 1983). In fact, autotomizing lizards generally possess fracture planes in the post-pygial vertebrae (Sheppard & Bellairs, 1972; Holder, 1960; Pratt, 1946) and the muscles in this region show a corresponding pattern of segmentation (Fig. 3). In this case the femoral retractor muscles must attach to the pygial vertebrae which are usually the first four or five of the caudal series.

It should also be noted that the investigators mentioned above used their animals within 48 hours of tail removal, a procedure that was carried out in the laboratory. Snyder (1949), for example, allowed only 15-20 minutes ('... to obviate the shock of removal') between cutting off the tails of lizards and using the animals in trials (1949, p. 136). It seems unlikely that lizards with actively functional tails would be able to run normally so soon after traumatic tail loss. By contrast, the water dragons described here had lost their tails before capture and in each case the tail was well healed and showed signs of regrowth. This difference may explain why water dragons were able to run bipedally with as much as 40% of the tail missing whereas the lizards used by Snyder were unable to do so when a third of the tail was removed.

Despite the fact that neither bipedal ability nor speed appeared to be seriously affected by less than severe tail damage, one significant effect of tail loss in water dragons was evident from the trackway records: at any given speed animals with abbreviated tails were found to take shorter strides (and axiomatically to have increased stride frequencies) than animals of the same size with complete tails (Fig. 4). To understand the significance of this increase in stride frequency it is necessary to look more closely at the relationship between the hindlimbs and the tail in sprawling tetrapods.

During lizard locomotion lateral undulations of the vertebral column generate a standing wave in the trunk region of the body. The nodes of the wave are located at the pectoral and pelvic girdles (Brinkman, 1981; Hamley, 1986). Posterior to the pelvic girdle the standing wave is transformed into a travelling wave that moves caudally along the tail. The base of the tail is flexed towards the protracted hindlimb during each cycle of hindlimb movement (Fig. 5). Then, as the hindlimb is retracted, the

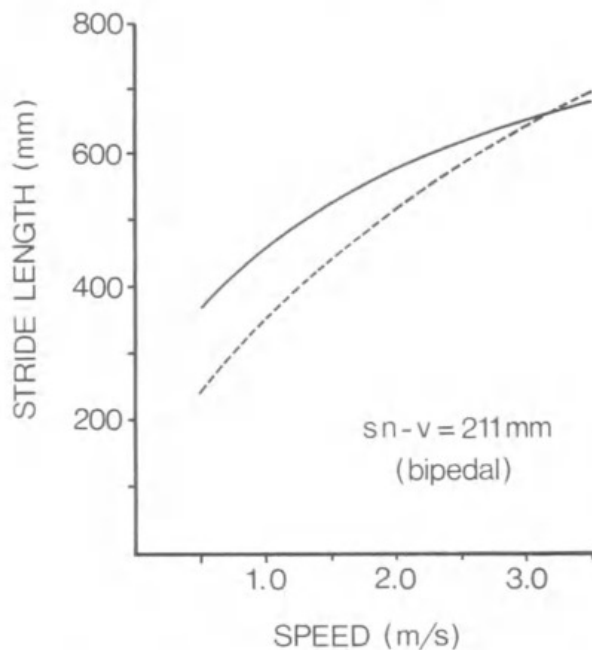


FIG. 4. Graph of stride length against speed for a lizard with partial tail loss (broken line) compared with a graph for a hypothetical animal of the same size with a complete tail (solid line).

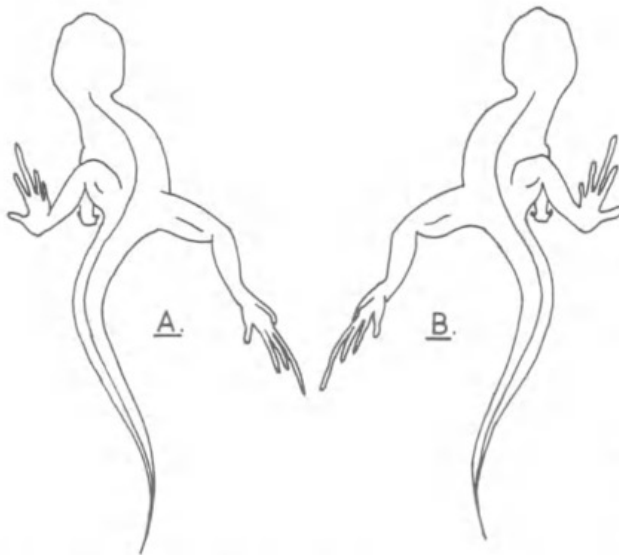


FIG. 5. Left (A) and right (B) hindlimb retraction showing extremes of tail flexion.

oscillation of the base of the tail to its opposite extreme supports what appears to be an isometric contraction of the caudi-femoralis musculature, presumably aiding in the most efficient use of the hindlimb retractor muscles. This mechanical coupling of hindlimb and tail means that the stride frequency and the frequency of tail oscillation must

be equal: changes in stride frequency require corresponding changes in the frequency of tail oscillation and vice versa. If the lizard's tail is considered to be a semi-rigid bar, attached at its proximal end, then the laws of simple harmonic motion will mean that:

1. When displaced laterally the tail will have a natural frequency of oscillation
2. This frequency will be dependent on both the rigidity of the tail (controlled by the segmented caudal musculature) and the length (mass) of the tail.

Hence, a lizard wishing to increase its stride frequency (and therefore its speed) during locomotion need only "stiffen up" its caudal musculature to achieve that effect. In addition, for a given degree of tail rigidity, a lizard with a damaged tail will have a higher frequency of tail oscillation (and, therefore, of stride frequency) than will a similar-sized lizard, with a complete tail, running at the same speed.

The relationship between tail length and stride frequency explains not only the observed increase in stride frequency for lizards with damaged tails, but also the commonly noted correlation between hindlimb length and tail length in cursorial lizards. Thus it can be seen that the tail of cursorial lizards contributes more to locomotion than simply acting as a counterbalance: by adjusting the frequency of tail oscillation (via the tension in the caudal musculature) cursorial lizards can use the simple harmonic motion of the tail as an aid to femoral retraction over a range of hindlimb stride frequencies. However, it should be noted here that stride frequency in lizards has a strong negative allometry when scaled against body mass (Hamley, 1986), which probably betrays an important size constraint in the functioning of such a system. Because of this size constraint, larger animals using caudi-femoralis musculature to retract the hindlimb need to be able to generate a high degree of tail rigidity to enable them to maintain a high stride frequency at reasonable energetic cost.

These findings have some interesting implications for the locomotion of extinct bipedal reptiles. Perhaps the most extreme ability to stiffen the tail was exemplified by the dromaeosaurid theropods *Deinonychus antirrhopus* (Ostrom, 1969 a,b) and *Velociraptor mongoliensis* (Barsbold, 1983). *Deinonychus* was a small (2m), agile predaceous dinosaur with a tail that comprised 36-40 segments and made up over half the length of the body. Ostrom (1969b) described the caudal skeleton as unremarkable in all respects except two: the prezygapophyses and chevrons of

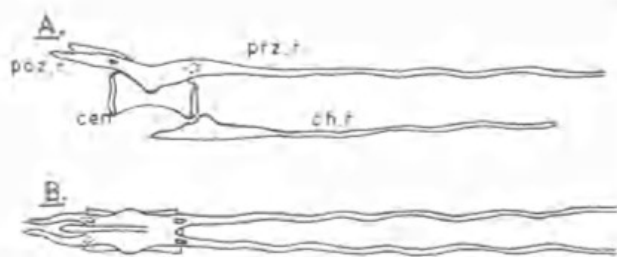


FIG. 6. Caudal vertebra of theropod dinosaur *Deinonychus antirrhopus* (after Ostrom, 1969b); prz. r. = prezygapophyseal rods; poz. r. = postzygapophyseal rods; cen. = centrum; ch. r. = chevron rods (A = right lateral view; B = dorsal view).

all but the proximal eight or nine segments were modified into extremely long bony rods that overlapped as many as ten preceding segments (Fig. 6). These bony extensions of the chevrons and prezygapophyses were nested together in such a way as to resemble the bundles of tendons that act as insertions for various caudal muscles in extant tetrapods. For example, the *M. extensor caudae lateralis* in lizards (such as *Iguana* and *Basiliscus*) inserts via bundles of tendons onto the extremities of the prezygapophyses, behind the fifth segment. As well, the long tendons of the *M. flexor caudae* in the above lizards and the *M. sacrococcygeus ventralis lateralis* in cats attach to the haemal arches in a way that is similar to the chevron rods of *Deinonychus*. These similarities, along with the periosteal-like histology of the rods, led Ostrom (1969b) to conclude that the caudal rods of *Deinonychus* were most probably ossified tendons.

Such bony rods would have served to stiffen the tail when extensor muscles attached to their anterior ends were contracted. However, the tail was not permanently inflexible, as is indicated by the presence of well-formed articular facets on the caudal vertebrae. What then was the function of a tail that could be stiffened to the degree indicated by the bony rods? In his descriptions of *Deinonychus*, Ostrom (1969a,b) suggested that the function of the caudal rods was to control the animal's equilibrium — that the stiffened tail of *Deinonychus* acted as a dynamic stabilizer, much like the balance pole of a tight-rope walker. Doubtless the tail of *Deinonychus* acted as a counterbalance, but it is also likely that the potential for extreme stiffening of the tail could have served to increase the natural frequency of tail oscillation, thereby allowing a greatly increased stride frequency. A predator such as *Deinonychus*

might have required a reasonable degree of speed and, perhaps more importantly, an extreme degree of agility — allowing it to use its clawed hindlimbs, either independently or in concert, in dealing with its prey. It is conceivable that *Deinonychus* mauled or eviscerated its prey in much the way that a cat will — kicking and slashing repeatedly at a particularly tenacious opponent. It seems possible that the synchronisation of movements between hindlimbs and tail could have hampered this ability and the extreme stiffness of the tail in *Deinonychus* might represent an evolutionary attempt to break that relationship. In fact, the constraints imposed by this relationship may well explain the change in hindlimb retractor musculature to the birdlike pattern seen in the more advanced theropod dinosaurs (Gatesy, 1987).

In addition to *Deinonychus* and *Velociraptor*, several genera of rhamphorhynchoid pterosaurs possessed bony caudal rods (Ostrom, 1969c). Ostrom's explanation of these rods (1969c) was that they may have allowed the kite-like vane at the end of the tail to act as an inertial stabilizer, thus implying a high degree of aerial manoeuvrability. Doubtless Ostrom is at least partly correct, but the presence of bony caudal rods may also have some bearing on the terrestrial mobility of rhamphorhynchoids. The cursorial ability of pterosaurs has been the subject of some controversy to date, with the main area of debate being the architecture of the pelvis and whether this indicated an 'erect' or 'sprawling' posture. Supporters of an erect posture suggest that pterosaurs were capable of fast and efficient movement, perhaps like dinosaurs (Padian, 1983). However, recent discoveries (Wellnhofer & Vahldiek, 1986; Molnar, 1987) indicate that a sprawling posture was more likely, and this has led Unwin (1987, p. 13) to conclude that "most, if not all, pterosaurs could manage only a clumsy waddle . . .". The identification of a sprawling posture with a clumsy inefficient style of locomotion is a common assumption, but not necessarily correct: the lizards investigated here are 'sprawlers' yet have a high degree of cursorial and scansorial ability. If the rhamphorhynchoids were agile bipeds, perhaps obliged to achieve a fast run before taking off, then their bony caudal rods may well have served to increase stride frequency through the relationship between hindlimbs and tail. The size constraints inherent in this relationship may also explain why the bigger pterosaurs dispensed with their tails altogether.

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