OBSERVATIONS ON THE AQUATIC LOCOMOTION OF YOUNG SALT-WATER CROCODILES (*CROCODYLUS POROSUS* SCHNEIDER)

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ABSTRACT

Swimming behaviour of young salt-water crocodiles was studied in capitivity by analysis of video films. Resting postures in fresh and salt water, escape responses, jumping and food handling behaviour were investigated.

INTRODUCTION

Although the terrestrial gaits of crocodilians have attracted much attention (see Frey, 1984 for review), their locomotion in water has been less studied. Fish (1984) has investigated the undulatory fast swimming of the American alligator, *Alligator mississippiensis*, while Turner, Tracy, Weigler and Baynes (1985) have correlated burst swimming speed with temperature in the same species. No detailed descriptions of swimming and associated behaviours in true crocodiles appear to have been published, and slow swimming in all crocodilians seems to have been ignored.

The availability of young salt-water crocodiles, *Crocodylus porosus*, in these laboratories, allowed the study of slow, medium and fast swimming in one of the most aquatic of living crocodilians. Resting postures in fresh and salt water, escape responses, jumping and food handling behaviour were also filmed and analysed.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Hatchling *Crocodylus porosus* were supplied by the Conservation Commission of the Northern Territories. They were held in running fresh water at 30°C and fed routinely upon chopped whole fish or squid. Occasionally they were given live food (cockroaches, crickets, shrimp or small crabs). Filming took place intermittently over several months during which period the animals ranged in weight from 70-220 g.

FILMING

All locomotion was filmed with a Panasonic F10 videocamera fitted with a 'high speed' shutter. Such shutters store an image for only 0.001 s during each video field, so freezing movement much more effectively than with a normal video camera. However, the video field frequency (25 fields s^{-1}) is unchanged and filming is only possible under conditions of bright lighting.

Crocodiles were filmed in a large plate glass tank (120cm long, 40cm high, 30cm wide) filled normally with fresh water at 30°C (occasionally sea water was used instead to investigate posture in a medium of greater density). The tank had a 2cm grid marked on the base and one of the long sides; these were backed with paper of neutral colour. The tank was illuminated from above and from each end to minimise shadow formation. The standard zoom/macro lens of the camera system was used, and the camera was mounted either 2m from the side of the tank or 1.5m above the water surface.

PROTOCOL

Swimming crocodiles were filmed from above, from the side and from head on to allow a 3 dimensional picture of locomotion to be constructed. In most cases the animals were allowed to swim spontaneously, but to achieve maximum speed animals were chased with the hand, or briefly restrained.

To study resting postures in fresh water and sea water, crocodiles were left until they quietly floated at the surface in fresh water; they were filmed continuously for about 15 minutes. They were then transferred to sea water and the process was repeated.

To study escape responses, the crocodiles were allowed to settle down in the tank so that they floated at the surface. Any sudden movement above the tank induced an escape reaction. To investigate behaviour during food capture, the animals were offered large cockroaches, some struggling in water, but others climbing on the walls of the tank well above the water surface.

ANALYSIS OF VIDEOTAPE

Motion was analysed by placing acetate sheets over the screen of the video monitor and making fine felt tip drawings from arrested video fields. The 2cm grid background allowed precise positional, size and distance data to be collected.

RESULTS

SWIMMING

When swimming slowly (<0.5 body lengths s⁻¹) the crocodiles use all four limbs, but with little tail motion. Each limb performs a simple drag-based propulsive cycle (Fig. 1). During the effective stroke the digits of the limb are spread to deploy the web (much larger in the case of the hind limbs) which is then pushed backwards at right angles to the direction of swimming (Fig. 2). At the end of the effective stroke the web is folded and brought forward in a recovery stroke. The limbs are synchronised ipsilateraly, so that one forelimb and the hindlimb on the opposite side of the body are on the effective phase of the limb stroke, while the other limbs are recovering (and vice versa). This low speed paddling, of typical tetrapod pattern, gives a steady speed as there is no period when propulsive power is not being generated.

Medium speed swimming (0.5-1.6 body length s⁻¹) is provided by combined action of the tail and limbs (Fig. 3). Propulsive waves pass rearwards along the tail with progressively increasing amplitude.

Fig. 2 A. Detail of movement of right rear limb (viewed from beneath) during slow swimming. Fields 1-6 represent the recovery stroke; fields 7-15 represent th effective stroke. B. Summary of timing of rear limb cycle; numerals represent successive video fields (0.04 s apart). Scale bar = 4cm.

Fig. 3 Medium speed swimming in *Crocodylus porosus* filmed from above. Numbers represent video fields (in this case 0.08 s apart; intermediate fields were omitted for clarity).
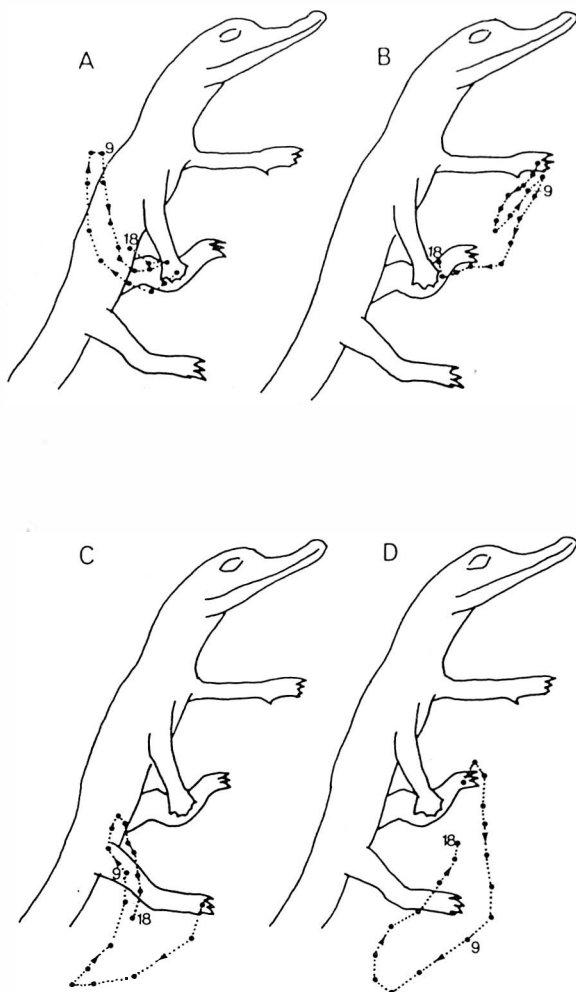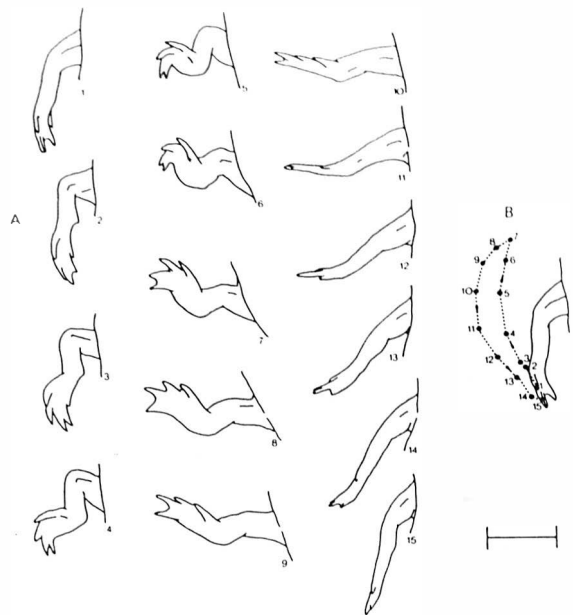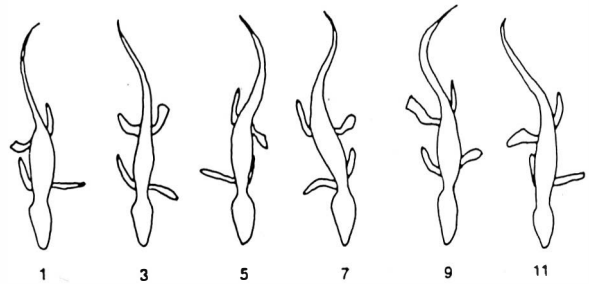

Fig. 1 Slow swimming in a specimen of *Crocodylus porosus* ascending from the bottom of a tank. Dotted lines indicate movements of each limb. Numerals refer to video fields (0.04 s apart) following the drawings (all made at field 1).

Faster swimming (1-2 body lengths s⁻¹) is accomplished by the propagation of travelling waves along the body and tail, all limbs being held immobile and close to the body to minimise drag (Fig. 4 A-E). Although it is obvious from this figure that the tail provides the bulk of the propulsion, it is also evident that the propulsive wave originates in the body anterior to the pectoral girdle, and is not simply a post-pelvic wave as described for the alligator by Fish (1984). Table 1 illustrates the relationship between crocodile swimming speed and the speed of propagation of the travelling wave along the tail. In all cases the propulsive wave travels rather more quickly than the animal's swimming speed. At least half to one wavelength (λ) occurs within the tail length at all times and the wave is not truly sinusoidal, since the amplitude increases (and λ decreases) towards the tip of the tail. These observations are in agreement with Fish (*op. cit.*) for *Alligator mississippiensis*.

When accelerating rapidly from a slow swimming mode to a fast swimming mode, the crocodiles sometimes go through a brief episode of combined tail beat and hindlimb paddling, but with immobile forelimbs; this lasts for no more than 2-3 leg beats before the fast swimming configuration supervenes. During deceleration the animals either progressively move from fast to medium to slow swimming, or they brake abruptly by extending all 4 limbs with spread webs.

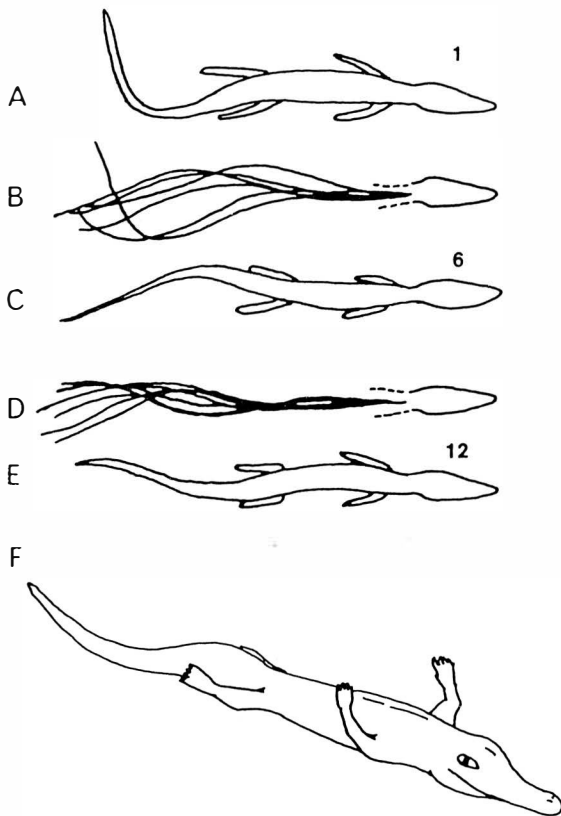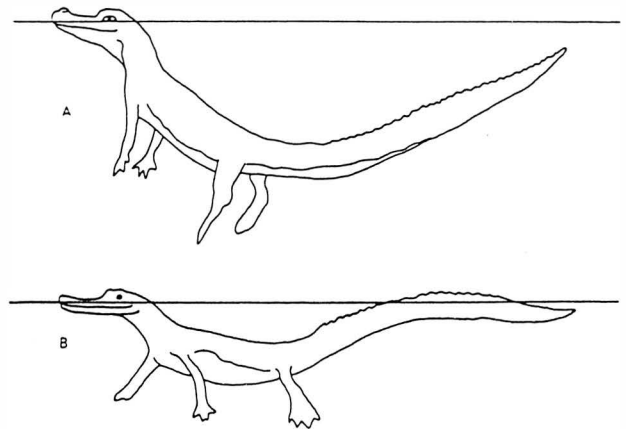Fig. 5   Surface resting postures of *Crocodylus porosus*. A. In fresh water. B. In sea water.

Fig. 4   Fast swimming in *Crocodylus porosus*. A. Posture at video field 1 (filmed from above). B. Drawing to show position of the midline of tail and body in video fields 1-6. C. Posture in video field 6. D. Drawing to show position of the midline of tail and body in video fields 6-12. E. Posture in video field 12. Interval between fields = 0.04 s. F. Posture of fast swimming *Crocodylus porosus* in shallow dive. Note raised fore limbs.

SURFACE RESTING POSTURE

The surface resting posture of young crocodiles is shown in Fig. 5. This posture is very common in hungry animals (presumably because it allows them to spot insects, fiddler crabs or mudskippers in the wild); recently fed animals usually rest on the bottom. In fresh water the top of the head is held out of water so that the eyes and nostrils are exposed. The body is held at about 45° to the horizontal and the tail projects upwards but does not reach the water surface. All four limbs are extended below the body, the hindlimb webs being widely spread (in preparation for the escape response — see below). In still water the crocodiles remain motionless between breaths. When the animal

Fig. 4F illustrates the posture of a crocodile swimming rapidly in a shallow dive. Although the hind limbs are always held parallel to the body axis during fast swimming, this is not the case for the forelimbs; during dives they trail in raised position (as in Fig. 4F), during ascents they trail below the body. In both cases the limb positioning may counteract rolling and yawing.

Trial No.	Swimming speed (v) (m s^{-1})	Wave speed (w) (m s^{-1})	w/v	Animal length (m)	Swimming speed (body l s^{-1})
1.	0.64	0.92	1.4	0.326	1.96
2.	0.33	0.43	1.3	0.310	1.06
3.	0.36	0.52	1.5	0.290	1.24
4.	0.35	0.38	1.1	0.310	1.13
5.	0.56	0.71	1.3	0.314	1.78
6.	0.57	0.71	1.2	0.312	1.83
7.	0.51	0.60	1.2	0.311	1.64
8.	0.43	0.46	1.1	0.311	1.38
Mean	0.47	0.59	1.3		1.50

TABLE 1: Relationship between swimming speed and tail travelling wave speed during fast swimming in young *Crocodylus porous*.

Species	Body length l m	Velocity v m s^{-1}	Reynolds number	v/l	Reference
Pleuronectes platessa (flatfish)	0.235	1.2	2.8×10^5	5	Blaxter & Dickson (1959)
Scomber scomber (mackerel)	0.350	3.0	1.0×10^6	9	Blaxter & Dickson (1959)
Aptenodytes forsteri (penguin)	1.000	2.3	1.8×10^4	2	Clark & Bemis (1979)
Chelonia mydas (green turtle)	0.110	0.9	9.4×10^4	8	Davenport *et al* (1984)
Mauremys caspica (f.w. turtle)	0.100	0.2	2.1×10^4	2	Davenport *et al* (1984)
Alligator mississippiensis (alligator)	0.460	1.0	4.6×10^5	2	Fish (1984)
Crocodylus porous (crocodile)	0.326	0.6	2.1×10^5	2	This study

TABLE 2: Comparison of maximum swimming speeds of aquatic vertebrates.

takes a breath the hind body and tail start to rise; this tendency is opposed by a slight forwards and upwards movement of both hindlimb webs (generating upwards thrust and transferring the centre of gravity forwards), causing the animal to bounce a little, though the head remains motionless. In sea water the surface resting posture is somewhat different, the whole animal being nearly horizontal and the dorsal part of the mid section of the tail projecting above the water surface. The limbs project sideways far more than in fresh water and the animal is less stable laterally, being prone to rolling.

ESCAPE RESPONSE

The escape reaction exhibited by crocodiles startled whilst floating at the water surface is shown in Fig. 6. The animal responds by simultaneously sweeping the spread webs of both hindlimbs (which are fully extended) forwards the upwards. This drives the animal downwards into the water column and transfers the centre of gravity forwards, helping to depress the head. The downward movement causes the tail to bend, but it is also flexed vigorously by the crocodile, the broad side of the tail being directed upwards. This action draws the body further into the water column, helped by the vertebral column adopting a ventral concavity (the animal 'crouches' in the water), and by sideways turning of the head. Within 0.68 s the animal is almost a body length below the water surface, horizontal and with the hindlimbs forward and the tail alongside the body. From this position (field 17 in Fig. 6) the crocodile accelerates away by straightening the tail and kicking back the hind limbs.

JUMPING AND FOOD CAPTURE

To capture insects above the water surface (in this case the glass of the tank, but presumably upon rocks or vegetation in nature) the crocodiles show remarkable jumping ability. Typical sequences are
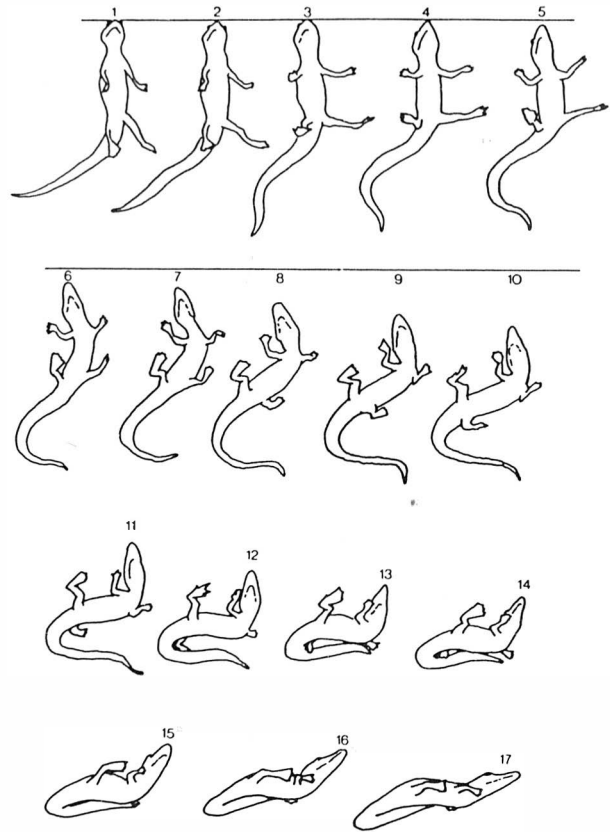

Fig. 6 Escape response of *Crocodylus porosus* startled when resting at the surface. Numerals indicate successive video fields (0.04 s intervals). The animal was startled between fields 1 and 2.

shown in Fig. 7, but hatchling crocodiles (unfortunately not filmed) sometimes jumped almost completely out of water to catch cockroaches. In preparation for a jump, the crocodile brings both hind limbs far forward and extends their webs. The tail is bent at right angles

Fig. 8   Water treading during food handling in *Crocodylus porosus*. Numerals represent video field numbers; black object represents insect prey.
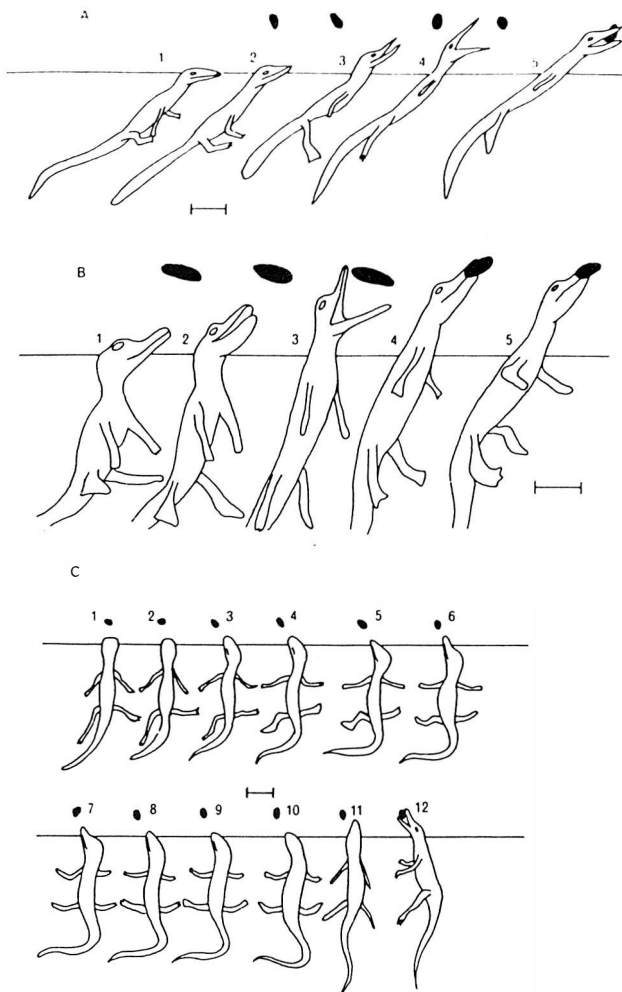

Fig. 7   Food capture by jumping in *Crocodylus porosus*. A. Filmed from the side. B. Detail of limb movements. C. Filmed from behind (except that the animal twisted between fields 11 and 12. Numerals indicate successive fields (interval 0.04 s); black objects represent cockroaches. Scale bars = 4cm.

to the body axis. To initiate the jump the hind limbs and tail are simultaneously driven backwards in a propulsive action lasting about 0.08 s. The head is driven upwards and forwards, the mouth starting to open as the snout clears the water. The animal accelerates as more of the body leaves the water, and the mouth gapes wide until snapped shut on the prey. Before jumping the neck and back are bent; both straighten during the jump.

When catching slow moving aquatic prey (e.g. crabs), or insects floating on the water surface, the crocodiles capture them by foot and tail powered lunges, similar in essentials to the jumps described above, but with less acceleration.

FOOD HANDLING AND WATER TREADING

Young *Crocodilus porosus* cannot swallow large food items under water (Davenport, 1987); this would involve opening the water seal between the back of the tongue and palate, causing water to flood into the oesophagus and stomach. Despite this problem the animals often retreat into water to swallow food, even
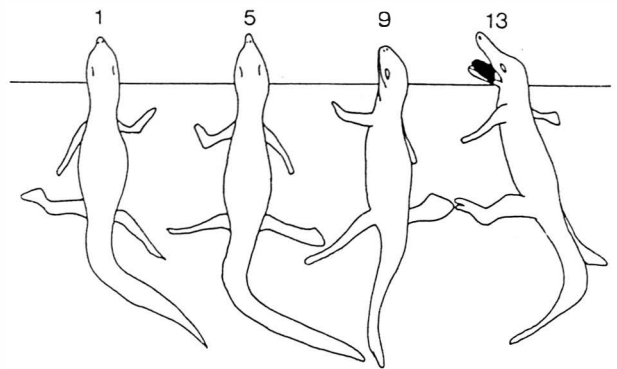
when it is captured on land. Swallowing is accomplished by adopting a vertical position in the water, by throwing the head back so that the snout points skywards, and by treading water vigorously with all four limbs to keep the whole head out of water (Fig. 8). Food is tossed around in the jaws until the longest axis of the food item is parallel with the body axis and swallowing is accomplished. The water treading (similar in pattern to low speed swimming) is obviously an energetic process. With medium sized prey items (e.g. small cockroaches) the crocodiles often caught several insects before starting a bout of water treading and swallowing.

DISCUSSION

Young crocodiles, like adults, spend most of their time in relative immobility; they are classic wait and strike predators. By use of the limbs and tail, a wide and flexible repertoire of movements are possible. The large hind limbs are of particular importance, their broad webs providing much of the force required to overcome inertia during escape reactions and in attacks on prey. The crocodiles' maximum length-specific swimming speed (v/e) is poor by comparison with other aquatic vertebrates (see Table 2), though their long, slender shape handicaps them to some extent in such comparisons. The peak length-specific swimming speed recorded for the salt water crocodile is close to that recorded for the alligator (Fish, 1984) and their anguilliform fast swimming mode is also generally similar (though we found that propulsive waves involved the body of the crocodiles and were not confined to the tail). The finding that the tail travelling wave is propagated at about 1.3 times the swimming speed also agrees with Fish's findings for the alligator. As Webb (1978) points out (for undulatory swimming in fish), longitudinal tail wave velocity (w) must exceed swimming speed for steady propulsive thrust to be developed, but if w greatly exceeds v, much energy is lost laterally to the wake; propulsive efficiency rises as w falls towards v.

Fish (1984) described the alligator as a low swimming speed, low acceleration and low efficiency organism, and cited the work of Schaller and Crawshaw (1982) on the caiman *Caiman crocodilus*,

and of Pooley and Gans (1976) upon the Nile crocodile *Crocodylus niloticus* to extend this hypothesis to crocodilians in general. These latter two studies demonstrated that adult crocodilians fished by snapping their jaws (sometimes with tail and foot powered lunges) at fish which had either strayed within range, or which had been herded into swallow, enclosed water. Our results for *Crocodylus porosus* generally support Fish's hypothesis, except in the case of the ability of hatchlings and juveniles to jump almost completely out of water to catch insects. It is increasingly clear that most crocodilians are insectivorous when young (Cott, 1961; IUCN, 1982), so it is probable that other species have the same jumping ability. Aquatic animals which jump out of water, either to catch prey or to avoid predators, exploit the much lower viscocity of air, which permits greatly enhanced acceleration.

Two features of aquatic movement in *Crocodylus porosus* merit further consideration; the frequent use of simultaneous movements of the hind limbs when rapid movement is required (whether forwards, as in jumps, or backwards, as in the escape response), and the involvement of the vertebral column in lunges and jumps. Both features may be related to the unique (amongst living reptiles) galloping ability of crocodiles upon land (Cott, 1961; Zug, 1974; Webb and Gans, 1982). Galloping involves the synchronous movement of the hind limbs and out of phase synchronous movement of the fore limbs, combined with alternate bending of the vertebral column into a strong ventral arch (when the hindlimbs are brought forward), and straightening of the arch during the propulsive phase (when the hind limbs are thrust backwards). When a young *Crocodylus porosus* jumps out of water to catch an insect, the limb and back movements correspond to half of the gallop stride described for the same species by Zug (1974); only the involvement of the tail in aquatic propulsion is different.

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