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Behavioural thermoregulation by Australian freshwater turtles: interspecific differences and implications for responses to climate change

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Abstract. The abilities of freshwater turtles to control their body temperatures by behavioural means have implications for activity, food ingestion and digestion, growth, reproduction and potential responses to climate change. I compared various forms of basking in nature, and responses to aquatic and aerial photothermal gradients in the laboratory, among three species of Australian chelid turtles: *Chelodina expansa*, *C. longicollis* and *Emydura macquarii*. Proclivity for behavioural thermoregulation varied substantially among these species, being highest in *C. longicollis* and lowest in *C. expansa*. However, *C. expansa* had a thermophilic response to feeding. For *C. longicollis* and *E. macquarii*, behavioural thermoregulation may enhance colonisation of more southerly latitudes or higher elevations as climatic warming proceeds. However, increasing air temperatures may pose a hazard to turtles dispersing or sheltering terrestrially (for example, when water bodies dry during drought). *C. longicollis* appears the best placed of the three species to avoid this hazard through its abilities to thermoregulate behaviourally and to aestivate in terrestrial microenvironments that are buffered against temperature extremes.

Additional keywords: basking, *Chelodina expansa*, *Chelodina longicollis*, *Emydura macquarii*, temperature.

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Introduction

The abilities of poikilothermic animals to control their body temperatures by behavioural means have growing significance as climate change alters their thermal environments (Kearney *et al*. 2009; Gvoždík 2012; Woods *et al*. 2015). In the case of reptiles, the potential for behavioural thermoregulation to modulate responses to climate change has been explored for several squamates (e.g. Aubret and Shine 2010; Buckley *et al*. 2015; Caldwell *et al*. 2017; Rubalcaba *et al*. 2019), but may also be relevant to turtles (Butler 2019).

Freshwater turtle species vary in their abilities and tendencies to alter their body temperatures by behavioural means. Individuals of many species leave the water periodically to bask in sunshine on logs or other objects, a behaviour termed aerial or atmospheric basking (Moll and Legler 1971; Ewert 1976). Hypothesised functions of aerial basking include both thermoregulatory and non-thermoregulatory benefits: elevation of body temperature to speed food digestion and enhance the availability of energy for growth and reproduction, vitamin D synthesis, drying of the skin and shell to assist ecdysis, reduction of body burdens of leeches, algae, fungi and bacteria, and resting in fast-flowing streams (Cagle 1950; Neil and Allen 1954; Boyer 1965; Shealy 1976; Acierno *et al*. 2006; Carrière *et al*. 2008; Bulté and Blouin-Demers 2010). Alternatively, turtles may float at the surface of water bodies with vertical thermal stratification, a behaviour known as aquatic basking (Moll and Legler 1971; Obbard and Brooks 1979). Semiaquatic basking also occurs, whereby a turtle rests on the bottom of shallow water or on a submerged object, with its carapace exposed to air (Boyer 1965; Auth 1975). Any form of basking necessitates a trade-off between its benefits and the associated sacrifice of foraging time, which may limit basking frequency and duration (Bulté and Blouin-Demers 2010; Clavijo-Baquet and Magnone 2017).

Several species of Australian chelid turtles have been observed to bask, but opinions about the thermoregulatory significance of this behaviour differ. Webb (1978) interpreted aerial basking as serving a thermoregulatory purpose because several behaviours of aerially basking captive chelids suggested prevention of overheating of the extremities while allowing the main body mass to warm to a desired temperature. However, Manning and Grigg (1997) found that aerial basking in a riverine population of *Emydura signata* resulted in only occasional elevation of body temperatures above water temperatures. These authors accordingly concluded that aerial basking was not of thermoregulatory significance in their study population, and suggested that the occasional elevated body temperatures that they observed could have been due to accidental exposure to solar radiation or 'behavioural fever' – a response to bacterial infection (Monagas and Gatten 1983). Manning and Grigg (1997) also speculated that aerial basking of *E. signata* might deliver non-thermoregulatory benefits such as inhibiting algal or fungal growth and promoting synthesis of vitamin D.

The capacity or incapacity of freshwater turtles to regulate their body temperatures has growing significance as human activities drive increases in average and extreme environmental temperatures globally. In Australia, average air temperatures have increased by ~1°C over the past century (Kirono *et al*. 2017), and a larger increase is likely in the present one (Grose *et al*. 2017). Correlative bioclimatic models predict substantial shifts in the distributions of Australian freshwater turtle species in response to projected climate change (Ihlow *et al*. 2012; James *et al*. 2017; Graham *et al*. 2019), but such models do not incorporate mechanistic considerations such as thermoregulatory ability, which may modify responses to rising temperatures (Kearney *et al*. 2009).

Here, I analyse data obtained in 1972–78 as part of a Ph. D. project at Monash University, Clayton, Victoria (Chessman 1978), and in minor follow-up studies in 1979–80, to assess the capacity for behavioural thermoregulation of three Australian species of chelid turtles (*Chelodina expansa*, *C. longicollis* and *Emydura macquarii*), and the possible influence of recent feeding. I analyse behaviour and body temperatures in nature and in two types of photothermal gradients in the laboratory. My aim is to shed further light on the capacity and propensity of Australian freshwater turtles for behavioural thermoregulation, its potential benefits, and the implications for responses to projected climate change. Whereas observations in natural environments can reveal the frequency of basking and its relationships to biological and environmental variables, experiments in artificial thermal gradients can ensure that preferred body temperatures are always attainable, in contrast to natural situations where such temperatures may be unachievable (Angilletta *et al*. 2002). Thus, field and laboratory studies can provide complementary information to understand thermoregulation.

Materials and methods

Study species

Chelodina expansa Gray, 1857, the broad-shelled turtle, is a long-necked species with a maximum carapace length of ~500 mm, distributed from south-eastern Queensland through western New South Wales and northern Victoria to south-eastern South Australia (Bower and Hodges 2014). It is carnivorous (Legler 1978; Chessman 1983*b*), inhabits running or standing water bodies that are permanent or near to permanent water (Chessman 1988*a*; Ocock *et al*. 2018), and is not known to aestivate.

Chelodina longicollis (Shaw, 1794), the eastern long-necked turtle, has a maximum carapace length of ~280 mm, and is naturally distributed from north Queensland to southern Victoria and south-eastern South Australia (Kennett *et al*. 2009). It is carnivorous (Chessman 1984*b*; Georges *et al*. 1986), occupies diverse running and standing water bodies, and is particularly adapted to temporary waters by a low rate of evaporative water loss, ability to aestivate, and proclivity for overland migration (Chessman 1984*a*, 1988*a*; Roe and Georges 2007, 2008*a*).

Emydura macquarii (Gray, 1830), the Macquarie turtle, is a polymorphic short-necked species (or species complex) with a maximum carapace length of >400 mm (Georges *et al*. 2006); it is widely distributed in eastern mainland Australia and adjacent islands (Georges *et al*. 2018). It is omnivorous (Chessman 1986; Spencer *et al*. 1998), inhabits running or standing waters that are permanent or near to permanent water (Chessman 1988*a*; Ocock *et al*. 2018), and is not known to aestivate. *Emydura krefftii* and *E. signata* are considered conspecific with *E. macquarii* by Georges and Thomson (2010).

Thermoregulation in nature

Turtles engaged in apparent aerial, aquatic or semiaquatic basking were observed in various parts of Victoria and southern New South Wales between 1972 and 1980, mainly in the Murray Valley between the Murray-Kulkyne Park (34.7°S, 142.5°E) and Torrumbarry (35.9°S, 144.5°E), and in the La Trobe Valley in Gippsland (38.1–38.2°S, 146.5–146.8°E). Some observations were opportunistic in the course of studies of various aspects of turtle ecology and others were targeted through visits to known basking sites.

Basking turtles were often too wary to be captured but some basking fully or partly out of the water were caught by approaching them rapidly from cover and enclosing them in a hand net. Some turtles floating in the warm surface layer of water bodies with vertical thermal stratification were captured by wading slowly into the water and extending a small net, attached to a 3–5-m-long handle, beneath them. Because turtles were generally observed for only a brief time before capture, the duration of prior basking was unknown and they were likely caught at various stages of the basking process.

Body temperatures of captured turtles were mostly determined with a Yellow Springs model 46 TUC telethermometer fitted with a 402 series probe, which was inserted through the cloacal vent for a distance of ~40–70% of the turtle's carapace length. In a few cases, rectal temperatures were taken with a small-diameter mercury thermometer. Air, water-surface and water-bottom temperatures coincident with basking observations were measured with the telethermometer or a standard mercury thermometer.

Thermoregulation in the laboratory

Turtles for experiments in laboratory photothermal gradients were obtained from the Murray Valley, ranged in mass from 100 to 3300 g, and included juveniles, adult males and non-gravid adult females. Prior to experiments, which took place in February–September (first series) or throughout the year (second series), they were housed for several months in plastic tubs of tap water (24 ± 2°C), with artificial lighting for 12 h per day (0700–1900 hours), and fed chopped meat with vitamin and calcium supplements, worms and fish. In order to test the hypothesis that basking is promoted by feeding as a means of enhancing digestion, they were tested in both series in two nutritional states: with no feeding in the week before testing (hereafter, fasted) and immediately after feeding to satiation (hereafter, fed).

Experiments were done during the daylight portion of the cycle to which the turtles had been acclimated. For the first series, a vertical photothermal gradient in water was established by suspending three or four 250-W heat lamps above a cylindrical tank of tap water 0.58 m wide and 0.87 m deep. Room temperature and lamp height were manipulated to establish thermal gradients from cooler bottom to warmer surface water of ~26–33°C or ~29–36°C. However, stirring of the water by turtle movement resulted in some deviation from these temperatures. A vertical wooden ladder with rungs 0.1 m apart, attached to one internal face of the tank, enabled turtles to rest at various depths, but they were not able to exit the water. Turtles (five *C. expansa*, seven *C. longicollis* and 16 *E. macquarii*) were placed individually in the tank, allowed 1 h or more to adjust to their new environment, and then removed at intervals of ~1 h (occasionally ~2–3 h) for measurement of body temperature by telethermometer as in the field. Individual turtles were tested on multiple occasions with 1–4 measurements per session. The telethermometer was also used to measure surface (50-mm depth) and bottom water temperatures in the tank at the same times as turtle body temperatures.

For the second series, a horizontal photothermal gradient in air was established in a rectangular chamber 2.6 m long, 0.8 m wide and 0.8 m deep, with a floor of asbestos sheeting. Three 250-W heat lamps were suspended at equal intervals along the central axis of the chamber at successive heights of 0.2, 0.4 and 0.6 m, and room temperature was not controlled. Turtles (seven *C. expansa*, eight *C. longicollis* and 14 *E. macquarii*) were placed in the chamber individually or in small groups (2–6 turtles), on multiple occasions, and deep-body temperatures were determined at intervals as for the first series, with 1–6 measurements per turtle per session. The air temperature at the coldest point in the chamber was measured with a mercury thermometer at the same time as measurements of turtle body temperatures.

Statistical analysis

Linear mixed models with restricted maximum-likelihood estimation were used to relate turtle body temperatures to environmental temperature (random effect), species and nutritional status (fixed effects), and interactions of these predictors. Separate analyses were conducted for aerial basking in the field, aquatic basking in the field, and the two series of laboratory experiments. Relationships to air, water surface and water bottom temperatures were also analysed separately, because these temperatures were highly correlated with one another. No analysis was done for semiaquatic basking in the field because sample sizes were low, and information on nutritional status was available only for the experiments. Turtle identity, nested within species, was included in the models for the experiments because multiple measurements were made on the same individuals. Linear regressions were also calculated for relationships between body and environmental temperatures. All tests were performed with XLSTAT 2020.1 (Addinsoft 2020), and F and P values were based on Type III tests.

Results

Thermoregulation in nature

No basking was observed for *C. expansa*, but apparent aerial, aquatic and semiaquatic basking were observed for both *C. longicollis* and *E. macquarii*. Although lotic waters were studied extensively, 91% of aerial and 100% of aquatic and semiaquatic basking observations were in lentic waters, especially oxbow lakes and farm ponds in the La Trobe Valley for *C. longicollis* and Lake Boga in the Murray Valley for *E. macquarii*. Basking was observed at all times of year except mid-winter (Table 1), and all three forms of basking were associated with maximum body temperatures in the range 32–34°C (Table 1).

Body temperature during aerial basking was significantly related to simultaneous air and water surface temperatures, and there was a significant difference between species and a significant interaction between species and water surface temperature (Table 2). In *C. longicollis*, body temperature during aerial basking was essentially independent of water surface temperature, whereas in *E. macquarii* the two had a strong positive correlation (Fig. 1). Body temperature during aquatic basking was significantly related to both water surface and water bottom temperatures, being below or about equal to the former and above or about equal to the latter, and there was no significant difference between species (Table 2; Fig. 2). Semiaquatic basking produced body temperatures similar to simultaneous water surface temperatures and above simultaneous water bottom temperatures.

Thermoregulation in the laboratory

Experiments with *C. expansa* in the vertical photothermal gradient in water were discontinued after initial testing because this species seldom left the bottom of the tank. However, *C. longicollis* and *E. macquarii* frequently swam or rested in the tank's upper or middle parts, achieving body temperatures that were often well above water bottom temperatures and sometimes about equal to water surface temperatures (Figs 3 and 4). Body temperatures of these species were significantly related to surface and bottom water temperatures, and there was a significant difference between species (Table 2), with body temperatures of *E. macquarii*

Table 1. Ranges of body temperatures of turtles captured while engaged in apparent aerial, aquatic and semiaquatic basking in nature

Basking type	Species	Period observed	Body temperature range (°C)
Aerial	*C. longicollis*	August–May	18.6–27.3 (n = 10)
	E. macquarii	September–June	12.8–34.2 (n = 39)
Aquatic	*C. longicollis*	September–May	17.8–32.2 (n = 34)
	E. macquarii	October–June	12.6–29.6 (n = 37)
Semiaquatic	*C. longicollis*	November	24.0 (n = 1)
	E. macquarii	October–June	12.0–33.2 (n = 11)

Table 2. Main effects and interactions for linear mixed models of relationships of turtle body temperature to environmental temperature, species and nutritional status

Significant results ($P < 0.05$) are shown in bold font

Data	Environmental temperature included	Main effect: environmental temperature	Main effect: species	Main effect: status	Interaction: environmental temperature × species	Interaction: environmental temperature × status	Interaction: species × status
Field: aerial basking	Air	**$F_{1,41} = 28.7$ $P < 0.001$**	$F_{1,41} = 1.4$ $P = 0.243$		$F_{1,41} = 1.9$ $P = 0.180$		
	Water surface	**$F_{1,38} = 80.2$ $P < 0.001$**	**$F_{1,38} = 5.5$ $P = 0.024$**		**$F_{1,38} = 6.7$ $P = 0.014$**		
Field: aquatic basking	Water surface	**$F_{1,56} = 176.9$ $P < 0.001$**	$F_{1,56} = 0.6$ $P = 0.451$		$F_{1,56} = 1.1$ $P = 0.289$		
	Water bottom	**$F_{1,55} = 37.3$ $P < 0.001$**	$F_{1,55} = 3.6$ $P = 0.063$		$F_{1,55} = 2.8$ $P = 0.102$		
Laboratory: vertical photothermal gradient in water	Water surface	**$F_{1,172} = 23.0$ $P < 0.001$**	$F_{1,172} = 1.1$ $P = 0.298$	$F_{1,172} = 0.3$ $P = 0.584$	$F_{1,172} < 0.1$ $P = 0.974$	$F_{1,172} = 0.24$ $P = 0.626$	**$F_{1,172} = 8.7$ $P = 0.004$**
	Water bottom	**$F_{1,170} = 22.2$ $P < 0.001$**	**$F_{1,170} = 7.5$ $P = 0.007$**	$F_{1,170} = 1.3$ $P = 0.254$	$F_{1,170} = 0.1$ $P = 0.787$	$F_{1,170} < 0.1$ $P = 0.914$	**$F_{1,170} = 11.7$ $P = 0.001$**
Laboratory: horizontal photothermal gradient in air	Minimum air	**$F_{1,529} = 289.6$ $P < 0.001$**	**$F_{2,529} = 3.2$ $P = 0.042$**	**$F_{1,529} = 12.1$ $P = 0.001$**	$F_{2,529} = 0.5$ $P = 0.606$	$F_{1,529} = 3.8$ $P = 0.052$	**$F_{2,529} = 6.0$ $P = 0.003$**

tending to be more elevated above water bottom temperatures than those of *C. longicollis* (Fig. 4). The main effect of nutritional status was not significant but there were significant interactions between species and nutritional status (Table 2), due to a slight tendency for *C. longicollis* to have higher body temperatures when fed than when fasted, and for *E. macquarii* to have higher body temperatures when fasted than when fed (Figs 3 and 4). Slopes of regressions of body on environmental temperatures were always substantially <1, especially for *C. longicollis* (Figs 3 and 4).

In the horizontal photothermal gradient in air, minimum air temperatures ranged from 6.4 to 29.5°C. The highest body temperature was 34.4°C and only four of 562 body temperatures exceeded 32.0°C, even though turtles could probably have achieved higher temperatures by basking beneath the lowest lamp for extended periods. *C. longicollis* and *E. macquarii* sometimes assumed an apparent basking posture under one of the lamps, but this behaviour was never observed in *C. expansa*. The main effects of minimum air temperature, species and nutritional status on body temperature were all significant, as was the interaction between species and nutritional status (Table 2). All three species achieved body temperatures well above minimum air temperatures when the latter was low, but similar to or slightly below minimum air temperatures when the latter was high (Fig. 5). The notable difference among the species was that fed *C. expansa* achieved higher body temperatures than fasted *C. expansa* when minimum air temperature was low, whereas for the other two species the relationship between body temperature and minimum air temperature was independent of nutritional status (Fig. 5). Slopes of regressions of body on environmental temperatures were always appreciably <1 (Fig. 5).

Discussion

All three species considered in this study showed some capacity to buffer their body temperatures against ambient temperature variation in environments that enabled them to do so. This capacity was demonstrated by slopes substantially <1 for regressions of body on environmental temperature both in nature and in the laboratory, particularly for *C. longicollis* (Figs 1–5). For example, in the vertical photothermal gradient in water in the laboratory, mean body temperatures of *C. longicollis* and *E. macquarii* were quite stable as surface and bottom water temperatures varied over a range of ~8°C (Figs 3 and 4). The turtles could have achieved this stability only by tending to select shallower water when ambient temperatures across the gradient were lower and deeper water when ambient temperatures across the gradient were higher.

The high thermoregulatory ability of *C. longicollis* may relate to its proclivity for terrestrial dispersal (Roe and Georges 2007, 2008*a*), because terrestrial activity exposes turtles to a greater range of environmental temperatures than those experienced in the water, including potentially lethal temperatures. However, terrestrial activity of *C. longicollis* often coincides with rainfall (Roe and Georges 2008*b*; Santori *et al*. 2018), which likely reduces risks of both overheating and dehydration.

C. expansa was never observed to bask, either aerially or aquatically. Unlike the other two species, *C. expansa* is an ambush predator (Legler 1978; Chessman 1983*b*), and this

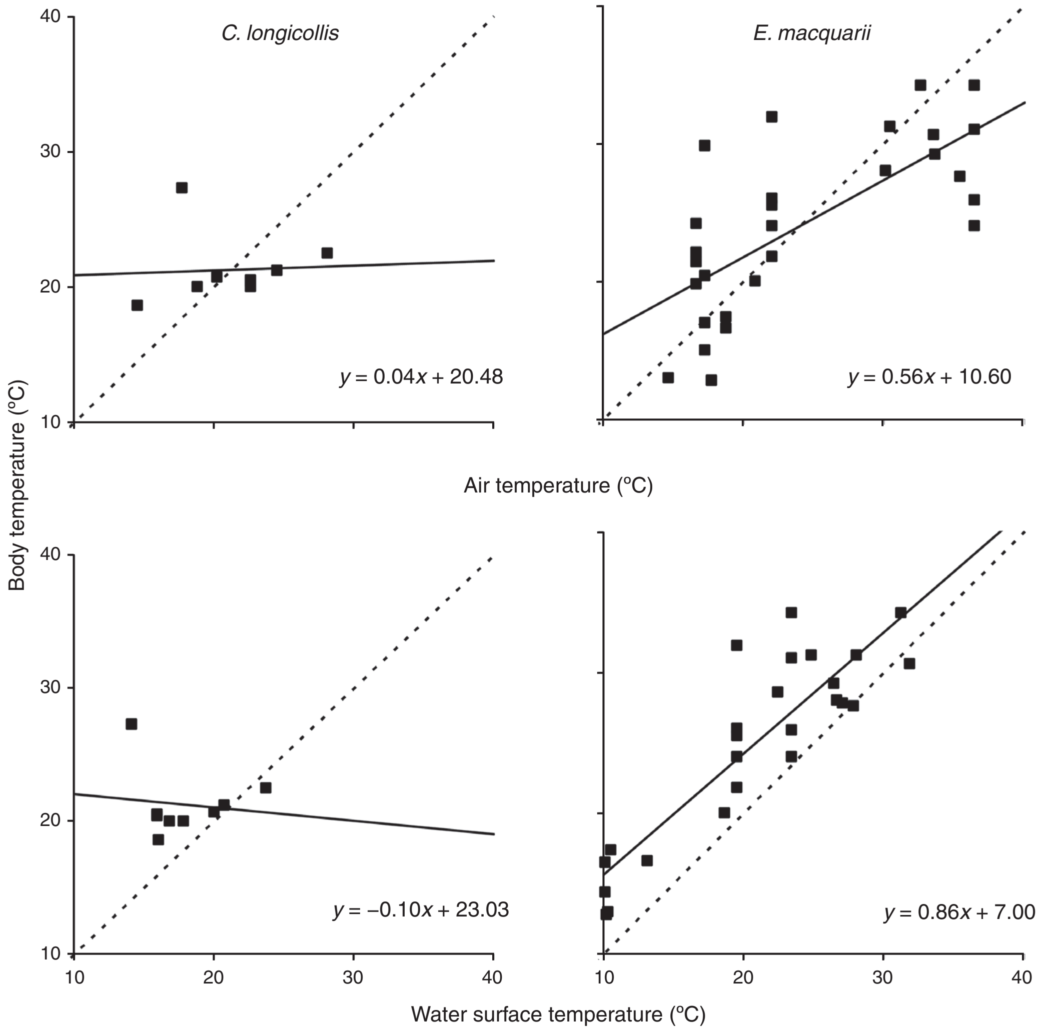

Fig. 1. Relationships of body temperatures of *C. longicollis* and *E. macquarii* to simultaneous air and water surface temperatures during apparent aerial basking in nature. Solid lines and equations are for linear regression and dashed lines represent equality of body and environmental temperatures.

feeding mode may require it to spend large amounts of time resting on the bottom of water bodies, or even buried in sediment with only the head exposed, waiting for prey to approach. Such a necessity could preclude devoting time to basking, which can be rare in other aquatic turtles that are ambush feeders, such as North American chelydrids (Ewert 1976; Brown *et al*. 1990; Brown and Brooks 1991; Harrel *et al*. 1996).

The effect of nutritional status varied among the three species and between the two experimental series. Previous research has also shown that the effect of nutritional status on basking behaviour, environmental temperature selection and body temperatures of turtles varies among both species and experimental conditions (Table 3). It may seem surprising that the effect of feeding was most evident in *C. expansa*, given its apparent reluctance to bask. However, the principal distinction was that when air temperature was low, fasted *C. expansa* tended to have lower body temperatures than fed *C. expansa* and both fed and fasted individuals of the other two species (Fig. 5). Thus a combination of fasting and low ambient temperature apparently reduced the thermophily of *C. expansa*, possibly by inducing a degree of dormancy given that this species appears to be the least cold adapted of the three (Chessman 1988*b*).

The observation that fasted individuals of *C. longicollis* and *E. macquarii* often selected warm and irradiated microenvironments when offered the opportunity to do so suggests that basking in those species may serve purposes other than enhancing food digestion, at least in part. For example, aerial basking, and perhaps even aquatic basking at the surface, might be explained by a requirement for periodic exposure to solar radiation to promote synthesis of vitamin D. This function could account for aerial basking of freshwater turtles often being an occasional activity (Manning and Grigg 1997; Singh 2018) that may occur especially on the first sunny day after a period of cloudy weather (Moll and Legler

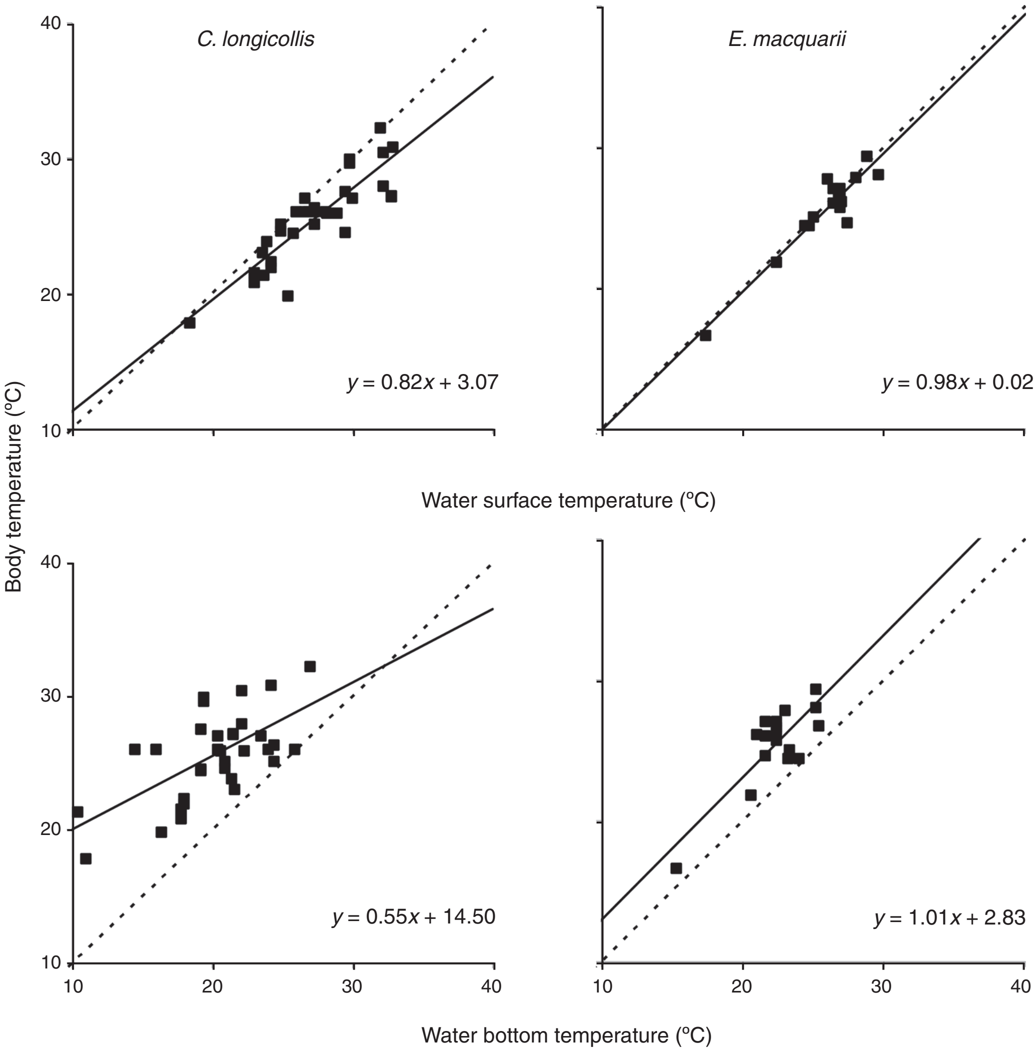

Fig. 2. Relationships of body temperatures of *C. longicollis* and *E. macquarii* to simultaneous water surface and water bottom temperatures during apparent aquatic basking in nature. Solid lines and equations are for linear regression and dashed lines represent equality of body and environmental temperatures.

1971; Auth 1975), or upon being released after a stay in captivity without basking opportunities (Shealy 1976).

In some cases, aerial basking by freshwater turtles may be motivated by ill health. For example, Dodd (1988) found that 20 of 32 aerially basking *Sternotherus depressus* that were examined for disease had advanced symptoms, and Ibáñez *et al*. (2014) reported that male *Mauremys leprosa* that spent more time aerially basking tended to have lower white blood cell counts and a higher frequency of infection with *Hepatozoon* spp. Leech removal has been suggested as an advantage of aerial basking (McAuliffe 1977), and detachment of leeches and harvesting by birds from aerially basking turtles have been reported (Vogt 1980; Selman and Qualls 2008, 2009). However, Readel *et al*. (2008) questioned this benefit because leeches can be very tolerant of desiccation. Chessman (1987) found that *E. macquarii* captured during aerial basking at Lake Boga had a higher incidence of obvious ailments (e.g. ulcers, lesions and eye infections) and parasitism by leeches than non-basking conspecifics. However, the difference was statistically significant only for a burden of more than five leeches.

C. expansa, *C. longicollis* and *E. macquarii* all appeared to consistently avoid raising body temperatures above ~34°C, a maximum close to that found for *E. signata* by Manning and Grigg (1997), and one that leaves a narrow safety margin to thresholds for thermal stress. The onset of uncoordinated movements has been observed at head and posterior body temperatures of ~38–39°C and ~31–36°C respectively in *C. longicollis*, and ~37–38°C and ~36–40°C respectively in *E. macquarii* (Webb and Johnson 1972). Heat-induced muscular spasms have been found to commence at head temperatures of ~42–44°C in *C. longicollis* and body temperatures of ~39°C in *C. expansa*, ~39–42°C in *C. longicollis* and ~40°C in *Emydura krefftii* (Burbidge 1967; Webb and Johnson 1972; Webb and

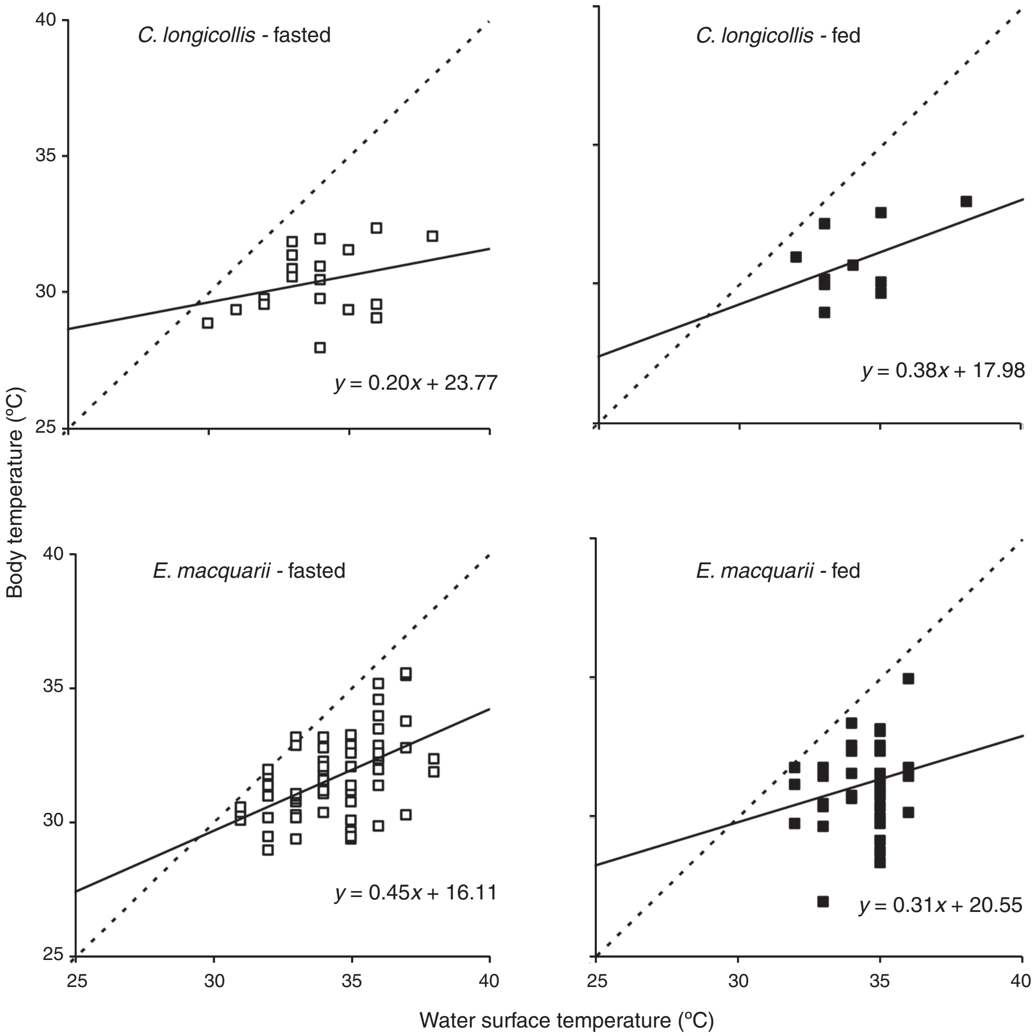

Fig. 3. Relationships of body temperatures of fasted and fed *C. longicollis* and *E. macquarii* to simultaneous water surface temperatures in a vertical photothermal gradient in water in the laboratory. Solid lines and equations are for linear regression and dashed lines represent equality of body and environmental temperatures.

Witten 1973). However, the physiological performance of ectotherms typically peaks close to their upper thermal tolerances (Kearney *et al*. 2009), and aerially basking aquatic cryptodires may leave an even slimmer safety margin, with reported body temperatures as high as 41.5°C (Rowe and Dalgarn 2009).

Average air and water temperatures in south-eastern Australia are projected to increase by ~2°C by the late 21st century (van Vliet *et al*. 2013; Olson *et al*. 2016). Such environmental warming could present both opportunities and threats to freshwater turtles: enhanced activity, feeding and growth when in the water, subject to availability of aquatic habitat and food, but increased risk of overheating and dehydration when on land (Chessman 2018). The current results suggest that, of the three species studied, *C. longicollis* will have the greatest capacity to behaviourally exploit the opportunities and avoid the threats, and *C. expansa* the least. For the latter, the response to warming is likely to be passive, with some range expansion where its distribution is limited by its apparently low level of adaptation to cold conditions (Chessman 1988*b*). For *C. longicollis* and *E. macquarii*, aerial or aquatic basking may enhance the potential to colonise more southerly latitudes or higher elevations, including where translocation by humans overcomes biogeographic barriers to dispersal, as in the introduction of *C. longicollis* to northern Tasmania (Fearn 2013). Aerial basking may also be of some advantage in rivers affected by releases of cold, hypolimnetic water from dams, although Singh (2018) inferred little such benefit for *E. macquarii* in the Murray River downstream of the Hume Dam. Even if the motivation for basking of *C. longicollis* and *E. macquarii* is primarily non-thermoregulatory, aquatic basking has the effect of intermittently raising body temperatures above bottom water temperatures, and aerial basking of raising body temperatures above surface water temperatures. Consequently, both forms of basking are likely to amplify food ingestion and digestion to

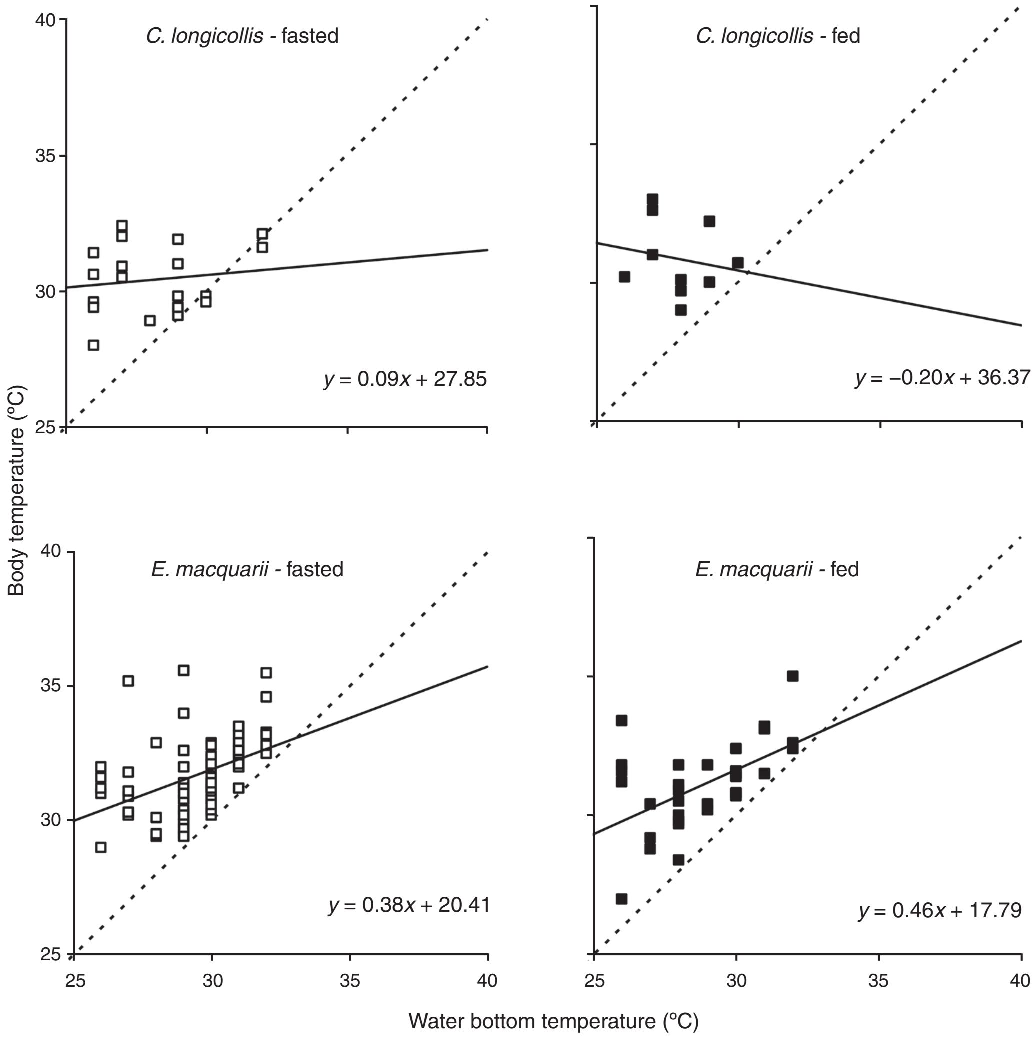

Fig. 4. Relationships of body temperatures of fasted and fed *C. longicollis* and *E. macquarii* to simultaneous water bottom temperatures in a vertical photothermal gradient in water in the laboratory. Solid lines and equations are for linear regression and dashed lines represent equality of body and environmental temperatures.

some degree, because both of these processes are enhanced at higher body temperatures in various freshwater turtle species (Kepenis and McManus 1974; Parmenter 1981; Avery *et al*. 1993; Spencer *et al*. 1998; Mitchell *et al*. 2012).

Increases in water temperatures are unlikely to be sufficient to threaten *C. expansa*, *C. longicollis* and *E. macquarii* at the warmer and more arid extremes of their ranges (Chessman 2018). However, given their critical thermal maxima of only ~40°C, higher air temperatures may be hazardous to turtles dispersing or sheltering terrestrially, for example as a result of water bodies drying under projected increases in the frequency and intensity of drought (Dai 2013; Feng *et al*. 2019). *C. longicollis* appears best placed to avoid this risk through its ability to thermoregulate behaviourally as well as its capacity for aestivation.

C. longicollis cannot swallow food out of water (author's obs.), and the duration of its aestivation in terrestrial environments could be limited by either starvation (Roe *et al*. 2008) or dehydration (Chessman 1978, 1984*a*). Chessman (1978) estimated that without access to water, a *C. longicollis* with a mass of 1 kg and could withstand evaporative water loss for a period of only 40 days at 34°C and 25% relative humidity, but 200 days at 8°C and 60% relative humidity, the lowest temperature and highest humidity considered. Roe and Georges (2007, 2008*a*) documented terrestrial aestivation of *C. longicollis* for apparently continuous periods of up to 480 days, although the turtles were monitored only monthly from April to August. These observations do not conflict with Chessman's (1978) predictions because temperature and humidity adjacent to the aestivating turtles were not reported, and they probably had intermittent opportunities to drink pooled rainwater (Roe *et al*. 2008). Since both metabolism and evaporative water loss of *C. longicollis* are positively related to temperature (Chessman 1984*a*, 2018), its apparent ability to select cooler microenvironments for aestivation (Chessman 1983*a*; Beck 1991), and the availability of such

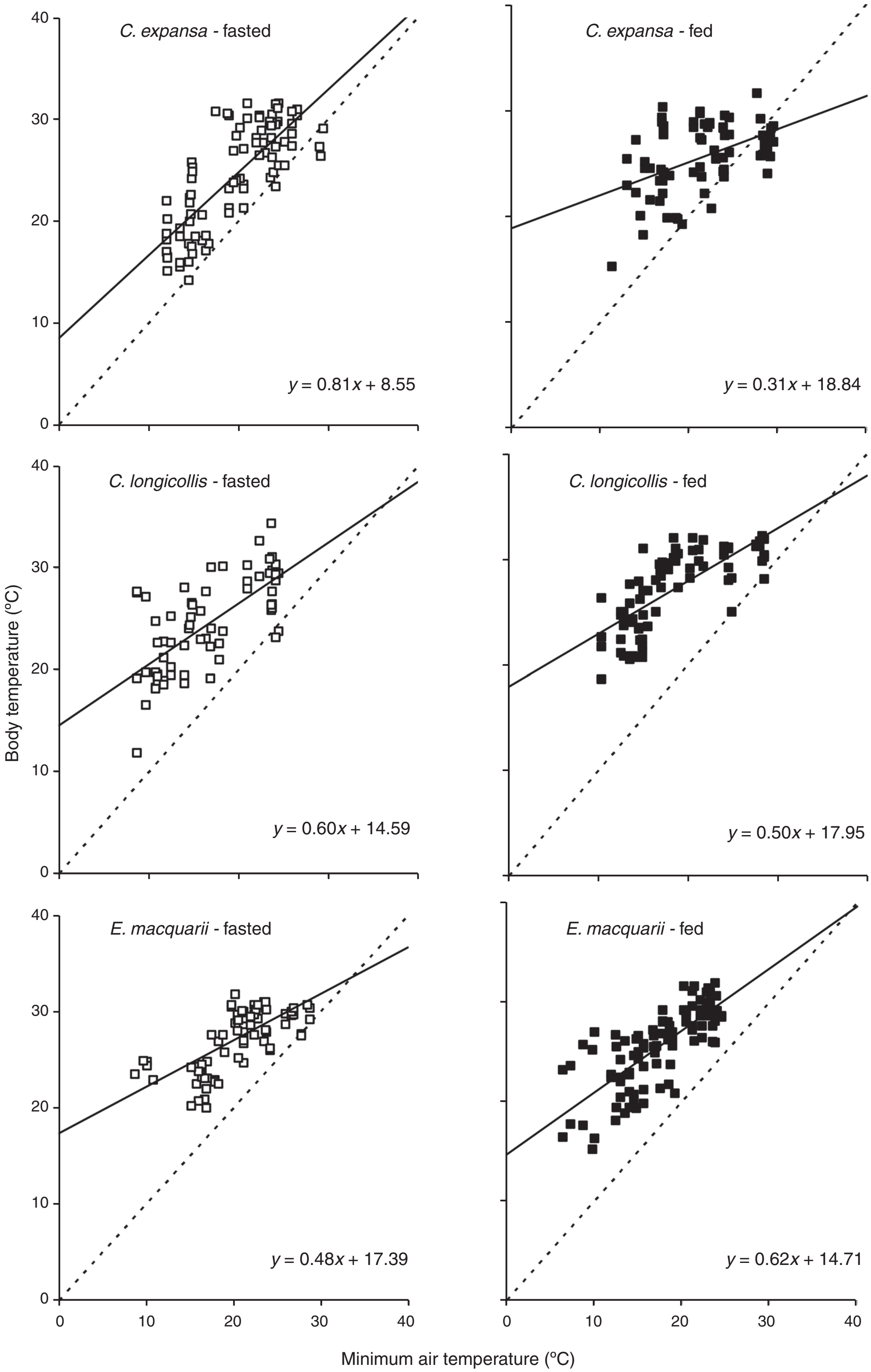

Fig. 5. Relationships of body temperatures of fasted and fed *C. expansa*, *C. longicollis* and *E. macquarii* to simultaneous minimum air temperatures in a horizontal photothermal gradient in air in the laboratory. Solid lines and equations are for linear regression and dashed lines represent equality of body and environmental temperatures.

Table 3. Summary of experimental findings comparing thermal responses of fasted and fed turtles

Species	Experimental setup	Finding	Reference
Chelydra serpentina	Aquatic thermal gradient	Fed turtles selected lower mean temperature if placed in cold end of gradient. No significant difference for turtles placed in middle or warm end of gradient	Knight *et al*. (1990)
Chrysemys concinna	Aquarium with basking platform	No significant difference in basking duration	Hennemann (1979)
Glyptemys insculpta	Terrestrial thermal gradient	Fed juvenile turtles had higher mean body temperature. No significant difference for adult males	Dubois *et al*. (2008)
Glyptemys insculpta	Terrestrial enclosures with water containers and basking sites	Fed juvenile turtles had higher mean body temperature under some circumstances. No significant difference for adult males	Dubois *et al*. (2008)
Mauremys leprosa	Aquarium with basking platform	Fed turtles had higher mean body temperature when basking ceased	Polo-Cavia *et al*. (2012)
Terrapene ornata ornata	Terrestrial thermal gradient	Fed turtles had higher mean body temperature	Gatten (1974)
Trachemys scripta	Aquarium with illuminated and non-illuminated basking platforms	Fed turtles had greater preference for illuminated platform	Moll and Legler (1971)
Trachemys scripta	Water tanks with basking platforms	Fed turtles had longer mean basking time in spring/summer. No significant difference in autumn/winter	Hammond *et al*. (1988)
Trachemys scripta elegans	Terrestrial thermal gradient	Fed turtles had higher mean body temperature	Gatten (1974)
Trachemys scripta elegans	Aquarium with basking platform	Fed turtles had higher mean body temperature when basking ceased	Polo-Cavia *et al*. (2012)
Not specified	Not specified	No difference in number basking or rapidity of basking	Boyer (1965)

microenvironments, could substantially affect its survival of prolonged drought.

Conflicts of interest

The author declares no conflicts of interest.

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