Diving through the thermal window: implications for a warming world

Hamish A. Campbell\textsuperscript{1,*}, Ross G. Dwyer\textsuperscript{2}, Matthew Gordos\textsuperscript{3} and Craig E. Franklin\textsuperscript{1}

\textsuperscript{1}School of Biological Sciences, University of Queensland, St Lucia, Queensland 4072, Australia
\textsuperscript{2}Centre for Ecology and Conservation, University of Exeter, Falmouth, Cornwall, UK
\textsuperscript{3}Aquatic Habitat Rehabilitation Unit, Wollongbar Agricultural Institute, 1243 Bruxner Highway, Wollongbar, New South Wales 2477, Australia

Population decline and a shift in the geographical distribution of some ectothermic animals have been attributed to climatic warming. Here, we show that rises in water temperature of a few degrees, while within the thermal window for locomotor performance, may be detrimental to diving behaviour in air-breathing ectotherms (turtles, crocodilians, marine iguanas, amphibians, snakes and lizards). Submergence times and internal and external body temperature were remotely recorded from freshwater crocodiles (\textit{Crocodylus johnstoni}) while they free-ranged throughout their natural habitat in summer and winter. During summer, the crocodiles’ mean body temperature was 5.2\textpm{}0.1°C higher than in winter and the largest proportion of total dive time was composed of dive durations approximately 15 min less than in winter. Diving beyond 40 min during summer required the crocodiles to exponentially increase the time they spent on the surface after the dive, presumably to clear anaerobic debt. The relationship was not as significant in winter, even though a greater proportion of dives were of a longer duration, suggesting that diving lactate threshold (DLT) was reduced in summer compared with winter. Additional evidence for a reduced DLT in summer was derived from the stronger influence body mass exerted upon dive duration, compared to winter. The results demonstrate that the higher summer body temperature increased oxygen demand during the dive, implying that thermal acclimatization of the diving metabolic rate was inadequate. If the study findings are common among air-breathing diving ectotherms, then long-term warming of the aquatic environment may be detrimental to behavioural function and survivorship.

\textbf{Keywords:} crocodilian; ectotherm; acclimatization; temperature; aerobic dive limit

1. INTRODUCTION

An ectotherm is by definition an animal whose body temperature varies with that of the ambient environmental temperature. Apart from one or two exceptions, these include all the fishes, amphibians, reptiles and invertebrates. The overbearing influence of temperature on the rate of metabolic processes means that for these animals ambient environmental temperature strongly influences ecological function (Portner & Farrell 2008). This close association means that acute and chronic shifts in ambient thermal conditions may be detrimental to an individual’s survival, and numerous cases have recently been reported of population decline and a shift in the geographical distribution of some ectotherms as a direct result of climatic warming events (Alford et al. 2007; Kutschera et al. 2007; Portner & Knust 2007; Farrell et al. 2008; McMenamin et al. 2008; Takasuka et al. 2008).

The structural and kinetic coordination of molecular, cellular and systemic processes results in animals optimizing performance within a limited thermal window (Portner & Farrell 2008). Beyond the upper and lower limits of this window, decrements in locomotion, growth, competitiveness, reproduction and immune competence will occur (Portner 2002). Confronted with a thermally generated reduction in performance, an organism may use behavioural and physiological strategies to mitigate negative effects. Behavioural strategies typically result in an avoidance of extreme ambient environmental temperatures and a selection of favourable thermal niches (Daly et al. 2008). If the animal cannot escape adverse ambient temperatures on the seasonal or longer-term time scale, then a reshaping of the thermal window may occur (Wilson & Franklin 1999; Franklin & Seebacher 2009). Knowing the capacity by which an organism can behaviourally compensate or physiologically acclimatize to long-term shifts in ambient environmental temperature may enable better prediction of its ecological response, and thus the long-term consequences of climatic change for the population.

Air-breathing diving animals provide a good model for examining the interplay between physiology and ecological function because diving behaviour is directly determined by the amount of stored oxygen and the rate it is used (Kooyman et al. 1980; Costa et al. 2004). The limitation by which animals can routinely dive without incurring an oxygen debt is defined by the diving lactate threshold (DLT; Butler 2006). Staying submerged beyond the limits of the DLT rapidly builds up...
2 H. A. Campbell et al. Diving through the thermal window

oxygen debt and results in exponential lengthening of the post-dive surface interval (PDSI) or, depending on the extent, a suspension of diving until normal lactate levels are re-established (Kooymans et al. 1980; Costa et al. 2004).

The close association between ambient temperature and body temperature in ectothermic animals means that at higher environmental temperatures, metabolic rate is proportionally increased (Q10 effect; Pough 1976; Jackson 2007). This causes a reduction in aerobic dive limit as a consequence of O2 being used more rapidly, and a reduction in available O2 stores (Herbert & Jackson 1985; Fuster et al. 1997; Prassack et al. 2001; Priest & Franklin 2002; Gordos et al. 2003a,b; Seebacher et al. 2005; Jackson 2007). Subsequently, a diving ectotherm faced with a higher body temperature would be required to reduce dive duration to maintain the dive within aerobic limits or, if dive duration remained constant, increase the duration of the PDSI to clear the anaerobic debt (lactate). Either of these modifications would reduce the amount of time the animal could remain submersed during a bout of diving activity.

Present and projected rises in the temperature of some marine and freshwater environments (Intergovernmental Panel on Climate Change 2007) would increase the body temperature of inhabiting ectothermic air-breathing diving organisms (marine and freshwater turtles, crocodilians, marine iguanas, sea and freshwater snakes), and may impinge on their diving performance. If this occurred, the animal’s ability to undertake diving-related ecological tasks could be impeded, survivorship reduced and a shift in the geographical distribution of the species may occur. Although it is known that acute rises in temperature significantly reduce dive performance in ectotherms (Priest & Franklin 2002; Clark et al. 2008), it is presently unclear how the diving performance of ectotherms responds to chronic rises in environmental temperature. Do ectotherms undergo adequate physiological acclimatization of the diving metabolic rate or is diving performance diminished?

This is a difficult question to answer empirically because numerous ecological factors influence the diving behaviour of an animal in the wild, while, in captivity, the environmental cues and stimulus for defining diving behavioural strategies are not present. In this study, we remotely monitored the diving behaviour, internal body temperature and the preferred microhabitat temperature of juvenile freshwater crocodiles (Crocodylus johnstoni) in the wild. The freshwater crocodile was a suitable ectothermic air-breathing diver to study; firstly, because it lives in an environment where it is exposed to a seasonal shift in environmental temperatures (approx. 8°C), but winter temperatures are not sufficiently low to induce hypometabolism (Seebacher & Grigg 1997; Seebacher et al. 2005); and, secondly, because they rest/sleep for prolonged periods on the river or waterhole substratum, surfacing to breathe when they approach their aerobic dive limit (Campbell et al. 2010). Thus, the effect of a long-term rise in temperature upon diving performance could be assessed in a free-diving ectotherm while minimizing physiological (activity, feeding) and ecological interference (predators, prey, conspecific interactions).

2. MATERIAL AND METHODS

(a) Animals and surgery

Freshwater crocodiles (C. johnstoni) were captured from a permanent waterhole (approx. 150 m in length, by 20 m wide, and between 1.5 and 3.0 m depth) in Lakefield National Park, Queensland, Australia (15.155840°S, 144.251992°E). The studies were undertaken in mid-June (n = 10) and late November 2007 (n = 10). Following capture by a set net, the crocodiles were sedated with 2 mg kg−1 body mass of Alfaxan CD-RTU (10 mg ml−1; Jurox, New Zealand), and a local anaesthetic (2–4 ml lignocaine, 20 mg ml−1 with adrenaline 1 part per 100 000; Troy Laboratories, Australia) was injected into the immediate area of tag attachment or implantation. All crocodiles were responsive to touch and auto-moving 1–2 h after surgery. They were released at the capture location 24 h post-surgery.

Throughout the duration of the study, data-loggers (iButton Thermocron, Dallas Semiconductor, Dallas, TX, USA) recorded air and water temperature at 0.15 (subsurface) and 1.5 m (on the bottom of the waterhole) depth every 20 min, within a shaded area of the waterhole.

(b) Remote monitoring of depth

The depth at the crocodiles dorsal surface was logged every 9 s using a time–depth–temperature recorder (TDTR; cylindrical dimensions = 60 mm L × 21 mm D; 15 g; Star-Oddi, Iceland) mounted on the nuchal shield. The device was attached using a plastic-coated multi-strap stainless steel wire to 4 × 1 mm holes drilled transversally through the raised dorsal scutes. Before deployment, all TDTRs were calibrated in the laboratory. Depth and temperature sensors were accurate to a resolution of 0.04 m and 0.1°C, respectively.

(c) Remote monitoring of temperature

The micro-niche temperature of each crocodile was recorded every 20 min by the TDTR (see above) mounted on the nuchal shield. The body temperature was measured simultaneously for each TDTR recording by temperature-sensitive radio transmitters (cylindrical dimensions = 40 × 22 mm; 15 g; Sirtrack, NZ) surgically implanted into the peritoneal cavity. A 4 cm lateral incision was made dorsal of the left hind-leg. The muscle layers were teased apart by a blunt dissection and the tag placed in a pocket under the abdominal muscle layer but external to the peritoneal cavity. The muscle layer was closed with two interrupted sutures (3-0 Ethicon cat gut), and the wound closed with six to eight interrupted sutures. Aseptic conditions were maintained throughout surgery. The transmitters emitted a radio pulse at a unique frequency for each animal. The pulse rate from each transmitter was temperature-dependent. The relationship between pulse rate and temperature was calibrated for each transmitter against a certified thermometer prior to implantation with an accuracy less than 0.3°C. During the study, the time elapsed for 10 consecutive pulses was used to calculate temperature.

To record the body temperature from free-diving crocodiles, a large four-prong radio antenna (Titley Electronics, Brisbane, Australia) was positioned at 10 m height above the waterhole. A receiving station was situated 110 m from the waterhole, from which the radio signal could be monitored without disturbance to the crocodiles. A scanning radio-receiver (Titley Electronics) continually recorded the received signals and scanned the frequency for each transmitter every 60 s; subsequently each transmitter was scanned
every 10 min. The audio output signal from the radio-
receiver was directed to a data acquisition system (Powerlab,
ADInstruments, Australia) that digitized the audio signal at a
sample rate of 100 Hz. The digital trace was recorded and
stored on a laptop computer (Toshiba) running CHART 5.1
software (ADInstruments).

(d) Statistical analysis
This study used a combination of general additive mixed
models (GAMMs) and general linear mixed models
(GLMMs) to describe patterns in diving behaviour and ther-
moregulation in C. johnstoni. General additive models
(GAMs) allow for nonlinear relationships between the
response variable and multiple explanatory variables (Wood
2004). Mixed models extend this framework, providing esti-
mates of the influence on the mean as well as the influence of
random effects on the variance, thereby accounting for the
non-independence of errors resulting from repeated
measures from the same individuals (Pinheiro et al. 2009).
Data from temperature sensors were analysed using a
GAMM with body temperature as the dependent variable,
season as a factor (summer and winter) and crocodile ID
as a random effect. A single measure of ‘environmental temp-
erature’ was derived from a principal components analysis
using the correlation between deep water, subsurface water
and micro-niche temperature to produce a single ‘environ-
mental temperature’ covariate. Principal component 1
(PC1) accounted for 95 per cent of the variance and was
used to make seasonal comparisons upon median and
distribution data, respectively. Welch’s t-test assuming
unequal variances was used to examine mean differences in
non-diving parameters between the two sampling periods.
Spearman’s rank-order correlation was used to examine the
relationship between dive duration and the PDSI for each
animal. All modelling was undertaken using the R statistical
software package (R Development Core T eam 2005).
GLMMs and GAMMs were carried out with the nlme
(Pinheiro et al. 2009) and mgcv (Wood 2004) packages,
respectively. ANOVAs were undertaken in STATAGRAPHICS
v. 5.1, and an effect was deemed significant if \( p < 0.05 \).

3. RESULTS

(a) Temperature
The average air temperature was 9.2°C warmer in summer
compared with winter (table 1). Surface water temperature
showed a seasonal shift of 7.8°C, while deep water temper-

ture showed a seasonal variation of only 4.8°C. This
resulted in a different thermal stratification in the water
column between the seasons (figure 1). In winter, surface
waters, warmed throughout the morning, were 1–2°C
warmer than deep water by 14.00, cooled rapidly after
15.00 and by 04.00 were 4.2°C cooler than the deep
water. In summer, surface waters were 3.4°C warmer
than deep water at 14.00 and never cooled to a tempera-
ture below that of the deep water. The mean daily
micro-niche temperature of the crocodiles was 5.1°C
warmer in summer than in winter (table 1). Micro-niche
temperature followed a similar daily profile to surface
water temperature for seasons, increasing rapidly during
the morning and decreasing throughout the late afternoon.
In winter, however, micro-niche temperature remained
relatively constant, whereas in summer, micro-niche
temperature remained similar to surface water temperature
throughout the night, but was significantly cooler than surface water temperature
between 14.00 and 16.00 (figure 1b).

Using the principal component for environmental
temperature, the GAMM indicated that \( T_b \) was affected
by environmental temperature equally across summer
and winter (REML: \( F_l = 0.63, \ p = 0.425 \); figure 2).

The relationship between the seasons was linear, but a

---

**Table 1. Environmental and internal body temperature (**\( T_b **)) in **C. johnstoni** (winter, \( n = 9 **)); summer \( n = 6 **); mean ±

<table>
<thead>
<tr>
<th>Condition</th>
<th>Winter</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>18.5 ± 4.2*</td>
<td>27.7 ± 4.2*</td>
</tr>
<tr>
<td>Surrounding rock</td>
<td>18.9 ± 6.4*</td>
<td>31.3 ± 2.0*</td>
</tr>
<tr>
<td>Surface water</td>
<td>21.3 ± 4.4*</td>
<td>29.1 ± 2.5*</td>
</tr>
<tr>
<td>Deep water</td>
<td>23.6 ± 0.2*</td>
<td>28.4 ± 1.3*</td>
</tr>
<tr>
<td>Daily micro-niche temp</td>
<td>23.9 ± 0.02</td>
<td>29.0 ± 0.02</td>
</tr>
<tr>
<td>Daily mean ( T_b )</td>
<td>23.9 ± 0.02*</td>
<td>29.1 ± 0.15*</td>
</tr>
<tr>
<td>Daily min ( T_b )</td>
<td>24.2 ± 0.12</td>
<td>28.0 ± 0.53</td>
</tr>
<tr>
<td>Daily max ( T_b )</td>
<td>27.2 ± 0.51*</td>
<td>32.2 ± 0.27*</td>
</tr>
</tbody>
</table>

* Asterisks denote a significance difference between the seasons, \( p < 0.05 \).
Figure 1. The relationship between the body temperature (Tb) of *C. johnstoni* (black circles; mean ± s.e.; n = 8) with micro-niche (black triangles; mean ± s.e.; n = 45) and deep water (white circles; mean ± s.e.; n = 45) temperature for each hour over the diel cycle in (a) winter and (b) summer. Plus symbols denote hours when Tb was significantly different from surface water temperature, and asterisks denote hours when Tb was significantly different from deep water temperature.

The nonlinear logistic function best fitted the data (REML: $F_{8.34} = 1862$, $p < 0.01$). This occurred because of dissociation between Tb and environmental temperature from linearity within each season and not between seasons. The within-season departure from linearity occurs because Tb does not equal the high surface water temperatures during summer afternoons or the low surface water temperatures during winter nights (figure 1). During these periods, Tb was more similar to micro-niche temperature than surface water temperature ($p < 0.05$). This modification of Tb by micro-niche selection resulted in Tb varying by approximately 2°C over the diel cycle in both summer and winter, despite the diel change in surface water temperature varying by greater than 6°C. It also helped to explain the reduced seasonal difference in Tb (5.2°C) compared with the seasonal variation in surface water temperature (7.8°C).

(b) Diving behaviour

In total, 6472 dives were recorded in winter, compared with 5935 dives in summer. However, data were successfully retrieved from more crocodiles in winter, and the mean number of dives exhibited per day was 38 per cent greater in summer (d.f. = 6 and 9, $W = 0.32$, $p < 0.05$). The median and maximum dive durations were significantly shorter in summer compared with winter (d.f. = 6 and 9, $W = 1.52$, $p < 0.05$; table 2), and the proportion of each day that the crocodiles were

submerged did not vary between the seasons (d.f. = 6 and 9, $W = 7.52$, $p = 0.76$). In both seasons, a large majority of dives were less than 20 min duration; during winter, however, a substantially greater proportion of time was spent on dives more than 40 min (figure 3). In summer, the crocodiles undertook about 0.83 ± 0.07 (mean ± s.e., $n = 6$) dives of more than 50 min in duration, compared with 12.6 ± 0.34 (mean ± s.e., $n = 9$) in winter.

The mean body mass of the crocodiles recorded in winter and summer was 7.3 ± 1.2 and 6.8 ± 2.1 kg, respectively. There was no significant difference in mean body mass between the two sample periods ($t_{9.6} = 1.65$; $p = 0.12$); however, the relationship between body mass and dive duration was significantly different between the seasons (REML: $F_{1} = 30.36$, $p < 0.01$). In summer, there was a positive nonlinear effect between dive duration and body mass, while in winter, body mass had little effect on dive duration (figure 4a).

In both seasons, dive duration increased at first light, approximately 1 h earlier in summer, illustrating an association between diving behaviour and photoperiod. A significant circadian rhythm was present in the duration

Table 2. Diving behaviour recorded in free-ranging *C. johnstoni* (winter, $n = 9$; summer, $n = 6$, mean ± s.e.m., median ± s.d.). Asterisks denotes a significance difference between the seasons, $p < 0.05$.

<table>
<thead>
<tr>
<th>season</th>
<th>winter</th>
<th>summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>median dive duration (min)</td>
<td>14.70 ± 0.26*</td>
<td>12.51 ± 0.23*</td>
</tr>
<tr>
<td>max dive duration (min)</td>
<td>77.01 ± 10.34*</td>
<td>48.77 ± 3.62*</td>
</tr>
<tr>
<td>no. dives per crocodile per day</td>
<td>47.94 ± 5.59*</td>
<td>66.16 ± 5.51*</td>
</tr>
<tr>
<td>time submerged (%)</td>
<td>38.52 ± 3.27</td>
<td>43.04 ± 4.31</td>
</tr>
<tr>
<td>post-dive surface interval (min)</td>
<td>5.22 ± 0.86</td>
<td>4.92 ± 0.95</td>
</tr>
<tr>
<td>dive depth (cm)</td>
<td>114.23 ± 18.25*</td>
<td>92.31 ± 15.43*</td>
</tr>
</tbody>
</table>
of the dives. The period of the circadian rhythm was 22.2 and 26.4 h (PS, 0.05). The period of the sine wave was similar for both seasons, and the relationship between dive duration and time of day was best explained by a nonlinear GAMM (REML: $F_{8.02} = 49.80, p < 0.01$).

However, dive duration during winter months was significantly greater at each period throughout the diel cycle. The relationship between dive duration and body mass was best explained by a linear GAMM (REML: $F_{1} = 30.36, p < 0.01$) and the relationship between dive duration and diel cycle was best explained by a nonlinear GAMM (REML: $F_{8.02} = 49.80, p < 0.01$).

Figure 3. Dive duration of *C. johnstoni* (mean ± s.e.) recorded in winter (*n* = 9; white bars) and summer (*n* = 6; black bars) as a proportion of the total time within each duration bin. Dive duration bins represent 0.8 min increments.

Figure 4. The best-fitting GAM model representing the relationship between dive duration of *C. johnstoni* with (a) body mass (REML: $F_{1} = 30.36, p < 0.01$) and (b) diel cycle (REML: $F_{8.02} = 49.80, p < 0.01$). The influence of winter (grey line) and summer (black line) upon this relationship is shown.

Figure 5. (a) The number of dives and (b) the proportion of time submerged by *C. johnstoni* over the diel cycle (winter, white circles, *n* = 9; summer, black circles, *n* = 8). Asterisk signifies hours that showed a significant difference between seasons.
for the reduced dive performance in summer was because of a higher rate of oxygen consumption during the dive. Because the crocodiles were inactive during the majority of these extended dives (Campbell et al. 2010), diving metabolic rate must have been greater. This result is similar to the effects of acute thermal exposure on diving in air-breathing ectotherms (Fuster et al. 1997; Priest & Franklin 2002; Jackson 2007), and implies that inadequate thermal acclimatization of the diving metabolic rate occurred between summer and winter.

This finding appears odd as numerous examples exist of ectotherms altering enzyme activity, cardiovascular function and metabolism in direct response to chronic changes in environmental temperature (Zari 1999; Hicks & Farrell 2000; Birkedal & Gessner 2004; Seebacher 2005; Seebacher et al. 2009), and crocodilians show significant changes in the activities of regulatory metabolic enzymes after only a few weeks of thermal acclimatization (Glanville & Seebacher 2006; Seebacher et al. 2009). Most field studies on the thermal biology of reptiles have however focused on their acclimatization to cold temperatures, and ectotherms from temperate regions that use hypometabolic strategies are often the study species.

In this study, behavioural rather than physiological acclimatization appeared to be the more significant seasonal response to temperature. During summer, the duration of the dives was reduced and a greater number of dives were undertaken during periods of the day when the crocodiles spent a high proportion of their time submerged. All C. johnstoni showed a significant positive correlation between dive duration and the PDSI in summer; however, during periods when Tb was lower, their DLT was extended. The summertime reduction in DLT would arise from a higher rate of oxygen consumption during the dive, as a direct result of a thermally induced higher spontaneous metabolic rate.

In a previous study, we found that the relationship between body mass and dive duration was a poor predictor of dive duration in C. johnstoni, and although DLT did scale allometrically with body mass, ecological factors exerted a greater influence on dive duration than oxygen reserves (Campbell et al. 2010). In this previous study, however, diving behaviour was studied only during winter months. The present study agrees with the previous findings for crocodiles examined during winter months, but when crocodiles are examined during summer months, dive duration does scale with body mass. This finding supports the theory that the crocodiles’ oxygen reserves were significantly more influential in controlling dive duration during summer than during winter, and, because dives were on average shorter during summer, we hypothesize that diving metabolic rate was greater.

It is difficult to assess and quantify the ecological ramifications for C. johnstoni as a direct consequence of a reduced dive performance during summer months. We can deduce that all crocodiles compensated for the restricted dive performance by undertaking a greater
number of dives during periods when a high level of submersion occurred. Chronic exposure to high ambient temperatures may be more detrimental to hatchlings owing to their higher mass-specific metabolic rates. The crocodiles used in this study were roughly 7 kg; extrapolation of DLT for a 70 g hatchling crocodile (using the allometric scaling exponent for aerobic dive duration in *C. porosus*; Wright & Kirshner 1987) shows that for the rise in Tb observed in this study, the DLT of a hatchling freshwater crocodile would be reduced from 11.36 to 7.1 min and diving beyond DLT would result in the crocodile needing to spend prolonged periods at the water surface to clear anaerobic debt. Further increases in ambient temperature would decrease DLT and the hatchlings would be required to spend greater periods of time at the water surface and vulnerable to predation from aerial and surface-feeding predators. Additionally, as metabolic rate rises with ambient temperatures, the energetic requirements of the crocodile would also increase. For an air-breathing animal that needs to dive to collect food, even slight restrictions on DLT may be detrimental to their foraging strategy, requiring them to push physiological limits and undertake a larger proportion of energetically costly anaerobic dives. A negative feedback loop can be envisaged, where the animal must engage in high-energy-cost foraging behaviour to satisfy growing metabolic demands.

All organisms exhibit a thermal window for optimal locomotor and metabolic performance. Living outside the limits of this window will reduce fitness, but within window boundaries, a broad plateau of thermal independence exists (Portner & Farrell 2008). The thermal constraints upon diving performance in *C. johnstoni* occurred under ambient temperatures, and transpired even though Tb fell well within their thermal window for locomotor performance (Elsworth et al. 2003). Similar seasonal reductions in dive duration have been observed in free-ranging turtles during summer (Carr et al. 1980; Bentivegna et al. 2003; Gordos et al. 2003a; Hochscheid et al. 2005; Bradshaw et al. 2007), and have also been shown to occur under experimental long-term thermal exposure (Clark et al. 2008), suggesting that inefficient thermal acclimatization of the physiological machinery responsible for diving may be common among ectothermic air-breathing divers. Further research is required to elucidate what feature of their diving physiology *C. johnstoni* were unable to thermally acclimatize, and to determine what constraints thermal-induced restrictions upon dive performance may place upon ecological function.

All research was undertaken with the University of Queensland’s, Animal Welfare Unit’s approval and a DERM Eco-Access permit. Funding was provided by ARC-Linkage with Australia Zoo as partners, Queensland Parks and Wildlife provided infrastructure and logistics. We would like to thank Paul O’Callaghan, Annabelle Olsson, Dave Leyland, Mariana Campbell and QPWS staff for their help during fieldwork, and Simon Blomberg of UQ for statistical advice.

**REFERENCES**


Herbert, C. V. & Jackson, D. C. 1985 Temperature effects on the responses to prolonged submergence in the turtle *B. a. maxima*.


