

Short Notes

Basking in the Australian water dragon *Physignathus lesueurii*; why do alpha males not respond to operative temperatures in the same way as adults and sub-adults?

Roger Meek¹, Roger A. Avery²

Abstract. Observations have been made on the behaviour of the Australian water dragon *Physignathus lesueurii* in southeast Australia. Physical models that explore the thermal environment at a similar spatial level as real lizards were related to ontogenetic changes in lizard behaviour. Current theory predicts that a heliotherm will bask in open locations to optimise heating rates in order to attain target body temperatures as quickly as possible. Movement to shaded or partially shaded areas then maintains thermal stability. Regression equations of basking intensity in relation to operative temperatures were employed to test this theory. The behaviour of adults, which were not alpha males, and sub adults was in agreement with the prediction, but the behaviour of alpha males was not: the regression coefficient did not differ significantly from 0. In general, sub adult lizards were more active and fed more often than larger lizards although this relationship changed with different times of the day. The results suggest differing costs for thermoregulation for different size classes, particularly in alpha males where territory defence has a key role.

Keywords: alpha-males, behaviour, lizards, operative temperatures.

The behaviour of lizards is intimately linked to the thermal aspects of their environment and temperature, mainly due to its impact on physiology, has played a key role in their behavioural evolution (Fox et al., 2003). In addition, size differences and their effects on heating and cooling rates may also influence behaviour and since they have no larval stage, juvenile and adult lizards have broadly similar ecological requirements and in general occupy similar environments. These effects can be readily observed. Consider a range of hypothetical heliothermic lizards of the same species ranging from juveniles to adults. When weather conditions are optimal they bask and achieve target body temperatures and are free from predatory or social in-

teractions. However, due to lower skin surface area to body mass geometry, larger lizards will experience an increase in basking time to attain target body temperatures and other activities may be delayed as a consequence. This is a crucial aspect of ectothermy, particularly if the animals are heliothermic; for example, compared to individuals that do not bask, giant tortoises can double the rate of increase in body temperature by basking (Gerlach, 2005). A heliotherm can be expected therefore, particularly during the earlier part of the day, to optimise basking opportunities in order to attain target body temperatures as quickly as possible. However in real lizards ecological costs may impact on behavioural thermoregulation, for instance predation pressures, food gathering opportunities, territory defence and reproductive behaviour may influence behaviour ontogenetically. We tested this hypothesis in the Australian water dragon *Physignathus lesueurii* in respect of the behaviour of alpha males during the breed-

1 - Rue Georges Clemenceau, Chasnais, 85400, France
e-mail: Rogermeek85@aol.com

2 - Bishops Avenue, Bishopsteignton, Devon, TQ14GRE, UK
e-mail: roger.avery1@btinternet.com

ing season. At this time territorial boundaries are being established and the level of agonistic behaviour between alpha males at its most intense and hence the possibility of conflict between social interactions and thermoregulatory behaviour most likely (e.g. Fox and Shipman, 2003). The focal lizards were from a colony of *P. lesueurii* living at the Australian Botanical Gardens, Canberra, ACT, a natural population used to the presence of humans enabling behaviour to be observed with minimum disturbance. Although predators that may have influenced thermoregulation were present (Huey, 1982) – for example the eastern brown snake *Pseudonaja textilis*, (Jenkins and Bartell, 1980) other additional factors that might influence thermoregulatory behaviour are minimal: it is a “low cost” thermal environment in the sense of Huey and Slatkin (1976).

The observations were made during the months of November and December 2000 at the Australian Botanical Gardens at the base of Black Mountain in Canberra, Australian Capital Territory. The focal population was mainly resident at the Tasmanian Garden. This habitat consisted of two large ponds of approximate diameters of 15-20 metres, one surrounded by large boulders and low growing vegetation. Tall trees of various species enclosed the second pond to the extent that only dappled sunlight reached the water surface or surrounding substrate. Most of the area was surrounded by native Eucalypt forest that also formed part of the dragons’ habitat. Behaviour patterns were defined in the following manner 1) *basking*, inactive and fully exposed to the sun’s rays 2) *partial basking*, the lizard was subject to a mosaic of sunlit and shaded light falling on the body 3) *shade*, no sunlight at all on the body of an inactive lizard and in overcast weather under vegetation cover and 4) *locomotory movement*, this is in general self explanatory but was recorded only if the animal actually traversed a set distance; movement to change orientation was not considered locomotory movement.

Data were categorized into three time periods: – morning, which was approximately 0830-1100 hours; midday, 1100-1400 hours and afternoon 1400-1700 hours. The behaviour of individual lizards was recorded continuously in terms of type of and duration of each bout of behaviour – e.g. basking, locomotory movement etc., by tracking each lizard. To minimise behaviour disturbance, lizards were observed and not captured. Total observation time for all animals totalled 75 hours 48 minutes. However, because of the difficulty of keeping track on lizards it was not always possible to follow certain animals for the complete daily period and hence some lizards had limited data sets that concerned particular periods of the day, nevertheless if the information was considered valid it was used. Our method

of recording behaviour also suffered from the disadvantage that there was no non-invasive means for distinguishing between adult males and adult females; alpha males could be distinguished on the basis of large size, proportionally larger heads and their coloration. Sub-adults could not be sexed non-invasively. There were thus three categories of lizards using the above criteria (1) alpha males ($n = 8$), these were very large animals with distinct secondary sexual colouration which are usually more than 25 cm snout to vent length, (2) other adults ($n = 8$) which were in general above 14 cm snout vent length. Determination of sex was not always unequivocal in these animals; for convenience, they are referred to throughout the remainder of this paper as ‘adults’, (3) sub-adults ($n = 5$) these were lizards of approximately between 6 and 14 cm snout vent length. Although we attempted to gather data on juveniles we found this almost impossible due to their particularly rapid movement in the dense vegetation.

To gather information on the general thermal qualities of the habitat operative temperatures were measured using 4 water filled black painted copper cylinders (Bakken, 1992) measuring 16.5 cm in length and 5.5 cm in diameter and 1 mm thick and placed in key locations of the habitat: – one in full sunlight where the highest operative temperatures were expected – defined here as $T_{o(open)}$, two were placed in dappled sunlight to record intermediate operative temperatures ($T_{o(dapple)}$) and one in full shade ($T_{o(shade)}$) to record the lowest operative temperatures. Alcohol thermometers were inserted into the centre of the cylinder. Measurements were made every 10 minutes or so or when there was a behaviour change. Operative temperatures were used rather than air temperatures as radiation load and the convective effects of wind also influence the temperature of an organism and hence they better represent an approximate single measure of the position of the lizard in the field environment (Bakken, 1992). Hollow-walled copper tubes have a low heat capacity and respond readily to changes in radiation levels and have value in predicting the amounts of time operative temperatures exceed physiological threshold temperatures and have been shown to simulate the body temperatures of live lizards reasonably accurately (e.g. Fox and Shipman, 2003). In *P. lesueurii* the physiological threshold body temperature that initiates panting is 34.8°C and hence by definition target body temperatures must be lower (Heatwole et al., 1973). It was assumed that the lizards could achieve target body temperature between the extremes of operative temperatures by locating in the appropriate microhabitats and could track operative temperatures in dappled sunlight by spending 50% of time in either sun or shade or by positioning half in sun and half in shade (Christian et al., 1983).

To avoid pseudo-replication and inflating the degrees of freedom, statistical analysis has been applied to the means of behaviours of individual lizards during the various time periods – early morning (before 1100 hrs) midday (1100-1400 hrs) and afternoon (after 1400 hrs). This was related the corresponding means of operative temperatures. Statistically this method employs the properties of the Central Limit Theorem, that is the mean of the means is equal to

the population mean. Regression analysis was used to relate operative temperatures to basking intensity with operative temperatures treated as the independent variable. In this test if operative temperatures had an effect on basking, the regression coefficient would be negative – basking would decline as operative temperatures increased, and be significantly different from 0. A *t*-test at $n - 2$ degrees of freedom (Bailey, 1981) was used to test this assumption and for differences between coefficients.

Figure 1 shows operative temperatures and the thermal environment that these lizards are operating in. Plotting basking against $T_{o(open)}$ (fig. 2) shows that adults and sub-adults fit the paradigm of a basking heliotherm – the amount of basking decreases with increases in operative temperature. The regressions coefficients gave:

$$\begin{aligned} \text{Basking} &= 165.0 - 3.26 \pm 0.60T_{o(open)}, \\ r^2 &= 61.8\%, \quad n = 20 \end{aligned} \quad (1)$$

for sub-adults,

$$\begin{aligned} \text{Basking} &= 159.0 - 3.19 \pm 0.70T_{o(open)}, \\ r^2 &= 74.4\%, \quad n = 9. \end{aligned} \quad (2)$$

The coefficients were not significantly different from each other ($p > 0.05$) but were significantly different from 0 (adults, $t = 5.18$, sub-adults $t = 5.44$, both $p < 0.001$). Therefore the data for adults and sub-adults were pooled and gave,

$$\begin{aligned} \text{Basking} &= 166.9 - 3.32 \pm 0.44T_{o(open)}, \\ r^2 &= 67.9\%, \quad n = 29 \end{aligned} \quad (3)$$

with, as expected, the regression coefficient again significantly different from 0, $t = 7.56$, $p < 0.001$. A graph of the pooled adult and sub adult data sets is shown in fig. 2 with a line running through the data representing equation (3). Statistically, alpha males did not fit the paradigm and gave,

$$\begin{aligned} \text{Basking} &= 56.3 - 0.86 \pm 0.68T_{o(open)}, \\ r^2 &= 8.9\%, \quad n = 18 \end{aligned} \quad (4)$$

with the regression coefficient not significantly different from 0 ($t = 1.28$, $p = 0.21$) and significantly different from both adults ($t = 2.7$,

$df = 34$, $p < 0.02$) and sub-adults ($t = 2.4$, $df = 28$, $p < 0.05$). Figure 2B shows the data with the regression line calculated from equation (4).

Alpha males travelled smaller distances in the early part of the day (before 1100 hrs, $mean = 9.6 \pm 7.6$ metres, $n = 5$). This peaked during the middle of the day ($mean = 28.8 \pm 23.6$ metres, $n = 6$) then declined from 1400 hrs onwards ($mean = 15.2 \pm 16.6$ metres, $n = 7$). However, the degree of overlap in the data sets was high and neither ANOVA nor repeated measures ANOVA was able to detect significant differences in the data (ANOVA on mean values; $F_{(2,15)} = 1.72$, $p = 0.21$). A similar general pattern was observed in adults where locomotory movement was low before 1100 hrs ($mean = 5.13 \pm 2.9$ metres) but increased through the day (1100-1400 hrs, $mean = 17.6 \pm 13.1$ metres; after 1400 hrs, $mean = 18.8 \pm 10.7$ metres) with the differences significant between early morning and the later part of the day ($t = 2.74$, $p = 0.02$, $df = 10$). These patterns of movement differed from sub-adults where the distances travelled were greater in the morning period ($mean = 29.3 \pm 3.1$, $n = 4$), presumably due to faster heating rates and hence attainment of working body temperatures earlier, but then declined as the day progressed (1100-1400 hrs, $mean = 14.7 \pm 11.3$, $n = 4$; after 1400 hrs, $mean = 12.6 \pm 9.8$, $n = 4$) with the differences significant ($F_{(2,9)} = 4.16$, $p = 0.05$).

Locomotory movement due to interactions with other individuals differed as the day progressed. In terms of the mean number of disturbances during time periods sub-adults ($n = 4$) were disturbed the most ($mean = 1.25 \pm 1.2$, $n = 12$) followed by disturbance to alpha males ($mean = 0.77 \pm 1.2$, $n = 18$); adults were least disturbed ($mean = 0.38 \pm 0.7$, $n = 18$). The statistical differences concerned the early morning period before 1100 hrs when sub-adults ($mean = 2.0 \pm 0.8$) were disturbed more frequently than alpha males ($mean = 0.6 \pm 0.9$, $t = 2.42$, $p = 0.046$). We did not observe adult dis-

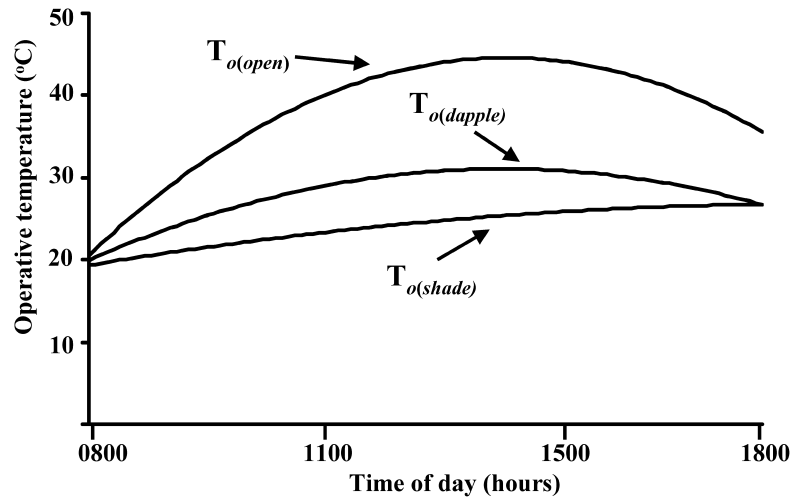


Figure 1. Changes in operative temperatures based on the mean values recorded per hour. The lines of best fit were found using polynomials and gave for $T_{o(open)}$, $y = -0.6255x^2 + 7.7551x + 20.558$; $T_{o(dapple)}$, $y = -0.294x^2 + 3.6169x + 19.935$ and $T_{o(shade)}$, $y = -0.0616x^2 + 1.3589x + 19.347$. For graphical clarity regression lines only are shown. See text for further discussion.

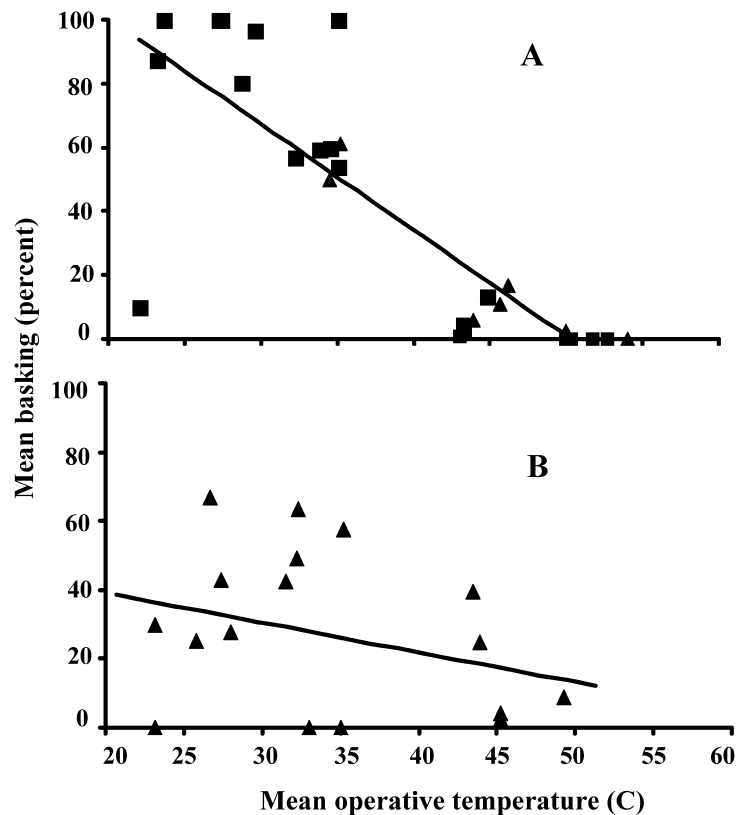


Figure 2. Differences in mean basking intensity in *P. lesueurii* in relation to changes in mean operative temperatures. Figure 2A shows pooled data sets for adults (square symbols) and sub adults (triangles); fig. 2B shows data for alpha males. The lines running through the data sets were calculated from equation (3) in fig. 2A and equation (4) in fig. 2B. See text for further details.

turbance before 1100 hrs but this did occur later in the day (1100-1400 hrs, $mean = 0.5 \pm 0.8$; after 1400 hrs, $mean = 0.6 \pm 0.8$). Conflict between alpha males was greatest between 1100-1400 hrs ($mean$ number of conflicts = 1.7 ± 1.5 per time period) and was minimal after 1400 hrs ($mean = 0.1 \pm 0.4$ per time period). These interactions between alpha males represent higher levels of aggression than seen in the other two classes, which were usually simple exchanges rather than more serious conflict. Sub-adults ($mean = 7.7 \pm 6.25$, $n = 12$) fed more frequently than either alpha males ($mean = 1.78 \pm 2.86$, $n = 18$) or adults ($mean = 3.25 \pm 4.39$, $n = 17$). Feeding was higher in sub adults for most of the day but was significantly higher only during the morning period (two sample t -tests, versus alpha males $t = 10.3$, $p = 0.002$, $df = 7$; versus adults $t = 9.9$, $p = 0.002$, $df = 3$).

The behaviour of adults and sub-adult *P. lesueurii* in general fitted the paradigm, particularly that of basking in relation to operative temperatures, which was high when operative temperatures were low and decreased as operative temperatures increased. Similarly locomotory movement and feeding in adults and sub-adults were as expected in a basking heliotherm, where after periods of basking locomotory activity tended to increase as the day progressed. For example, high levels of early morning locomotory movement and feeding in sub adults were presumably due to faster heating rates and the earlier attainment of thermal optimum body temperatures. The behaviour of alpha males did not follow this pattern. Basking was non-linear, gross distances travelled throughout the day were approximately equal in each time period and there were higher incidences of conflict. The latter in particular indicates that not all *P. lesueurii* behaviour was thermoregulatory and that territory defence has a key behavioural role. Conflict between alpha males, which was observed almost routinely at the same time each day and often between the

same individuals, must impose a constraint on other activities.

Does territory defence involve operative temperatures? The relationship is often complex, but it is known that when operative temperatures are optimal, male lizards may be intolerant of home range overlap by other males (e.g. Fox and Shipman, 2003) and this is what we appear to have observed in *P. lesueurii*. Late emergence from overnight aquatic retreats in alpha male *P. lesueurii* is also of interest and may in part be a consequence of low initial water temperatures (19-21°C) that only slowly increased to 24-25°C. Why do alpha males spend the night in water? A possibility is that site tenure in aquatic areas is critical for alpha males but the cost of remaining in water overnight is that low early morning water temperatures – and hence low body temperatures, impose a constraint on territory defence in the early part of the day by restricting body temperature elevation. The relationship between behaviour and operative temperatures in lizards is complex and it is known that certain species may remain active at high temperatures to defend territory (Gier, 2003; Fox and Shipman, 2003). For example, *Dipsosaurus dorsalis* tolerates very high midday high temperatures as a cost of maintaining above ground activity to defend territory in desert habitats (Gier, 2003). However, this is not always the case. An alternative strategy was found in male *Sceloporus merriami* where territory defence and mate acquisition is achieved by abandoning high temperature microhabitats in the morning and elevating body temperatures in the evening, thus extending habitat use (Grant, 1990); a similar strategy has been observed in the Australian *Pogona barbata* but over seasons (Schauble and Grigg, 1998).

Intense territory defence is possibly a seasonal activity and in lizards it is known that males attempt to defend and monopolise territories important to females at certain times of the year. For example, nesting sites are a key resource and may be defended by males (review in Fox et al., 2003) and in our study area

were located in open sunny locations close to the territories of two alpha males (Meek et al., 2001). This might suggest that *P. lesueurii* defends thermal space as found in certain other lizards (e.g. Gill, Perez-Mellado and Guerrero, 1990). However, microhabitats exposed to the sun, although optimal for a heliotherm, may also be thermally lethal at certain times of the day and hence difficult to defend – at our site operative temperatures approached 60°C, and thus special strategies to defend territory may be required. A final point is to note that our data are based on the mean values of individual lizards and operative temperatures, which reduces the sample sizes and hence the degree of certainty in the results. This obviously sets limits on the amount of insight we have into *P. lesueurii* behaviour and so further studies are needed to clarify this interesting aspect of their ecology.

Acknowledgements. We thank the Australian Botanical Gardens, in particular Greg Sattler, for allowing us to work on the water dragons living in the gardens. Special thanks also to members of the Frost family, Jim, Charlie and Jeanette for their generous hospitality and assistance throughout the study period.

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Received: June 12, 2007. Accepted: September 24, 2007.