

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Webb, G. J. W., and C. Gans, 1982. Galloping in *Crocodylus johnstoni*—a reflection of terrestrial activity? *Records of the Australian Museum* 34(14): 607–618. [31 December 1982].

doi:10.3853/j.0067-1975.34.1982.244

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

Australian Museum science is freely accessible online at
www.australianmuseum.net.au/publications/
6 College Street, Sydney NSW 2010, Australia



GALLOPING IN *CROCODYLUS JOHNSTONI* — A REFLECTION OF TERRESTRIAL ACTIVITY?

GRAHAME J. W. WEBB

Department of Herpetology, The Australian Museum, Sydney, N.S.W.

(Present addresses: School of Zoology,

The University of N.S.W., P.O. Box 1, Kensington. N.S.W. 2033, Australia,

and Conservation Commission of the N.T., P.O. Box 38496, Winnellie, N.T. 5789.)

and

CARL GANS

Division of Biological Sciences, The University of Michigan, Ann Arbor,
Michigan 48109, U.S.A.

SUMMARY

Crocodylus johnstoni commonly gallop when released after being caught and handled. Galloping is a bounding gait and, in addition to increased velocities, it allows crocodilians to rapidly negotiate obstacles such as rocks and logs when on land. Bound length and gallop velocity both increase with increasing snout-vent length, but not in the same proportion: small *C. johnstoni* bound more frequently than larger ones.

INTRODUCTION

Although living crocodilians may spend appreciable portions of the day and night on land, the terrestrial excursions of most species rarely extend far from water. The observations of Cott (1961) that "when disturbed ashore a Nile crocodile's immediate reaction is to make for water with speed" may be applied to most crocodilians. Yet the suite of terrestrial movement patterns (belly slide, high walk and gallop; Cott, 1961; Zug, 1974) shows little sophistication. Typically a disturbed crocodile will burst into a rapid high walk or belly slide (depending on the slope of the bank), sometimes colliding with trees and rocks before hitting the water "with tremendous impact" (Cott, 1961) and submerging. Galloping, as a form of crocodilian terrestrial locomotion, has been observed rarely (Cott, 1961; Zug, 1974), and then only in juveniles.

During a field study of *Crocodylus johnstoni*, the endemic Australian freshwater crocodile, it was found that individuals surprised on banks, and about 80% of 250 juveniles and adults released after being marked, galloped back to the water. As the gallop is spectacular, and had hitherto rarely been described in crocodilians, the opportunity was taken to collect preliminary data on it.

During the dry season (May to November), *C. johnstoni* frequently inhabits a variety of permanent and temporary pools, and overland travel between them seems commonplace, although there is little quantitative data on the frequency of such excursions. This paper describes the movement and attempts to interpret the common use of galloping by *C. johnstoni* as part of an adaptive suite reflecting greater terrestrial activity.

METHODS

This study was carried out during August/September, 1978, along the McKinlay River (131°30'E; 12°55'S), a major tributary of the Mary River System in the Northern Territory. At this time, the McKinlay River consisted of a river bed containing isolated pools separated by stretches of sand and rock. Many of these pools contained *C. johnstoni*, as did the semipermanent billabongs (= lagoons or remnants of oxbows) on either side of the main stream bed.

The crocodiles were being caught as part of a study of growth and movement (G. W.) and most were taken at night with fine nets (Webb and Messel, 1977). Until morning, they were individually tethered in the water, with heavy cord tied around and through the jaws. They were then measured, weighed, sexed, numbered (by removing a sequence of caudal scutes) and released; no anaesthetics were used.

Specimens were released on flat or sloping banks, and were annoyed until they moved to escape. They usually moved freely when they could see the water, though in some situations they turned and attempted to bite and could not be induced to 'escape' at any speed. Two tapes, colour marked at 50 cm and 1 m intervals were usually placed along the escape route.

Water temperatures and body temperatures were between 28° and 31°C; air temperatures in the shade were usually between 34° and 38°C.

Analysis of movement is based on 40 sequences of galloping (asymmetrical movement; Hildebrand, 1966) performed by individual *C. johnstoni* between 23 and 107 cm snout-vent length (SVL; approximately half total length if the tail tip is complete). Using a Nizo 801 Macro Camera, fifteen sequences were filmed at 24 f.p.s. from various angles between 1400 and 1700 hr on a clear day with intermittent cloud cover. An additional 25 sequences were recorded on 35 mm film with a motor-driven (3.4 f.p.s.) still camera and 300 mm lens. For comparison, 12 sequences of symmetrical movement were filmed with the movie camera at both 24 and 56 f.p.s. The cine films were analysed frame by frame on a Kodak Ektagraphic MFS 8 analytical projector. The stills were printed, joined in sequence, and then analysed. Distances travelled by animals between individual frames were measured using both the dimensions of each crocodile (head length in particular) and the colour-coded tapes as reference scales. Statistical methods follow Zar (1974).

RESULTS

A. TERRESTRIALITY

During August/September 1978, 269 *C. johnstoni* were caught in the McKinlay River area. The catching was essentially restricted to permanent and temporary pools, and when not actually catching, little time was spent in the area. Still, the following observations indicate that terrestrial activity is not unusual:

1. While catching in the drying pools of the mainstream, tracks leading from one pool to another over distances between 100 m and 400 m were common.
2. On 4 September, 1978 at 2030 hr a female *C. johnstoni* (SVL = 68 cm) was located on a gravel hill 53 m from a permanent pool. It was high walking towards the pool when encountered, and after being caught and released, galloped for 15 m, then shifted to a symmetrical pattern until it reached a dry gulley (20 m further on) that was connected to the pool.



Fig. 1. A *C. johnstoni* (98 cm SVL) located 75 cm from water in the shade of a dry undercut bank.

3. On 24 August, 1978 at 1320 hr a male *C. johnstoni* (SVL = 98 cm) was located in shade beneath a dry undercut bank, 75 m from a temporary pool (Fig. 1). Tracks indicated that the individual had passed through this pool after leaving a permanent one 20 m further on where a much larger *C. johnstoni* was sighted.
4. On 30 August, 1978, 7 days after the crocodiles in a permanent pool had been caught, marked and released, a set of tracks was discovered directed away from this pool and heading upstream in the river bed. These were followed for 2½ km to the next permanent pool; on the way they entered and left two temporary pools.
5. On 3 September, 1978, two hatchling *C. johnstoni* (approx. 9 months old) were caught amongst dry sticks and flood debris, 25 m and 11 m from the bank of a permanent pool.

It is probably significant that all these observations were made during the dry season, there having been no rain for at least 5 months. The ground over which the animals travelled was parched.

B. MOVEMENT SEQUENCES

The literature suggests that crocodylians progress by three patterns when on land; (1) belly slide, (2) high walk, and (3) gallop (Cott, 1961; Zug, 1974; Webb, 1977). The first two are symmetrical and the other asymmetrical in the terminology of Hildebrand (1966). In a belly slide, a crocodylian propels itself downhill by undulatory movement. The limbs are usually folded back along the sides of the body, though the hind limbs may be used for the initial propulsion. The high walk is characterized by the lifting of the trunk, which is suspended between symmetrically moving limbs; the tail typically swings from side to side with the tip dragging. In a gallop, the hind limbs (and usually the forelimbs as well) move asymmetrically in time, the two sides moving in parallel in what is essentially a series of bounds or hops. The back arches vertically and the tail, which is more or less straight, moves up and down.

1. Belly slide. Our *C. johnstoni* did not practice belly sliding, but the surfaces they traversed were never more than 30° inclined to the horizontal, and were generally hard, dry and rough, consisting of caked sand, rocks and debris with some parts roughened by the dried spools of water buffalo (*Bubalus bubalis*). The belly slide actually consists of a walk in which the animal does not lift the trunk off the ground and assists propulsion by body undulation. At low velocities on firmer substrates, the belly slide is perhaps better described as a crawl.

2. High walk. The so-called 'high walk' proved much more diverse than previously described, particular sources of variation being the extent to which the trunk was levered off the ground, the extent to which the limbs were spread laterally, and the velocities attained. Analysis of the slowed down film sequences (particular some in which the animals were travelling towards the camera) documented substantial variability in the lateral and vertical excursions of the hindlimbs. If on slightly rough ground, the pace would differ from stride to stride and often the moving hindlimb would delay its forward travel for 0.05 to 0.10 sec and stabilize the posterior trunk while the anterior column was rotated toward the opposite side. Other variants involved the degree to which the trunk and girdles were bent, to which the hindlimb was rotated medially before firm contact with the ground, and the angles in the vertical plane, at which the limb segments were to each other, and to the trunk. Our records are not sufficient to characterize this variability in detail, though the following categories of high walk were evident:

a. *Classical high walk* — As described by Cott (1961) and Zug (1974), in which velocities are relatively low, the trunk is held high off the ground by the extended limbs and decidedly ventriflexed, and the limbs have little lateral spread.

b. *Running* — At higher (and lower) velocities when the trunk is carried lower, so that the hind limbs are not fully extended, they may begin cycling more irregularly and less frequently than the forelimbs. The body, driven by two symmetrically moving hindlimbs, is tilted downward between the driving strokes and upward during them. While the foot position is close to the centerline, the toes are not just placed into and rolled out of contact with the ground. Rather, there is significant slippage between the hindfeet and the ground.

3. Gallop. A run sometimes transforms itself into a gallop, in which both hindfeet hit the ground in parallel within a single stroke. This transformation is signalled by a shift in the angle of the trunk to the ground (becoming 15° to 20°), a lifting of the head (to 30° to the ground) and a folding and unfolding pattern of hindlimb movement (Fig. 2). Often however, the gallop is initiated from a resting position, the first movement being an asymmetrical bound.

The pattern of limb and trunk movements in a typical gallop sequence can be deduced from Fig. 2, in which the frequency of bounds is sufficiently out of phase with the (3.4 f.p.s.) filming rate that each frame represents a different stage of a bound. In a resting position, the femur is more or less horizontal (to the ground in lateral view), the tibia is vertical, and the tail is extended straight, horizontally and in contact with the ground. The initial bound is accomplished by a raising of the anterior body on the front legs, and a rapid unfolding of the hindlimbs such that the femur becomes more or less vertical and tibia horizontal. This unfolding of the limbs raises the acetabulum, an action which appears to be assisted by a marked ventriflexing of the tail (Fig. 2a). The last points of contact with the substrate are the tail tip and hind toes.

As the hindlimbs unfold, the forelimbs simultaneously move forward, first swinging outward, then tilting under the trunk (Figs 2a, b, c); an initial bound essentially terminates when the anteriorly directed forefeet make contact with the substrate. The forelimbs then bend slightly, decreasing the angle between the humeral and radio-ulnar portions, and rotate (Figs 2c, d, e) as the momentum continues to move the trunk forward on them (Figs 2c, d, e).

After the initial unfolding of the hindlimbs (Figs 2a, b), they are refolded and swung outward and anteriorly (Fig. 2c) before being unfolded again (Figs 2d, e). They are fully extended when they make contact with the substrate either next to or anteriorly to the point of contact of the forefeet (Figs 2d, e).

When the hindlimbs are leaving the ground (Figs 2a, b) the thoracolumbar vertebral column is often slightly dorsiflexed, extending the reach of the forelimbs. Following contact between the forelimbs and the substrate (Fig. 2c), the column is always ventriflexed, extending the hindlimb contact anteriorly.

Although the gallop appears more regular than the high walk, irregularities are noted. These are most pronounced within the first few bounds, or when a crocodile grades into or out of a gallop from a run, or when rough or broken terrain is encountered. Sometimes the forefeet make contact with the ground while still pointed posteriorly, in which case the head and thorax hit the substrate, and the animal temporarily collapses. Often the left or the right foreleg leads the other, such

that they are not truly in parallel. Sometimes the forefeet and hindfeet appear to leave the ground at the same instant, giving the impression that the animal is stotting, though this is uncommon. We repeatedly noted series of three to five bounds during which the head was gradually lowered. The next sequence incorporates a marked dorsiflexion of the anterior body. When confronted with either a rise in ground level or an obstruction, animals would often change their angle of attack to the ground by lifting the forequarters; they would then cantilever or propel themselves over the obstruction.

The mean velocities for individual crocodiles are shown on Fig. 3. These data are calculated from filmed (cine or motor drive) sequences of at least three bounds and include crocodiles travelling on a variety of substrates. The animals essentially chose their own path to the water, and the analysed sequences may or may not involve encounters with sand, rough terrain or obstructions. In 78% of sequences there was a definite acceleration after the first bound, though by the third bound, this was usually minimal. For example, the crocodile in Fig. 2 (the first two frames are not included on the figure) has a velocity profile of 14.3, 14.0 (both off sandy bank), 15.0, 16.4, 15.7 and 16.3 km/hr.

Figure 3 shows the relationship between velocity and size. Analysis of variance indicates the correlation is significant at the 0.1% level (Fig. 3; $r^2 = 0.42$). Velocity (V) in km/hr can thus be predicted from snout-vent length (SVL) in cm using the formula: $V = 7.33 + 0.0818 \text{ SVL} \pm 1.78 \text{ km/hr}$ (standard error of estimate; Zar, 1974). Relative to body length, the distance covered per bound remains relatively constant (1.3 SVL; Figure 4; $r^2 = 0.86$), the absolute length of each bound increasing with SVL. Bound length (B) in cm can be predicted from SVL in cm using the formula: $B = 1.90 + 1.26 \text{ SVL} \pm 8.2 \text{ cm}$ (S.E.E.).

Using the above formulae it can be shown that small crocodiles bound more frequently than larger ones when galloping. For example, a 30 cm SVL *C. johnstoni* could be expected to gallop at $9.8 \pm 1.8 \text{ km/hr}$, with a bound length of $39.7 \pm 8.2 \text{ cm}$; it would need 6.8 bounds/s. An 80 cm SVL *C. johnstoni* would only need 3.8 bounds/s to be galloping at its velocity of $13.9 \pm 1.8 \text{ km/hr}$; bound length = $102.7 \pm 8.2 \text{ cm}$.

The higher correlation values for bound length ($r^2 = 0.86$) than velocity ($r^2 = 0.42$) suggest that adjustment to rough terrain involves variations in propulsion forces during contact rather than changes in the distance travelled per bound.

Our observations suggest that the movements grade into each other. However, there is a bimodal distribution of velocities, with the crawl and classical high walk being used for slow locomotion, and the run and gallop for fast locomotion, with occasional intermediates.

DISCUSSION

A. TERRESTRIAL ACTIVITY

Crocodylians emerge from the water for a variety of reasons, though such emergences are usually restricted to the immediate bank area. This implies that the biological roles of emergence can be satisfied there, which would appear the case with basking, skin drying and short-term escape from other crocodiles in the water (aggressive dominant animals or potential predators).

More protracted demands are imposed during nesting activities, when

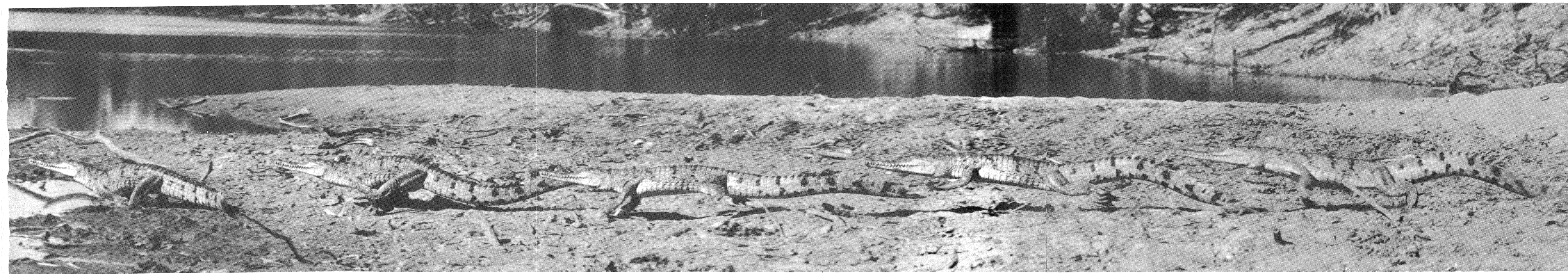


Fig. 2. *C. johnstoni* (107 cm SVL) galloping along a sand bar. The speed of the motor-drive (3.4 F/s) was sufficiently out of phase with the bounds to demonstrate the sequence of limb movements. From right to left, a to e.

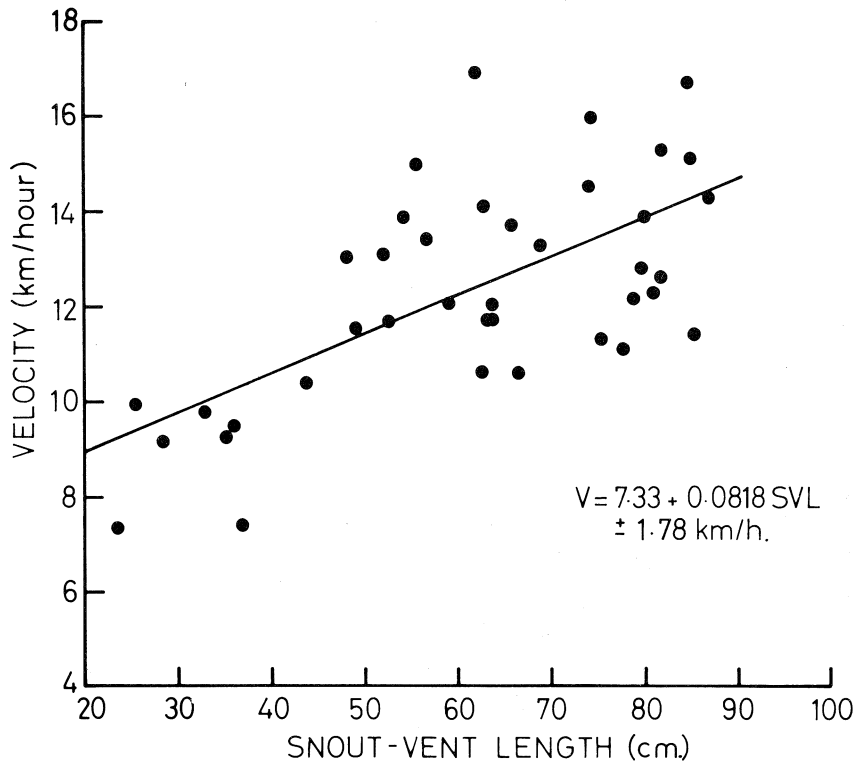


Fig. 3. The relationship between velocity and snout-vent length in galloping *C. johnstoni*.

crocodilians move overland to locate suitable nesting sites, usually within 100 m of permanent water. They continually circle the nest during construction, and may regularly visit the nest during incubation (see for example Cott, 1961; Neill, 1971; Pooley and Gans, 1976; Staton and Dixon, 1977; Webb *et al.*, 1977).

Most crocodilians seem to have the ability to traverse long distances (1 km +) over dry parched country. This permits some species to return to permanent water from areas in which they may have become stranded during floods (e.g. *C. niloticus*; Cott, 1961); however, in others, it is a more regular occurrence and permits them to utilize temporary, seasonally filled bodies of water which may otherwise be unavailable. Such water sources may offer refuges to socially displaced or disturbed individuals, and be a source of concentrated food as water levels recede (see Staton and Dixon, 1975; Gorzula, 1978; pers. observations).

Finally, terrestriality may be associated with foraging. Crocodilians will travel overland to carcasses of dead animals (Pooley and Gans, 1976; pers. observations), and may themselves hunt prey on land, although there are few records of this; *C. porosus* for example has been found on land beneath flying fox colonies, and once approaching a snake moving on an exposed mud bank.

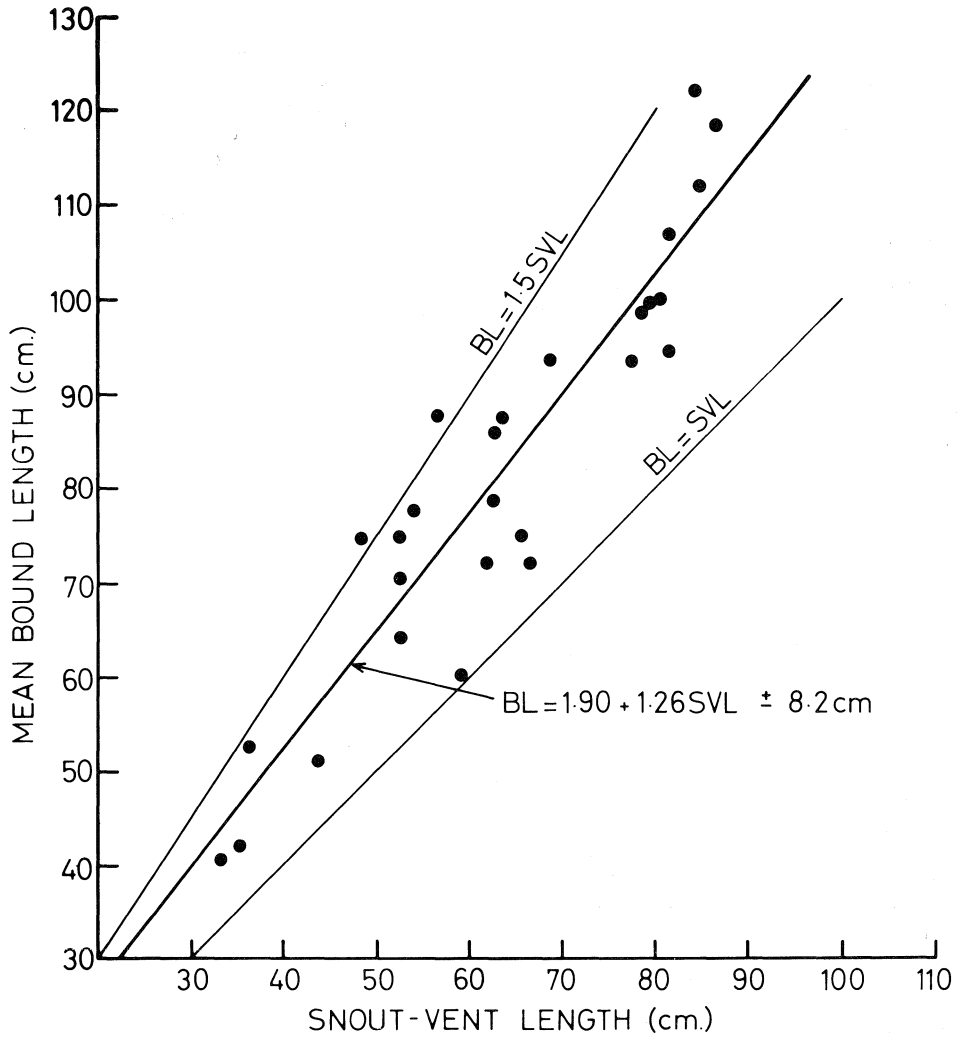


Fig. 4. The relationship between bound length and snout-vent length in galloping *C. johnstoni*.

Most crocodylians that have been studied exhibit terrestriality of the above-mentioned type; however, it appears that few crocodylians show specializations for the utilization of isolated bodies of temporary water in hot dry country. *Caiman c. crocodilus* (Staton and Dixon, 1977; Gorzula, 1978) and possibly *Crocodylus palustris* (Whitaker, pers. comm.) appear to be such exceptions, as is *Crocodylus johnstoni*. Observations indicate that *C. johnstoni* is appreciably more terrestrial than the narrowly sympatric *C. porosus*. In the habitat of the former in Northern Australia there is abundant water during the floods of the wet season (November to May). As the dry season progresses the bodies of water shrink, and overland travel between temporary and/or permanent pools or streams appears common.

Greater terrestriality of the type exhibited by *Crocodylus johnstoni* could be expected to enhance selection for a more extensive motor repertoire, as the animals require several modes of progression. There is a need for a slow steady (perhaps intermittent) walk for travelling overland without the animals being forced onto the glycolytic pathway. The trunk must be held high above the substrate when traversing areas with broken rocks and flood debris, and, more recently, those roughened by buffalo spoor. The high walk meets these requirements. However, predators, now including man, force the crocodiles to cross such terrain rapidly. Speed, coupled with the ability to negotiate obstructions, such as rocks and logs, is then advantageous.

B. GAITS

The fact that we failed to observe the belly slide in *Crocodylus johnstoni* in the McKinlay River probably means only that the animals in question were not tested on suitable substrates. The mud banks occupied by *C. porosus* on the tidal rivers facilitate slippage and the few *C. johnstoni* in such areas do belly slide (personal observations and H. Messel, pers. comm.).

During the classical high walk, the limbs place the feet under or close to the centreline of the body so that the foot remains in contact with the ground during the power stroke, which is fore to aft. However, this rotation of the pelvic girdle and the concomitant undulation of the trunk only occurs when the trunk is lifted fairly high; it is also seen when a crocodile is running. When the trunk is raised only slightly (when crawling in contrast to belly-sliding) the limbs are more straddled and there is little vertebral undulation. Use of either the classical highwalk (slow), the run (fast), or an intergrade, is probably a reflection of the speed required in a particular situation.

The gallop clearly allows increased speed over irregular surfaces. A single stride is slightly longer than the snout-vent length, but varies with the slope and regularity of the terrain (and perhaps the amount of slide after impact). Maximal galloping velocities observed were in the order of four times those of slow high walks, and twice the velocities of a fast high walk (or run). Due to a computational error, the galloping velocities reported by Zug (1974) were in error by an order of magnitude (Zug, pers. comm.). A most important aspect of the gallop however, is that it allows the animals to leap or bound over obstructions such as logs, rocks or small gullies. Such obstacle negotiation often requires an irregularity in a sequence of gallops; the bound length immediately before an obstacle may be reduced, and the subsequent power stroke is delivered in a more vertical direction that allows clearing of the obstacle.

An interesting aspect of rapid locomotion in *C. johnstoni* is the variability associated with it. Thus a crocodile may gallop from a resting position (more usual), or

begin a fast high walk which is gradually transformed into a gallop. Even when galloping, the limb placement can alter, particularly where irregular surfaces are being negotiated. In a number of cases released *C. johnstoni* could not be induced to elicit any rapid escape behaviour (gallop or fast high walk). Such reluctance has not been observed in the wild, and was presumed to reflect the physiological state of the animal. The lactate build up during the capture process could take more than twelve hours to drop to normal levels (compare with Bennett and Dawson, 1977). A further possibility is that in the wild, most long distance terrestrial excursions seem to take place at night (as with *Caiman c. crocodilus*; Staton and Dixon, 1977; Gorzula, 1978), whereas all our animals were released during the day, mostly in bright sunlight.

It would seem important to note that selection on crocodilian motor systems most likely matches the aquatic aspects of their niche. Consequently, adaptations specifically for terrestriality must represent an adaptive compromise between two rather extreme roles. Limbs of crocodilians must have proportions consistent with their use in maintaining the animal in the more usual 'shallow edge of the bank' posture, and must be able to be folded against the trunk during the undulating movements associated with swimming; they are rather short for an effective gallop.

Finally, there are a number of aspects of crocodilian galloping which are unclear. Is the capacity to gallop a recent development, or an ancestral one? It may well be that the majority of extant crocodilians can gallop if placed in the type of environment in which *C. johnstoni* are found in the McKinlay River, although *Caiman crocodilus* and *Crocodylus palustris* appear to live in similar habitats and have not been observed galloping (Dixon and Whitaker, pers. comm.). Thousands of observations of locomotion of *C. porosus* in the tidal areas of Northern Australia have revealed only a few which galloped; Zug (1974) filmed *C. porosus* galloping in New Guinea. Fossil evidence has been used to suggest that galloping was extremely well developed in some crocodilians. Thus, Walker (1970) concluded from limb structure that the Upper Jurassic *Hallopus victor* had a "hare-like bounding gallop" as its most probable form of fast locomotion.

Unfortunately, there is a scarcity of information on locomotory patterns of extant crocodilians in the wild, and it is thus not possible to be certain that the regular use of galloping by *Crocodylus johnstoni* is as unique as it would appear. However, the results do indicate the utility of and need for further research on crocodilian locomotory behaviour. Then perhaps, it will be possible to determine whether or not there are structural correlates associated with galloping in extant crocodilians.

ACKNOWLEDGMENTS

We are grateful to the Conservation Commission of the Northern Territory and the Australian Research Grants Committee for funding the research on freshwater crocodiles, of which this paper forms a part. Ross Sadlier, Phil Hauser, John Barker, David Lindner and Stephanie Bush assisted with this study. The work of Gans was supported by participation in a U.S./Australia Co-operative Science Project at the Department of Zoology of the University of Western Australia, and by a John Simon Guggenheim Memorial Fellowship. James Dixon and Romulus Whitaker supplied observations on *Caiman crocodilus* and *Crocodylus palustris* respectively. Harry Messel and George Zug provided useful comments, and we thank Harry Messel for the opportunity to view crocodiles in some tidal situations. We are grateful to Dave Lindner for his cordial guidance and hospitality while in the field and at Berrimah.

GALLOPING IN *CROCODYLUS JOHNSTONI*

REFERENCES

- Bennett, A. F. and W. R. Dawson 1977. Metabolism. In "Biology of the Reptilia." (C. Gans and W. R. Dawson, eds.). Academic Press, London, 5(3): 127-223.
- Cott, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile, *Crocodylus niloticus*, in Uganda and Northern Rhodesia. *Trans. Zool. Soc. Lond.*, 29(4): 211-311.
- Gorzula, S. J. 1978. An ecological study of *Caiman crocodilus crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. *Oecologica*, 35: 21-34.
- Hildebrand, M. 1966. Analysis of the symmetrical gaits of tetrapods. *Folia Biotheor.*, 6: 9-22.
- Neill, W. T. 1971. The last of the ruling reptiles: alligators, crocodiles and their kin. Columbia Univ. Press, New York, 486 pp.
- Pooley, A. C. and C. Gans 1976. The Nile Crocodile. *Scient. Amer.* 234(4): 114-124.
- Staton, M. A. and J. R. Dixon 1975. Studies on the dry season biology of *Caiman crocodilus* from the Venezuelan Llanos. *Mem. Soc. Cienc. Nat. La Salle* 35: 237-265.
- Walker, A. 1970. Studies of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. *Phil. Trans. Roy. Soc. Lond.*, Ser. B., 257: 323-372.
- Webb, G. J. W. 1977. The natural history of *Crocodylus porosus*, II. Growth, movement, river distributions and general comments. Chapter 15 in "Australian Animals and their Environment." (H. Messel and S. T. Butler, eds.). Shakespeare Head Press, Sydney, pp. 285-312.
- Webb, G. J. W. and H. Messel 1977. Crocodile capture techniques. *J. Wildlife Manag.* 41(3): 572-575.
- Webb, G. J. W., H. Messel and W. Magnusson 1977. The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. *Copeia*, 1977 (2): 238-249.
- Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N. J.
- Zug, G. R. 1974. Crocodilian galloping. An unique gait for reptiles. *Copeia*, 1974 (2): 550-551.