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# Diving Behaviour of a Reptile (*Crocodylus johnstoni*) in the Wild: Interactions with Heart Rate and Body Temperature

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## ABSTRACT

The differences in physical properties of air and water pose unique behavioural and physiological demands on semiaquatic animals. The aim of this study was to describe the diving behaviour of the freshwater crocodile *Crocodylus johnstoni* in the wild and to assess the relationships between diving, body temperature, and heart rate. Time-depth recorders, temperature-sensitive radio transmitters, and heart rate transmitters were deployed on each of six *C. johnstoni* (4.0–26.5 kg), and data were obtained from five animals. Crocodiles showed the greatest diving activity in the morning (0600–1200 hours) and were least active at night, remaining at the water surface. Surprisingly, activity pattern was asynchronous with thermoregulation, and activity was correlated to light rather than to body temperature. Nonetheless, crocodiles thermoregulated and showed a typical heart rate hysteresis pattern (heart rate during heating greater than heart rate during cooling) in response to heating and cooling. Additionally, dive length decreased with increasing body temperature. Maximum diving length was 119.6 min, but the greatest proportion of diving time was spent on relatively short (<45 min) and shallow (<0.4 m) dives. A bradycardia was observed during diving, although heart rate during submergence was only 12% lower than when animals were at the surface.

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## Introduction

Evolution is to a large extent driven by selection pressures that arise as a result of, or fluctuate with, changes in an organism's biotic or abiotic environment (Schluter 2001; Ogden and Thorpe 2002). Many lineages of terrestrial vertebrates and invertebrates have secondarily and independently recolonised aquatic environments and presumably gained selective advantages by adopting a semiaquatic ecology. The pronounced physical differences between air and water impose different selection pressures on anatomical and physiological traits of semiaquatic animals. For example, many semiaquatic vertebrates have independently evolved anatomical features that facilitate locomotion in water (webbed feet, finlike appendages, dorsoventrally flattened tails, etc.), although behavioural patterns, such as foraging behaviour and avoidance of predation (Mori 2002; Mori et al. 2002; Halsey et al. 2003; Heithaus and Frid 2003), often encompass movement between the two media. Behaviour is accompanied by physiological traits, particularly metabolic and cardiovascular ones (Burggren 1988; Southwood et al. 1999; Elliott et al. 2002; Kanatous et al. 2002; Gordos and Franklin 2002; Halsey et al. 2003), that must respond to the unique characteristics of both aquatic and terrestrial environments.

Crocodylians evolved from ancestral terrestrial archosaurs in the Late Triassic (Parrish 1993) and secondarily became aquatic (Parrish 1997). Although modern crocodylians are proficient in terrestrial locomotion (Frey 1988; Reilly and Elias 1998), much of their ecology is geared toward an aquatic lifestyle (Frey and Salisbury 2001; Elsworth et al. 2003; Seebacher et al. 2003). Crocodylians possess a number of cardiovascular characteristics (Axelsson and Franklin 1997; Franklin and Axelsson 2000) that, even if they have not evolved in response to exploiting aquatic habitats, make the animals well disposed for aquatic behaviour and diving (Grigg et al. 1985). In laboratory trials, crocodylians have shown pronounced bradycardia in response to submergence in water, which was interpreted as an adaptation to diving because of its presumed reflection of decreased tissue perfusion and, hence, oxygen conservation (Wilber 1960; Andersen 1961; Wright et al. 1992). Additionally, crocodylians have the capacity to bypass the pulmonary circuit by a right-to-left cardiac shunt (Franklin and Axelsson 2000) that may play a role during diving, although the functional significance of such a shunt is not resolved (Grigg and Johansen 1987; Jones and Shelton 1993; Axelsson and Franklin 1997). Laboratory experiments on diving bradycardia may be confounded by stress-induced autonomic

responses (Gaunt and Gans 1969; Weinheimer et al. 1982; Wright et al. 1992; Altimiras et al. 1998), so that part of our aim was to investigate diving bradycardia in undisturbed animals in the wild.

Ectotherms must also reconcile essential terrestrial thermoregulatory behaviour, such as basking in high-irradiation environments, with non-thermoregulatory behavioural demands that may be almost entirely restricted to water, for example, reproduction, social interactions, and feeding (Seebacher 1999; Seebacher and Grigg 2001; Vliet 2001). In many reptiles thermoregulation is closely tied to the cardiovascular system, and at least heart rate may be strongly influenced by thermoregulatory behaviour. Numerous laboratory studies have shown that heart rates are significantly higher during heating than during cooling (Bartholomew and Tucker 1963; Grigg et al. 1979; Grigg and Seebacher 1999). Animals may gain selective advantage from this heart rate pattern (known as heart rate hysteresis) by controlling rates of heating and cooling and thereby increasing the time spent within a preferred thermal range during the day (Seebacher 2000). Heart rate during heating changes in response to heat load received at the animal surface (Franklin and Seebacher 2003), and the hysteresis pattern results from complex physiological control mechanisms (Seebacher and Franklin 2001, 2003). Given the reliance of crocodilians on water for thermoregulation (Seebacher 1999; Seebacher et al. 2003), we were particularly interested in confirming laboratory findings of this evolutionarily significant pattern in crocodiles moving in their natural habitat and in determining the interaction between diving ecology and physiological thermoregulation.

## Material and Methods

### Study Site and Animals

We captured freshwater crocodiles, *Crocodylus johnstoni* ( $N = 6$ ) at Lakefield National Park, Queensland, Australia. Monitoring equipment attached to the largest study animal (26.5 kg) was irreparably damaged, so that we obtained data from five animals (mean mass =  $9.88 \pm 1.97$  kg [SE], range = 4.00–16.00 kg). Crocodiles were caught by set nets in a section of an intermittent creek that forms a permanent water hole (ca. 150 m  $\times$  20 m) even in the dry season (June–August), when the study was conducted. Water depth was estimated by sounding the ground with long poles, and maximum depth was ca. 3.5 m, with an estimated average of 1.5–2.0 m throughout the length of the water hole. After capture, the animals were transported to a base 2 km distant from the water hole, where monitoring equipment was attached; crocodiles were held for no longer than 24 h, after which they were released at their site of capture. Monitoring of diving behaviour and physiological data did not commence until 2 d after release, and all animals were recaptured at the end of the recording period to remove externally attached monitoring equipment.

Water temperatures at 0.25 m depth were measured with dataloggers (iButton Thermocron, Dallas Semiconductor, Dallas) every 5 min during the study and averaged  $21.85 \pm 0.48^\circ\text{C}$  (SE), ranging from  $20.50^\circ\text{C}$  to  $24.50^\circ\text{C}$ . Solar radiation was measured on the ground next to the water hole every 5 min with a pyranometer (Sol-Data, Silkeborg, Denmark) connected to a datalogger (Data Electronics, Melbourne, Australia).

### Diving Behaviour

Custom built time-depth recorders (TDRs; cylindrical dimensions = 55 mm  $\times$  16 mm, mass = 16 g; Lotek Marine Technologies, St. John's, Canada) were used to measure diving behaviour. The recorders were attached to the nuchal (dorsal neck) shield of crocodiles, so that TDRs were above water when crocodiles floated at the surface. TDRs were programmed to record pressure every 4 s while on the crocodiles. Before deployment, TDRs were calibrated in a water tank (1.5 m depth) to obtain the relationship between pressure and water depth. TDRs are accurate to 0.04 m, but their zero line at the water surface drifts over the period of deployment by 0.1 m, so that we set the diving threshold at 0.25 m, that is, only TDR recordings of  $>0.25$  m depth were considered to reflect diving, and all data presented were corrected for this drift (i.e., we set the zero line for dives at 0.25 m). Activity of crocodiles was defined as vertical movements of  $>0.1$  m. We obtained diving data for  $4.4 \pm 0.6$  d (SE) for each crocodile. This excluded the first two days of diving data we obtained upon release of the animals after instrumentation.

### Body Temperature

Body temperature was measured with temperature-sensitive radio transmitters surgically implanted into the peritoneal body cavity of crocodiles. Surgery was performed under local anaesthesia (Lignocaine) and aseptic conditions. Transmitters were calibrated in a temperature-controlled water bath (Julabo, Seelbach, Germany) against a certified thermometer before im-

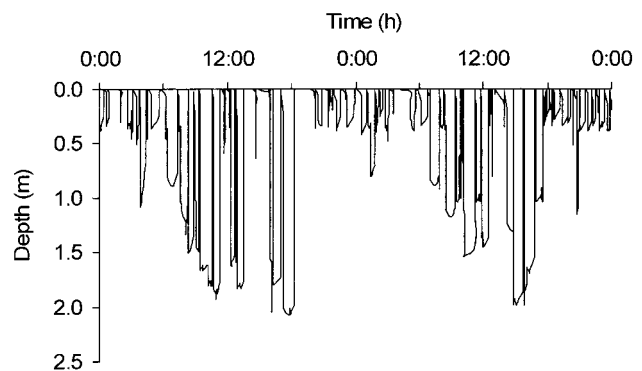


Figure 1. Example of a diving record (from a 5.4-kg crocodile)

Table 1: Diving data from individual freshwater crocodiles, *Crocodylus johnstoni*

Animal No.	Body Mass (kg)	Logging Duration (d)	Dives Logged	Mean Dive Time (min)	Maximum Dive Time (min)	Percent Time Submerged
1	5.4	6	84	26.8	94.7	26.4
2	4	5	146	20.2	75.3	40.3
3	16	4	106	13.3	67.9	24.4
4 <sup>a</sup>	26.5					
5	9.2	3	58	30.3	117.5	40.7
6	14.8	3	29	17.8	119.6	18.1

Note. Logging days refer to the duration over which dive records were analysed (i.e., 2 d after the crocodiles were released).

<sup>a</sup> Time-depth recorder damaged during deployment, data not retrievable.

plantation and were accurate to 0.1°C. The temperature-dependent time intervals between transmitter signals were measured either directly with a stopwatch or by an automated recording system. During automated recordings, output signals from telemetry receivers (Titley Electronics, Ballina, Australia; Telonics, Pasadena, CA) were recorded by a computerised data acquisition system (PowerLab, AD Instruments, Sydney, Australia) connected to a laptop computer. The PowerLab and computer were powered by a DC-to-AC inverter (Dick Smith, Sydney, Australia) connected to a 12-V truck battery.

#### Heart Rate

Heart rate was monitored by heart rate telemetry transmitters (Sirtrack, Havelock North, New Zealand) that were triggered by the electric signal (ca. 100  $\mu$ V) generated by the depolarisation of the cardiac muscle. Transmitters had external attachment point for two electrodes (temporary cardiac pacing leads, Medtronic, Minneapolis, MN), one of which was placed ventral to the heart and the other at the dorsal surface across the heart from the first electrode. Transmitters were attached externally with tape to the base of the tail, and electrode wire was passed under the skin from the transmitter to the location of the electrode; electrodes consisted of braided stainless steel wire coated in biologically inert plastic coating. Signals from heart rate transmitters were received in the same way as for body temperature transmitters. Probably owing to shifting of the electrodes or impaired contact as a result of air pockets, we obtained data from only four crocodiles (mean mass  $8.65 \pm 2.08$  kg [SE]).

#### Analysis

Diurnal patterns of activity and diving depth data were grouped into four 6-h periods per day (0000–0600, 0600–1200, 1200–1800, and 1800–0000 hours) and analysed with a repeated-measures ANOVA with “crocodile” as factor and “period” as

repeated measure. Additionally, we used only three days of data for each crocodile in the analysis, to ensure equal sample sizes.

The effect of body mass on average and maximum dive length, dive depth, and percent of time spent diving was analysed by Type 1 linear regressions. Similarly, the effect of body temperature on dive time and the proportion of total dive time spent on dives of different length were analysed by linear regression.

Heart rate during heating and cooling was analysed by

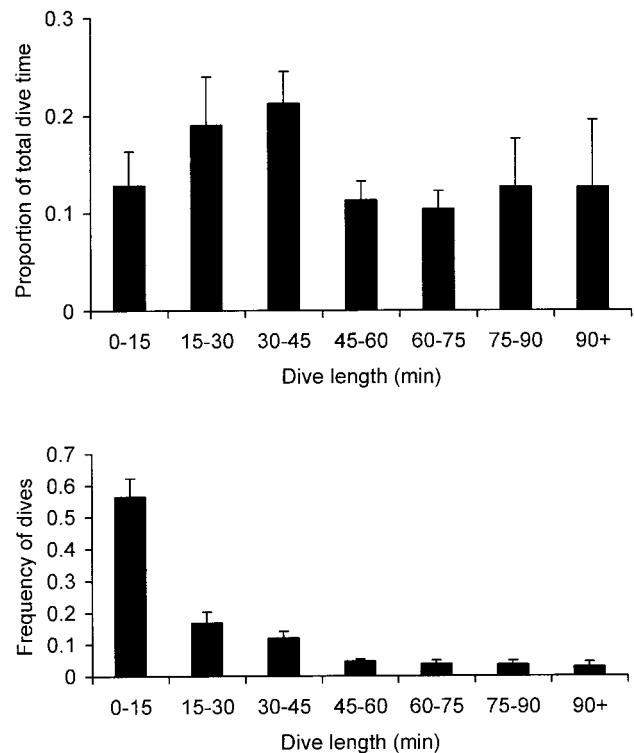


Figure 2. Distributions of dive lengths (mean  $\pm$  SE) for *Crocodylus johnstoni* in 15-min interval blocks. *Top*, Proportion of dives relative to total dive time; *bottom*, frequency of dives in relation to dive length.

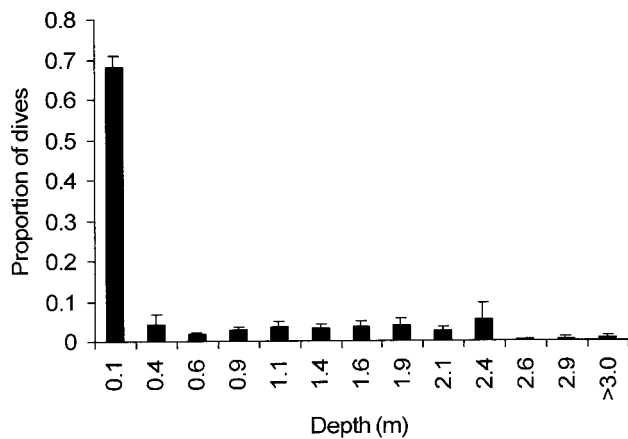


Figure 3. Mean  $\pm$  SE dive depth of crocodiles. Maximum dive depth exceeded 3 m, but most dives were shallow ( $<0.4$  m). Data are summarised into bins, with the values on the X-axis showing the maximum of a bin (e.g., 0.6 indicates dives between 0.4 and 0.6 m).

ANOVA with crocodile and heating/cooling as factors and body temperature as covariate. In the analysis, we used only those heating and cooling episodes that occurred on land or at the water surface, to avoid confounding effects of diving. We obtained heart rates during heating and cooling from only three animals (mean =  $8.47 \pm 3.79$  kg [SE]). Heart rates during diving and at the surface were compared within crocodiles by  $t$ -tests, and only those instances were used when body temperature did not vary by more than  $1^\circ\text{C}$  between surfacing and diving, to avoid confounding effects of temperature.

## Results

An example of a diving profile for a 5.4 kg crocodile is shown in Figure 1. Individuals spent between 18% and 41% of their time submerged (Table 1), although the greatest proportions of the dives were short in duration, less than 15 min (Fig. 2), and were shallow, 0.4 m or less (Fig. 3). The greatest proportion of total dive time was taken up by these shallow, short dives (Figs. 2, 3). Mean dive times for individuals ranged between 13 and 30 min, with maximum dive durations exceeding 60 min for all animals (Table 1). Two animals (5 and 6) performed dives that approached 2 h in duration (Table 1). Dives greater than 60 min generally occurred at depths greater than 1.5 m.

Activity of crocodiles changed significantly during the day ( $F_{3,255} = 8.50$ ,  $P < 0.001$ ). The animals were most active between 0600 and 1200 hours (Fig. 4, *top*) and least active at night (1800–0000 hours), and there were no differences between individuals ( $F_{4,85} = 2.03$ ,  $P = 0.098$ ). This pattern was reflected in the dive depth, which varied significantly during the day ( $F_{3,255} = 25.62$ ,  $P < 0.0001$ ), and crocodiles dived deepest at their most active time period (0600–1200 hours). At night, when the animals were least active, they spent most of the time

at the surface or on shallow dives (Fig. 4, *middle*). There were, however, significant differences between individuals ( $F_{4,85} = 8.077$ ,  $P < 0.0001$ ), and the interaction between crocodile and diving depth was significant ( $F_{12,255} = 4.22$ ,  $P < 0.001$ ), indicating that while individuals showed the same patterns of activity, the depth to which they dived varied. Diving activity and depth corresponded with daylight hours, but peak activity preceded periods of maximum solar irradiation and daily peak body temperatures (Fig. 4, *bottom*). Individual differences were not owing to differences in body mass, and there was no significant relationship between body mass and dive length or depth (average length, maximum length, average depth, percent of time diving, all  $F_{1,4} < 6.0$ ,  $P > 0.09$ , and  $R^2 < 0.55$ ; data not shown).

Mean dive length decreased with increasing body temperature during the dive ( $Y = 52.73 - 1.21X$ ,  $F_{1,6} = 7.14$ ,  $P < 0.05$ ,

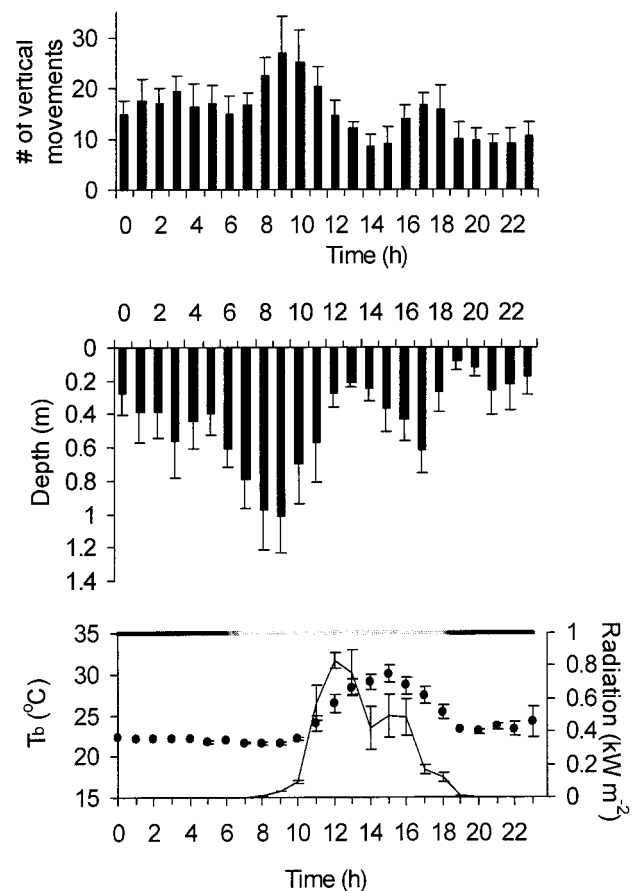


Figure 4. Diurnal patterns of diving behaviour. Activity was expressed as the mean ( $\pm$  SE) number of vertical movements per hour (*top*), and the corresponding mean ( $\pm$  SE) depths are shown (*middle*). Patterns of diving activity paralleled natural light cycles (indicated by the solid bar at the top of the bottom panel: black = darkness, dark gray = twilight, light gray = daylight), but peak activity preceded maxima in mean ( $\pm$  SE) body temperature (*bottom*, circles) and mean ( $\pm$  SE) solar radiation (*bottom*, solid line).

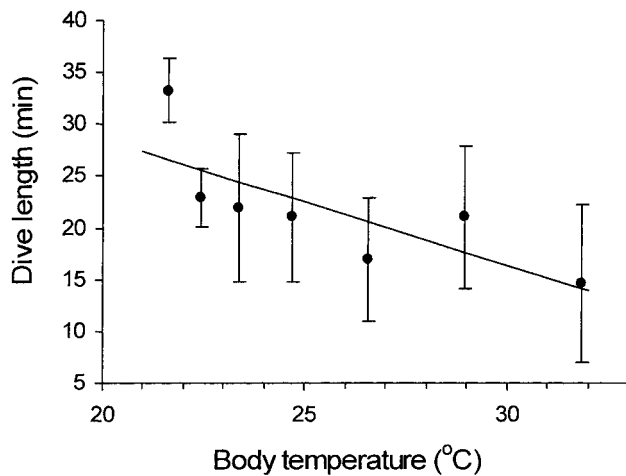


Figure 5. Mean ( $\pm$ SE) dive length decreased linearly with increasing body temperature.

$R^2 = 0.51$ ; Fig. 5), but there was no relationship between dive depth and body temperature (linear regression,  $F_{1,6} = 3.61$ ,  $P = 0.12$ ).

*Crocodylus johnstoni* exhibited a bradycardia during submergence, and heart rate was on average 11.9% lower while diving than heart rate immediately before the dive (Fig. 6, top). This difference in heart rate was significant in three crocodiles (2:  $t_{42} = -3.29$ ,  $P < 0.002$ ; 3:  $t_{26} = -2.99$ ,  $P < 0.004$ ; and 5:  $t_{16} = -3.21$ ,  $P < 0.003$ ), and the same trend existed in a fourth animal (1), but we obtained heart rate data from only two dives, which precluded statistical analysis (Fig. 6, bottom). Heart rate was significantly faster during heating than during cooling ( $F_{1,55} = 59.70$ ,  $P < 0.0001$ ; Fig. 7, bottom), and heart rate increased significantly with body temperature ( $F_{1,55} = 11.24$ ,  $P < 0.001$ ). In the example (Fig. 7, top), heart rate increased as the animal heated, and when body temperature reached 32°C the animal moved into the water briefly, which coincided with a sharp drop in heart rate. The animal resurfaced and cooled at the surface, but heart rate nonetheless remained considerably below heating values.

## Discussion

Crocodiles are diurnally active and spend most of the night at the water surface. Interestingly, we found that the diving activity of *Crocodylus johnstoni* increased with first light in the morning and that this occurred before body temperature increased or radiation levels became high enough for basking. Social behaviour and foraging often occur underwater in crocodilians (Webb et al. 1982; Vliet 2001), and if *C. johnstoni* in our study performed any of those activities while diving, they did so at body temperatures (22–23°C) considerably less than the average daily maximum (29–30°C). Performance in ectothermic reptiles is temperature dependent, and it is thought that the importance

of thermoregulation in reptiles is to attain optimal (preferred) temperatures (Seebacher and Grigg 1997) for activity in particular (Angilletta et al. 2002). However, the behaviour of *C. johnstoni* is contrary to this notion, as the animals did not synchronise thermoregulation with their peak of activity. Thermal sensitivity of locomotor performance originates primarily from the temperature-induced constraints on muscle performance and metabolic potential (Guderley and St. Pierre 2002; Johnston and Temple 2002). It may be that metabolic and muscular demands of crocodiles during their normal behaviour never reach their full potential at the higher “preferred” temperature, so that the reduced potential at the lower body temperature does not pose a physiological constraint on activity. Additionally, metabolic processes may be relatively temperature insensitive and plastic within individuals (Guderley and St. Pierre 2002; Seebacher et al. 2003), so that activity may not be significantly curtailed as a result of lower body temperature in the morning.

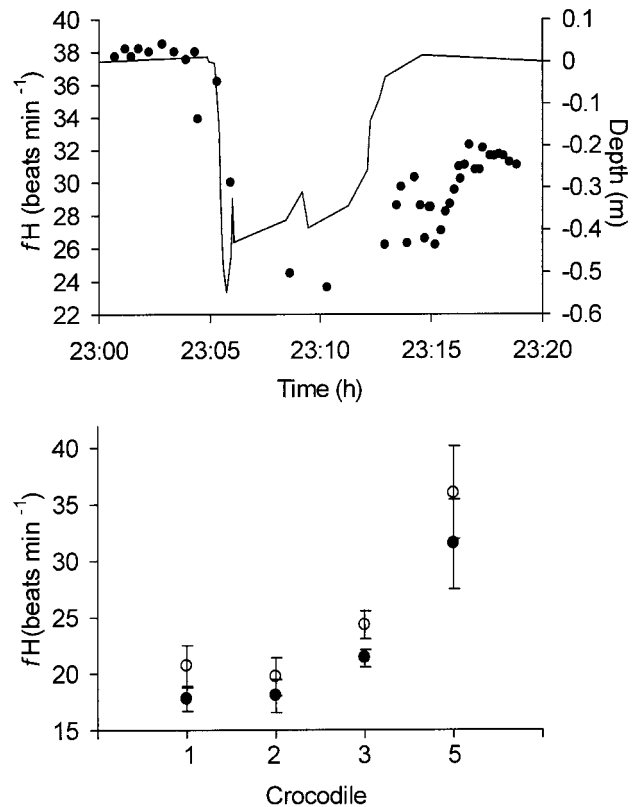


Figure 6. Mean heart rate ( $fH \pm$ SE) decreased significantly during diving compared to heart rate immediately before the dive in three crocodiles (2, 3, and 5), and the same trend existed in a fourth animal (1), but we obtained heart rate data from two dives only (bottom: filled circles = heart rate during diving, open circles = heart rate immediately before the dive). In a typical record of a diving episode (from crocodile 3; top) heart rate (circles) decreases immediately after the animal dived (curve).



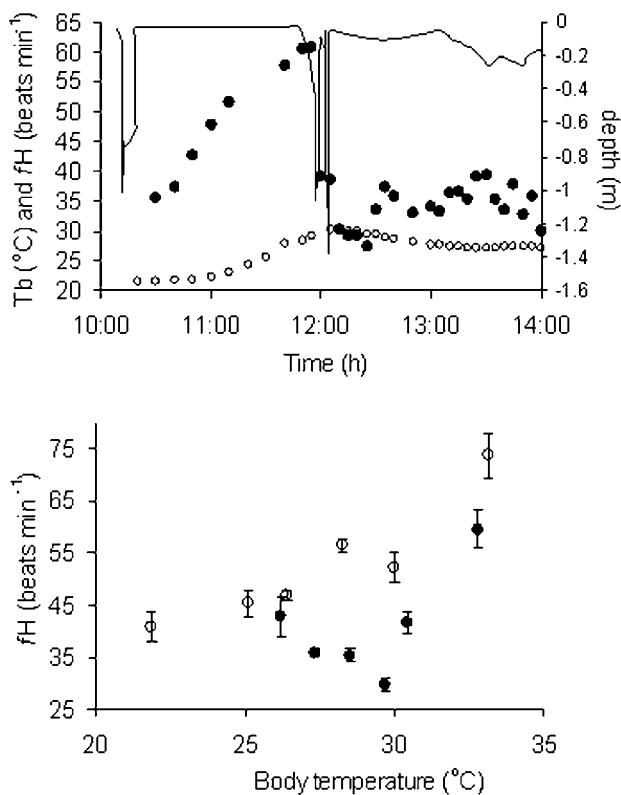


Figure 7. Mean heart rate ( $fH \pm SE$ ) was significantly faster during heating than during cooling, and heart rate increased significantly with body temperature (*bottom*). In the example (*top*), heart rate (*filled circles*) increases as the animal heats (*open circles* = body temperature). As body temperature reaches 32°C, the animal moves into the water briefly (*curve* = diving record), which coincides with a sharp drop in heart rate. The animal resurfaces and cools at the surface, but heart rate nonetheless remains considerably below heating values.

Diving activity of *C. johnstoni* decreased and body temperature increased as radiation levels peaked at the water hole. This pattern probably reflects prolonged basking periods at that time (Seebacher and Grigg 1997; Seebacher 1999). The advantages of heating after activity may be to facilitate physiological rate functions, such as assimilation of food, and recovery from locomotory activity. Short (<5 min) voluntary dives in estuarine crocodiles (*Crocodylus porosus*) in captivity are aerobically fueled (Wright 1987), but *C. johnstoni* in the wild routinely dived for much longer than 5 min, so that it is unlikely that diving behaviour was entirely supported by aerobic metabolism (Mori 2002). Hence, the relatively inactive period at a high body temperature following activity peaks may serve to accelerate recovery by reoxidising lactic acid to pyruvate. Regardless of the asynchrony in the timing of activity and peak body temperatures, the animals did thermoregulate. Opportunistic observations revealed typical basking behaviour (F. Seebacher and C. E. Franklin, personal observations; data not shown) and,

importantly, crocodiles displayed the typical cardiovascular changes in response to heat (i.e., faster heart rates during heating than during cooling) that have previously been described from laboratory studies (Grigg and Alchin 1976; Franklin and Seebacher 2003). Heart rate hysteresis significantly increases the efficacy of thermoregulation by conferring control over heating and cooling rates on the animals and, thereby, extending periods during the day that can be spent at preferred body temperatures (Seebacher 2000). Interestingly, diving bradycardia would augment the temperature-induced hysteresis in animals that dive after basking, although the two mechanisms operate independently from each other (Figs. 6, 7). Diving bradycardia in wild *C. johnstoni* was less pronounced than previously reported for crocodylians in the laboratory. It is likely that the bradycardia in the laboratory was augmented by a stress response, although if crocodiles in our study were active while diving, heart rates may have been elevated, leading to an underestimate of the magnitude of the bradycardia. The diving response (bradycardia, vasoconstriction) in mammals is primarily mediated by the autonomic nervous system (Elliott et al. 2002), while heart rate hysteresis during heating and cooling in a lizard is primarily controlled by prostaglandins and, to a lesser extent, by cholinergic and adrenergic mechanisms (Seebacher and Franklin 2001, 2003). Maximum dive time in *C. johnstoni* was considerably longer than in most endothermic species (e.g., Elliott et al. 2002) and much longer than voluntary dives reported in a laboratory setting (20 min; Wright 1987; Wright et al. 1992). Lower aerobic metabolic rates would account for the difference between ectotherms and endotherms, and the likelihood of increased adrenergic stimulation (stress) in captive animals would explain the shorter dive times in the laboratory.

Optimal diving models for endothermic vertebrates predict that the relationship between dive time and surface time (recovery) is nonlinearly related to body mass (Watanuki and Burger 1999; Mori 2002). The lack of allometry in *C. johnstoni* diving behaviour is most likely the result of a relatively narrow range of body mass of the study animals. Rates of oxygen consumption in crocodylians are mass dependent (Wright 1986), so that the depletion of oxygen stores during diving would be slower in larger animals, which would therefore be expected to have the potential for longer dives.

#### Acknowledgments

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