

Blood concentrations of lactate, glucose and corticosterone in dispersing hatchling sea turtles

Carla M. Pereira^{1,*}, David T. Booth¹, Adrian J. Bradley² and Colin J. Limpus³

¹Physiological Ecology Group, School of Biological Sciences, University of Queensland, QLD 4072, Australia

²Vertebrate Stress and Neurobiology Laboratory, School of Biomedical Sciences, University of Queensland, QLD 4072, Australia

³Aquatic Threatened Species and Threatening Processes Unit, Queensland Government Environment and Heritage Protection, PO Box 2454, Brisbane, QLD 4001, Australia

*Author for correspondence (carla.limapereira@uqconnect.edu.au)

Biology Open 2, 63–67

doi: 10.1242/bio.20123046

Received 5th September 2012

Accepted 18th October 2012

Summary

Natal dispersal of sea turtles is an energetically demanding activity that is fuelled primarily by aerobic metabolism. However, during intense exercise reptiles can use anaerobic metabolism to supplement their energy requirements. We assessed anaerobic metabolism in dispersing hatchling loggerhead and flatback turtles by measuring the concentrations of blood lactate during crawling and at different times during the first four hours of their frenzy swim. We also measured concentrations of blood glucose and corticosterone. Blood lactate (12.13 to 2.03 mmol/L), glucose (6.25 to 3.8 mmol/L) and corticosterone (8.13 to 2.01 ng/mL) concentrations decreased significantly over time in both loggerhead and flatback hatchlings and no significant

differences were found between the species. These results indicate that anaerobic metabolism makes a significant contribution to the dispersal phase of hatchling sea turtles during the beach crawl and the first few hours of the frenzy swim.

© 2012. Published by The Company of Biologists Ltd. This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial Share Alike License (<http://creativecommons.org/licenses/by-nc-sa/3.0>).

Key words: Swimming frenzy, Anaerobic metabolism, Glucose, Lactate, Corticosterone, Sea turtle, Hatchling

Introduction

Once they emerge from their nest, sea turtle hatchlings frantically crawl down the beach towards the sea and then engage in a frenzy swim, which rapidly takes them off-shore to reach oceanic currents (Bustard, 1972; Salmon and Wyneken, 1987). During this period hatchlings face high near-shore predator pressure that decreases as they move further offshore (Gyuris, 1994; Gyuris, 2000; Salmon et al., 2009; Whelan and Wyneken, 2007). Reptiles such as sea turtles have a limited aerobic capacity (Bennett, 1978) and during intensive exercise they supplement their energy requirements with anaerobic metabolism (Bennett, 1982) with a subsequent production and accumulation of lactate (Gleeson, 1996). Studies on the natural history and physiology of nest emergence, beach crawl and the off-shore frenzy swimming dispersal of hatchling sea turtles indicate that these processes are extremely vigorous and energy demanding (Wyneken and Salmon, 1992; Wyneken, 1997; Booth, 2009; Pereira et al., 2012). Although primarily fuelled by aerobic metabolism (Wyneken, 1997; Booth, 2009; Pereira et al., 2012), tissue lactate concentrations increase during these activities indicating that anaerobic metabolism also plays a major role at this time (Dial, 1987; Baldwin et al., 1989; Hamann et al., 2007).

Sea turtle hatchlings typically exhibit frantic swimming behaviour when they first enter the water, but this decreases in the first few hours before they settle into a sustained swimming effort for up to 24 hours (Wyneken and Salmon, 1992; Wyneken, 1997; Booth, 2009; Pereira et al., 2011; Pereira et al., 2012).

However, the intensity of swimming varies between species (Wyneken and Salmon, 1992; Pereira et al., 2011). Green turtle (*Chelonia mydas*) hatchlings are the most vigorous swimmers followed by loggerhead turtle (*Caretta caretta*) hatchlings, with flatback turtle (*Natator depressus*) and leatherback turtle (*Dermodochelys coriacea*) hatchlings being less vigorous (Wyneken and Salmon, 1992; Pereira et al., 2011; Pereira et al., 2012). These differences in swimming intensity are expected to be reflected in differences in the use of anaerobic metabolism and therefore differences in blood lactate concentrations.

In reptiles, aerobic and anaerobic metabolism is influenced by steroid hormones, which control metabolic processes (Nelson, 2005; Neave, 2008). Glucocorticoid hormones influence physiological processes such as lipolysis, gluconeogenesis, lactate release from muscles (Neave, 2008) and increases in blood glucose concentration (Munck and Koritz, 1962). Glucocorticoids are involved in adjusting physiological process in response to environmental cues particularly in animals that undergo seasonal changes as part of their life history, such as migration, breeding and hibernation (McEwen and Wingfield, 2003). Emerging from a nest, crawling down the beach then entering a frantic swim may be a series of events that are influenced to some degree by glucocorticoids (Hamann et al., 2007). In reptiles, corticosterone (B) is one of the major glucocorticoids produced (Nelson, 2005) and is known to vary in concentration at different stages of sea turtle life history including the natal dispersal phase (Hamann et al., 2002; Hamann et al., 2005; Hamann et al., 2007). Hence, as with blood lactate concentrations, the patterns of

exercise activity exhibited by sea turtle hatchlings are expected to result in changes in blood corticosterone concentration.

In this study we investigate blood lactate, glucose and corticosterone concentration in hatchling turtles through the beach crawl and early frenzy swim to test the hypothesis that these parameters will vary in a systematic way with the varying exercise intensity of different species. In particular, we predict that loggerhead turtles experience intermediate changes in these physiological variables as a result of their moderate swimming effort and that flatback hatchlings experiences the smallest changes because of their relative low swimming effort (Pereira et al., 2011; Pereira et al., 2012). This is the first study to report data regarding changes in concentrations of blood lactate, glucose and corticosterone in flatback hatchling turtles and data regarding glucose and corticosterone concentrations in loggerhead hatchling turtles during the early stages of the dispersal phase.

Materials and Methods

Study site

This study was conducted at Mon Repos Conservation Park (24°48S, 152°27E), located on the east coast of the Australian mainland (Pfaller et al., 2009). Annual nesting of loggerhead (*Caretta caretta*) and flatback (*Natator depressus*) turtles occur every year at this rookery (Limpus et al., 1984; Limpus and Limpus, 2003; Limpus, 2007; Limpus, 2008).

Terrestrial and swimming activities

Data collection took place between the 21st January and the 18th February 2011. The beach was patrolled throughout the night to monitor nests of loggerhead and flatback turtles. When hatchlings were found emerging from a nest, a total of 18 hatchlings were collected from the nest and transported dry to the laboratory in a bucket lined with sand, a process that took around 15 minutes. During this transport time hatchlings were actively crawling around inside the bucket, a behaviour that is similar to their terrestrial movement from the nest to the sea.

Each trial consisted of one terrestrial treatment (crawling) and five swimming treatments (15 minutes, 30 minutes, 1 hour, 2 hours and 4 hours). We did not collect blood at emergence because it was difficult to sample on the beach. Once in the laboratory three hatchlings were sampled for blood and classified as a 'crawling' treatment. The remaining 15 hatchlings were allocated to the swimming treatments. Each hatchling was placed in a separate tank (34 cm long×28 cm wide×19 cm high) filled with 16 cm of sea water at ambient temperature (25–28°C) and a low intensity light was placed at one end of the tank to encourage unidirectional swimming. Each hatchling was fitted with a lycra harness attached to a monofilament tether that was fixed to a wooden stake attached to the top of the tank. The tether length was adjusted so that hatchlings could swim freely but could not touch the sides or bottom of the tank. The stretched tether provided resistance to forward motion that encouraged continuous swimming. At the end of each sampling period three hatchlings had a blood sample taken and were then released into the ocean.

Measurement of blood variables

A 200–300 µl blood sample was collected from a branch of the jugular vein using a 27 gauge needle and 1 ml heparinized syringe following the method of Bennett (Bennett, 1986). Blood lactate and glucose concentrations were immediately analysed with an I-STAT one Blood Analyzer (Heska, Colorado USA) using GC4+ and 6+ cartridges (Abbott Laboratories, USA), respectively. The remaining blood was centrifuged to separate the blood cells (discarded) from the plasma that was preserved at –10°C until later analysis of corticosterone. Plasma corticosterone was analysed by radioimmunoassay (RIA) as described in Bradley using a 10 µl sample (Bradley, 1987; Bradley, 1990). Corticosterone standards ranged from 0 to 1000 pg and standards were made up in methanol using corticosterone purchased from Sigma Chemical Co, USA. Radiolabelled corticosterone ([1,2,6,7-³H(N)] corticosterone) was purchased from PerkinElmer NEN Radiochemicals, USA and 20,000 dpm was added to both standards, samples and external controls. A standard curve was plotted using AssayZap software (Biosoft, Cambridge, UK). The intra- and inter- assay coefficients of variation were 8.4 and 7.1% respectively. The assay sensitivity was 10 pg.

Statistical analysis

Blood concentrations of corticosterone, lactate and glucose were analysed using a MANOVA, followed by a Repeated Measures ANOVA (each clutch was considered as just one individual that was sampled repeatedly over time).

Results were reported as means ± SE and statistical significance assumed if $P < 0.05$.

Results

A total of 132 loggerhead hatchlings and 79 flatback hatchlings had blood samples taken although there was not enough blood in some samples to perform measurements on all three variables (Table 1). Lactate and corticosterone blood concentration data were log transformed to comply with the statistical assumptions of normality and homoscedasticity before statistical analysis. The MANOVA analysis revealed significant differences between all variables ($P < 0.01$). The Repeated Measures ANOVA showed significant differences over time but not between species and with the exception of lactate there were no species*time interactions (Table 2).

Loggerhead turtle hatchling blood lactate, glucose and corticosterone concentration decreased significantly with time from crawling until trials ended after 4 hours of swimming (Table 2; Fig. 1). Most of these decreases in concentration occurred between crawling and two hours of swimming (Fig. 1). Flatback turtle hatchlings had a similar pattern, with blood concentrations of all variables decreasing throughout time (Table 2), although there was a slight increase in blood lactate after 1 hour of swimming (Fig. 1) and this was the cause of the interaction between species and time for this variable.

Discussion

Our results show that flatback and loggerhead turtle hatchlings have a similar use of anaerobic metabolism as indicated by the similar patterns of change in blood lactate concentration. In both species, anaerobic metabolism decreased with time but the use of anaerobic metabolism persisted for longer in flatback turtle hatchlings than in loggerhead hatchlings. Dial (loggerhead turtles), Baldwin et al. (loggerhead and green turtles) and Hamann et al. (green turtles) have reported lactate concentrations at different times during the beach crawl and early stages of the frenzy swim in hatchling sea turtles (Dial, 1987; Baldwin et al., 1989; Hamann et al., 2007). Although all studies indicate anaerobic metabolism plays an important role during this period, results differ between studies due to differences in methodology and species. Dial and the current study found lactate to be highest after the beach crawl (Dial, 1987), while Baldwin et al. found lactate continued to accumulate in blood when hatchlings swam across the reef flat (Baldwin et al., 1989). Baldwin et al. reported a fall in blood lactate in hatchlings swum in an aquarium because they power-stroked only briefly and remained mostly on the surface with the head above the water, and for loggerhead turtles blood lactate concentration was just 1.7 mmol/L after 15 minutes of 'swimming' in the aquarium (Baldwin et al., 1989). In the current study, however, hatchlings swam almost continuously as they were tethered and could not touch the sides or bottom of the swimming container and loggerhead hatchling blood lactate concentration was four times greater averaging 6.9 mmol/L after 15 minutes of swimming. Baldwin et al. found that blood lactate concentrations peaked at ~13 mmol/L after 15 minutes of swimming across the reef flat and that they were greater in green turtle hatchlings than in loggerhead turtle hatchlings (Baldwin et al., 1989). In contrast, Hamann et al. found blood lactate concentrations in green turtle hatchlings to be only 4.5 mmol/L after 30 minutes of swimming but to be extremely

Table 1. Sample size for each measured variable at each sampling time for data reported in Fig. 1. Numbers in brackets indicate number of clutches represented in sample.

| Species and sampling time | Blood lactate concentration | Blood glucose concentration | Blood corticosterone concentration |
|---------------------------|-----------------------------|-----------------------------|------------------------------------|
| Loggerhead | | | |
| crawl | 20 (8) | 12 (7) | 23 (8) |
| 15-minute swim | 21 (8) | 13 (7) | 22 (8) |
| 30-minute swim | 16 (8) | 10 (7) | 19 (8) |
| 1-hour swim | 21 (8) | 15 (7) | 23 (8) |
| 2-hour swim | 20 (8) | 8 (7) | 22 (8) |
| 4-hour swim | 18 (8) | 10 (7) | 20 (8) |
| Flatback | | | |
| crawl | 10 (4) | 11 (5) | 13 (5) |
| 15-minute swim | 7 (4) | 5 (5) | 10 (5) |
| 30-minute swim | 8 (4) | 9 (5) | 10 (5) |
| 1-hour swim | 8 (4) | 8 (5) | 13 (5) |
| 2-hour swim | 6 (4) | 6 (5) | 12 (5) |
| 4-hour swim | 8 (4) | 9 (5) | 14 (5) |

high (24 mmol/L) after two hours of swimming (Hamann et al., 2007). The pattern of blood lactate concentration change reported for green turtle hatchlings reported in Hamann et al. (Hamann et al., 2007) is unexpected because green turtle hatchlings generally decrease their swimming effort as the time spent swimming increases (Burgess et al., 2006; Booth, 2009; Ischer et al., 2009; Booth and Evans, 2011).

As expected, blood lactate concentrations of loggerhead hatchlings were lower than those reported for green turtle hatchlings, which is consistent with the less vigorous swimming behaviour of loggerhead hatchlings compared to green turtle hatchlings (Pereira et al., 2011; Pereira et al., 2012). We also expected blood lactate concentrations of flatback turtle hatchlings to be lower than loggerhead turtle hatchlings because they are less vigorously swimmers (slower power-stroke rate and less frequent power-stroking bouts) (Pereira et al., 2011). However, this was not the case, as lactate concentration was not significantly different between the species during the beach crawl and first hour of swimming. Indeed, contrary to our expectation, from two hours onward blood lactate concentration in flatback hatchlings increased slightly although it continued to decrease in loggerhead hatchlings. A possible explanation for this increase in blood lactate concentration of flatback hatchlings may be that lactate is being released from the muscles to the blood, which will then be transported to the liver and converted back into glucose (gluconeogenesis), either for immediate use or to be stored as glycogen.

The fact that anaerobic metabolism in flatback hatchlings is similar or even exceeds that of loggerhead hatchlings, but swimming effort is relatively lower in flatback hatchlings (Pereira et al., 2011), suggests that it is the aerobic component of flatback hatchling swimming effort that is relatively lower compared to loggerhead hatchlings. This hypothesis is supported

by the finding that aerobic metabolism of flatback turtles decreases much more sharply than in loggerhead turtle hatchlings within the first two hours of swimming (Pereira et al., 2012).

The pattern of changes in the concentrations of glucose and corticosterone seems to reflect the changes in blood lactate concentration. Both aerobic and anaerobic muscle metabolisms are fuelled by glucose and during heavy exercise glucose is mobilised from glycogen stores in the liver. During prolonged exercise liver glycogen stores become depleted and other sources of fuel such as lipid and proteins are gradually mobilised (Brooks, 1987; Horowitz and Klein, 2000; Hamann et al., 2007). Hence in loggerhead and flatback turtle hatchlings elevated concentrations of corticosterone during crawling and early swimming are correlated with glucose being released from the liver and a consequent increase in blood glucose concentration. Subsequently blood glucose concentration falls as the liver glycogen stores are depleted.

Ecological interpretation

The 'predation risk' hypothesis suggests that offshore swimming behaviour of hatchling sea turtles is moulded by the interaction of three factors that contribute to survivorship: predator pressure in near-shore waters, swimming distance to oceanic currents and hatchling size (Chung et al., 2009; Salmon et al., 2009). Green turtle hatchling swimming behaviour is more vigorous than that of loggerhead and flatback hatchlings (Pereira et al., 2011; Pereira et al., 2012), which indicates a strategy moulded primarily by the need for a rapid escape from near shore predator rich waters (Gyuris, 1994). Loggerhead turtle hatchlings swimming behaviour is similar to but not as vigorous as green turtle hatchlings (Pereira et al., 2011; Pereira et al., 2012; Wyneken, 1997), which suggests that is also primarily moulded

Table 2. Results of Repeated Measure ANOVAs for differences in blood lactate, glucose and corticosterone concentration in loggerhead and flatback turtle hatchlings and across time intervals. *F*=F value, *P*=probability.

| Factor | Blood lactate | Blood glucose | Blood corticosterone |
|--------------------------|---------------|---------------|----------------------|
| Species $F_{(1,1)}$ | 1.17 | 0.45 | 2.15 |
| Species <i>P</i> | 0.31 | 0.53 | 0.20 |
| Time $F_{(1,5)}$ | 11.9 | 8.10 | 3.98 |
| Time <i>P</i> | <0.001 | <0.001 | <0.001 |
| Species*time $F_{(1,5)}$ | 2.70 | 0.60 | 2.48 |
| Species*time <i>P</i> | 0.03 | 0.70 | 0.06 |

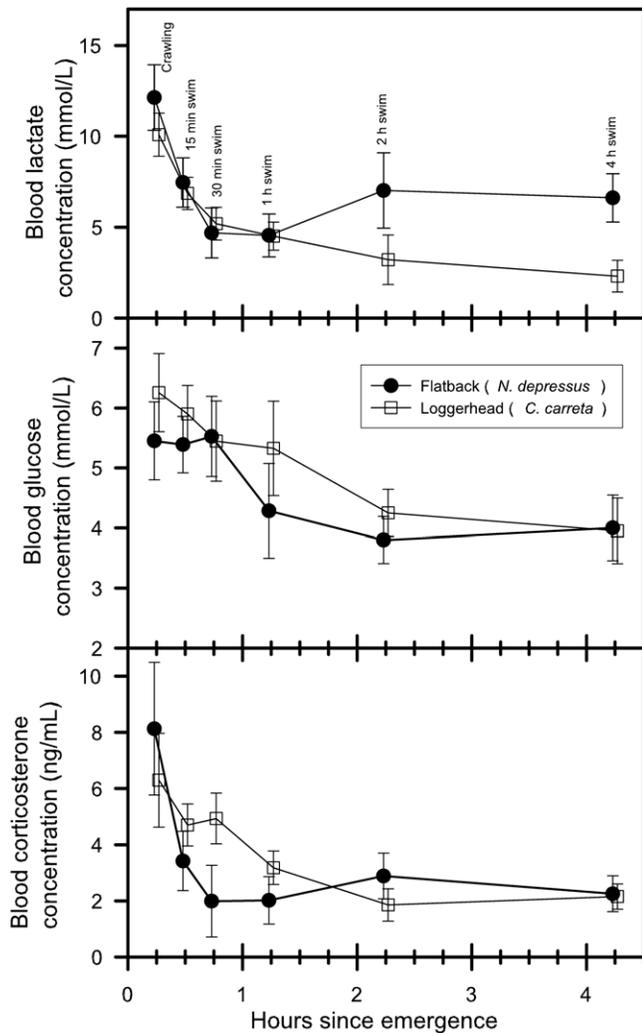


Fig. 1. Blood lactate, blood glucose and blood corticosterone concentration from crawl until 4 hours of frenzy swimming in loggerhead (*C. caretta*) and flatback (*N. depressus*) turtle hatchlings from the Mon Repos rookery. Sample sizes for loggerhead and flatback turtles are listed in Table 1.

by a need to rapidly escape predator rich near shore waters. Flatback hatchlings, however, experience a sharper decrease in their swim effort and aerobic metabolism within the first two hours of the swimming frenzy (Pereira et al., 2011; Pereira et al., 2012) and they maintain a similar level of swimming activity for the first four days after entering the water (Salmon et al., 2009). Our results do not allow us to make strong inferences about the role of anaerobic metabolism on dispersal strategies but it supports the idea that near-shore predation pressure is a potential driver for the frantic and energetically expensive swimming effort typical of the initial stages of the frenzy swim.

In summary the current study and previous studies (Dial, 1987; Baldwin et al., 1989; Hamann et al., 2007) indicate anaerobic metabolism is used extensively during the beach crawl and at least the beginning of the frenzy swim during natal dispersal of sea turtle hatchlings. The additional use of anaerobic metabolism allows hatchlings to maximize their physical activity and thus minimises the time they spend on the beach and in the shallow near-shore waters where predators are in their highest concentration.

Acknowledgements

This research conforms to Australian Animal Welfare laws and was approved by a University of Queensland Animal Ethics Committee (approval no. SBS/228/10). We thank Christina Burger, the Mon Repos Conservation Park staff and volunteers and the DERM Turtle Conservation Volunteers for the help provided during the field work. This study was co-financed by the European Social Fund (ESF) and Fundação para a Ciência e a Tecnologia (FCT) as part of a doctoral scholarship [SFRH/BD/44139/2008 to C.M.P.].

Competing Interests

The authors have no competing interests to declare.

References

- Baldwin, J., Gyuris, E., Mortimer, K. and Patak, A. (1989). Anaerobic metabolism during dispersal of green and loggerhead hatchlings. *Comp. Biochem. Physiol.* **94A**, 663-665.
- Bennett, A. F. (1978). Activity metabolism of the lower vertebrates. *Annu. Rev. Physiol.* **40**, 447-469.
- Bennett, A. F. (1982). The energetics of reptilian activity. In *Biology Of The Reptilia* (ed. C. Gans and F. H. Pough), pp. 155-199. London; New York: Academic Press.
- Bennett, J. M. (1986). A method for sampling blood from hatchling loggerhead turtles. *Herpetol. Rev.* **17**, 43.
- Booth, D. T. (2009). Swimming for your life: locomotor effort and oxygen consumption during the green turtle (*Chelonia mydas*) hatchling frenzy. *J. Exp. Biol.* **212**, 50-55.
- Booth, D. T. and Evans, A. (2011). Warm water and cool nests are best. How global warming might influence hatchling green turtle swimming performance. *PLoS ONE* **6**, e23162.
- Bradley, A. J. (1987). Stress and mortality in the red-tailed phascogale, *Phascogale calura* (Marsupialia: Dasyuridae). *Gen. Comp. Endocrinol.* **67**, 85-100.
- Bradley, A. J. (1990). Failure of glucocorticoid feedback during breeding in the male red-tailed phascogale *Phascogale calura* (Marsupialia: Dasyuridae). *J. Steroid Biochem. Mol. Biol.* **37**, 155-163.
- Brooks, G. A. (1987). Amino acid and protein metabolism during exercise and recovery. *Med. Sci. Sports Exerc.* **19** Suppl, S150-S156.
- Burgess, E. A., Booth, D. T. and Lanyon, J. M. (2006). Swimming performance of hatchling green turtles is affected by incubation temperature. *Coral Reefs* **25**, 341-349.
- Bustard, R. (1972). *Sea Turtles: Natural History And Conservation*, p. 220. London; Sydney: Collins.
- Chung, F. C., Pilcher, N. J., Salmon, M. and Wyneken, J. (2009). Offshore migratory activity of hawksbill turtle (*Eretmochelys imbricata*) hatchlings, I. Quantitative analysis of activity, with comparisons to green turtles (*Chelonia mydas*). *Chelonian Conservation and Biology* **8**, 28-34.
- Dial, B. E. (1987). Energetics and performance during nest emergence and the hatchling frenzy in loggerhead sea turtles (*Caretta caretta*). *Herpetologica* **43**, 307-315.
- Gleeson, T. T. (1996). Post-exercise lactate metabolism: a comparative review of sites, pathways, and regulation. *Annu. Rev. Physiol.* **58**, 565-581.
- Gyuris, E. (1994). The rate of predation by fishes on hatchlings of the green turtle (*Chelonia mydas*). *Coral Reefs* **13**, 137-144.
- Gyuris, E. (2000). The relationship between body size and predation rates on hatchlings of the green turtle (*Chelonia mydas*): is bigger better? In *Sea Turtles Of The Indo-Pacific: Research, Management & Conservation* (ed. N. Pilcher and G. Ismail), pp. 143-147. London: ASEAN Academic Press.
- Hamann, M., Jessop, T., Limpus, C. and Whittier, J. (2002). Interactions among endocrinology, seasonal reproductive cycles and the nesting biology of the female green sea turtle. *Mar. Biol.* **140**, 823-830.
- Hamann, M., Jessop, T. S., Limpus, C. J. and Whittier, J. M. (2005). Regional and annual variation in plasma steroids and metabolic indicators in female green turtles, *Chelonia mydas*. *Mar. Biol.* **148**, 427-433.
- Hamann, M., Jessop, T. S. and Schüble, C. S. (2007). Fuel use and corticosterone dynamics in hatchling green sea turtles (*Chelonia mydas*) during natal dispersal. *J. Exp. Mar. Biol. Ecol.* **353**, 13-21.
- Horowitz, J. F. and Klein, S. (2000). Lipid metabolism during endurance exercise. *Am. J. Clin. Nutr.* **72** Suppl, 558S-563S.
- Ischer, T., Ireland, K. and Booth, D. T. (2009). Locomotion performance of green turtle hatchlings from the Heron Island Rookery, Great Barrier Reef. *Mar. Biol.* **156**, 1399-1409.
- Limpus, C. J. (2007). *A Biological Review Of Australian Marine Turtles. 5. Flatback Turtle Natator Depressus (Garman)*. Brisbane: Queensland Government.
- Limpus, C. J. (2008). *A Biological Review Of Australian Marine Turtles. 1. Loggerhead Turtle Caretta Caretta (Linnaeus)*. Brisbane: Queensland Government.
- Limpus, C. J. and Limpus, D. J. (2003). Loggerhead turtles in the Equatorial and Southern Pacific Ocean: a species in decline. In *Loggerhead Sea Turtles* (ed. A. B. Bolten and B. E. Witherington), pp. 199-209. Washington: Smithsonian Books.
- Limpus, C. J., Fleay, A. and Baker, V. (1984). The flatback turtle, *Chelonia depressa*, in Queensland: reproductive periodicity, philopatry and recruitment. *Australian Wildlife Research* **11**, 579-587.

- McEwen, B. S. and Wingfield, J. C.** (2003). The concept of allostasis in biology and biomedicine. *Horm. Behav.* **43**, 2-15.
- Munck, A. and Koritz, S. B.** (1962). Studies on the mode of action of glucocorticoids in rats. I. Early effects of cortisol on blood glucose and on glucose entry into muscle, liver and adipose tissue. *Biochim. Biophys. Acta* **57**, 310-317.
- Neave, N.** (2008). *Hormones And Behaviour: A Psychological Approach*, p. 366. Cambridge; New York: Cambridge University Press.
- Nelson, R. J.** (2005). *An Introduction To Behavioral Endocrinology*, 3rd edition, p. 816. Sunderland: Sinauer Associates.
- Pereira, C. M., Booth, D. T. and Limpus, C. J.** (2011). Locomotor activity during the frenzy swim: analysing early swimming behaviour in hatchling sea turtles. *J. Exp. Biol.* **214**, 3972-3976.
- Pereira, C. M., Booth, D. T. and Limpus, C. J.** (2012). Swimming performance and metabolic rate of flatback *Natator depressus* and loggerhead *Caretta caretta* sea turtle hatchlings during the swimming frenzy. *Endang. Species Res.* **17**, 43-51.
- Pfaller, J. B., Limpus, C. J. and Bjorndal, K. A.** (2009). Nest-site selection in individual loggerhead turtles and consequences for doomed-egg relocation. *Conserv. Biol.* **23**, 72-80.
- Salmon, M. and Wyneken, J.** (1987). Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J. Exp. Mar. Biol. Ecol.* **109**, 137-153.
- Salmon, M., Hamann, M., Wyneken, J. and Schauble, C.** (2009). Early swimming activity of hatchling flatback sea turtles *Natator depressus*: a test of the 'predation risk' hypothesis. *Endang. Species Res.* **9**, 41-47.
- Whelan, C. L. and Wyneken, J.** (2007). Estimating predation levels and site-specific survival of hatchling loggerhead seaturtles (*Caretta caretta*) from South Florida beaches. *Copeia* **2007**, 745-754.
- Wyneken, J.** (1997). Sea turtle locomotion: mechanisms, behavior and energetic. In *The Biology Of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 165-198. Boca Raton: CRC Press.
- Wyneken, J. and Salmon, M.** (1992). Frenzy and postfrenzy swimming activity in loggerhead, green and leatherback hatchling sea turtles. *Copeia* **1992**, 478-484.