

Cool running: locomotor performance at low body temperature in mammals

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Mammalian torpor saves enormous amounts of energy, but a widely assumed cost of torpor is immobility and therefore vulnerability to predators. Contrary to this assumption, some small marsupial mammals in the wild move while torpid at low body temperatures to basking sites, thereby minimizing energy expenditure during arousal. Hence, we quantified how mammalian locomotor performance is affected by body temperature. The three small marsupial species tested, known to use torpor and basking in the wild, could move while torpid at body temperatures as low as 14.8–17.9°C. Speed was a sigmoid function of body temperature, but body temperature effects on running speed were greater than those in an ectothermic lizard used for comparison. We provide the first quantitative data of movement at low body temperature in mammals, which have survival implications for wild heterothermic mammals, as directional movement at low body temperature permits both basking and predator avoidance.

Keywords: body temperature; lizard; marsupial; running speed; torpor

1. INTRODUCTION

Locomotor performance is fundamental for many behaviours, including predator avoidance, territoriality, mating interactions and foraging, and therefore directly relates to an animal's fitness and survival [1,2]. Locomotor performance has been examined in detail with regard to size and maximum aerobic capacity in mammals, whereas temperature effects on running speed over a wide range of body temperatures (T_b) have been quantified only in ectotherms, such as lizards [1,3]. However, low T_b are also expressed in many heterothermic mammals and birds during torpor that is characterized by controlled and pronounced reductions of T_b and metabolism [4]. While torpor is the most effective means for energy conservation available to endotherms [4–7] and torpid animals can sense external stimuli [8], its widely assumed downside is a lack of directional movement [9], and thus an increased vulnerability to predation [10]. In contrast, recent studies have shown that small arid zone marsupials and elephant shrews (Macroscelidea), which

regularly use torpor in the wild, are in fact capable of moving while torpid at low T_b . These mammals move to basking sites and expose themselves to solar radiation to passively rewarm from torpor, which minimizes the energetic costs of raising T_b at the end of a torpor bout [11–14]. Currently, there are no data on the effects of low T_b , characteristic of torpor, on running speed in mammals. A previous study on round-tailed ground squirrels (*Spermophilus tereticaudus*) revealed no difference in speed over a 11°C T_b range, however, the minimum T_b measured was 30°C [15], which is above that often used to define torpor ($T_b < 30^\circ\text{C}$).

As locomotor function is crucial for movement in some torpid mammals, both when moving to basking sites and/or avoiding predators, we investigated running speed as a function of T_b in three small (11.7–35 g) dasyurid marsupials that use torpor and basking in the wild [14,16,17]. A similar-sized agamid lizard was examined to provide a comparison with an ectothermic species.

2. MATERIAL AND METHODS

Our study animals were four kalutas (*Dasykaluta rosamondae*, mean body mass \pm s.d.; 35.1 ± 2.0 g) trapped in Port Hedland, Western Australia (20°18' S, 118°36' E), six captive-bred dunnarts (*Sminthopsis crassicaudata*, 17.5 ± 1.9 g), five planigales (*Planigale gilesi*, 11.7 ± 1.3 g) captured at Kinchega National Park, New South Wales, Australia (32°32' S, 142°17' E) and three jacky lizards (*Amphibolurus muricatus*, 24.2 ± 8.7 g) caught near Armidale, New South Wales, Australia (30°32' S, 151°40' E).

All animals were run on an illuminated 5 m \times 20 cm running track and were videotaped with a Samsung digital camera to determine running speeds (for detailed methods, see the electronic supplementary material). Running speed was recorded over a range of T_b that was measured using small implantable temperature-sensitive transmitters or using a thermocouple to measure the rectal/cloacal temperature.

Torpor was induced in the marsupials to obtain running speed at low T_b by exposing them to low ambient temperatures (T_a) and removing food overnight. To achieve the desired T_b in the lizards, animals were placed into temperature-controlled cabinets for more than 2 h with a T_a range of 5–38°C. For both mammals and lizards, T_b was measured immediately before each run, and running speed was recorded over a range of T_b , as the animal re-warmed. Maximum running speed was recorded for each T_b over a distance of high continuous running speed.

3. RESULTS

All animals were able to move at low T_b (kalutas 17.9°C; dunnarts 15.3°C; planigales 14.8°C; lizards 8.4°C) and exhibited similar sigmoid curves of running speed against T_b (figure 1). Running speed was significantly affected by T_b (ANOVA with mixed procedure; kalutas: $F_{18,22} = 24.14$, $p < 0.001$; dunnarts: $F_{22,41} = 57.82$, $p < 0.001$; planigales: $F_{25,51} = 154.13$, $p < 0.001$; lizards: $F_{24,19} = 38.77$, $p < 0.001$); individuals of each species did not differ in their thermal response (ANOVA with mixed procedure; kalutas: $F_{1,2} = 4.62$, $p = 0.16$; dunnarts: $F_{1,4} = 0.00$, $p = 0.96$; planigales: $F_{1,3} = 6.63$, $p = 0.08$; lizards: $F_{1,1} = 5.86$, $p = 0.25$).

Maximum running speed ranged from 2 to 3 m s⁻¹ and occurred between T_b 35°C and 40°C in all species. Although maximum running speeds in the small planigales were lower than in the larger kalutas and lizards (Tukey's, $p < 0.05$), running speed and body mass were only weakly correlated (linear regression; $r^2 = 0.44$, $p < 0.01$), likely because of the small mass range. The effect of T_b on running speed differed significantly among species (ANOVA with mixed procedure; $p < 0.05$), with the exception of planigales and dunnarts ($p > 0.05$). At T_b 20°C, running speed differed significantly

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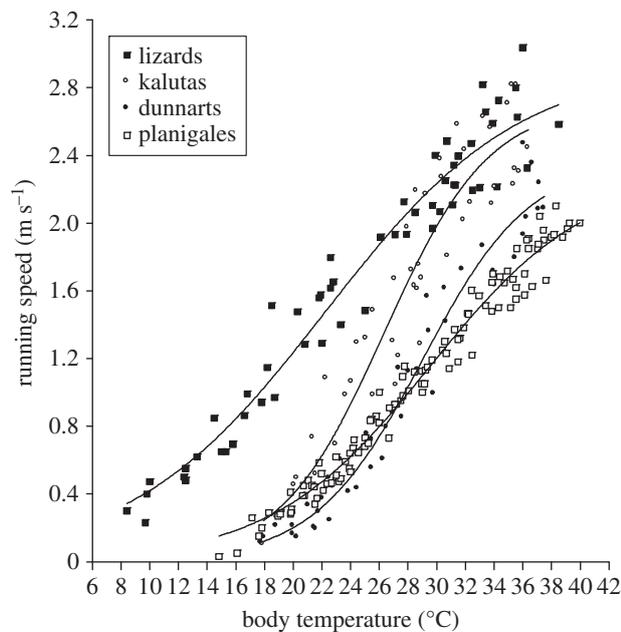


Figure 1. Running speeds over a range of body temperatures (T_b) of planigales, kalutas, dunnarts and lizards. Data points represent maximum values of individuals of a species at the measured T_b . Running speed against T_b was fitted with sigmoid curves: [planigales: $y = 2.31/(1 - e^{-(x-29.53)/5.54})$; kalutas: $y = 2.71/(1 + e^{-(x-26.37)/3.63})$; dunnarts: $y = 2.38/(1 + e^{-(x-29.01)/3.77})$; lizards: $y = 2.95/(1 + e^{-(x-22.21)/6.81})$].

between the marsupials and the lizard (Tukey's, $p < 0.05$); in the marsupials, running speed was less than 0.5 m s^{-1} , whereas in the lizards, running speed was approximately 1.5 m s^{-1} . At T_b approximately 10°C , running speed in the lizards was less than 0.5 m s^{-1} , similar to the marsupials at T_b approximately 20°C .

In all species, running speed at T_b $30\text{--}40^\circ\text{C}$ showed a lower thermal dependence (low Q_{10} coefficients of 1.3–2.0) than at T_b $20\text{--}30^\circ\text{C}$ (Q_{10} coefficients of 1.8–6.5; figure 2; paired t -test, $p < 0.05$). At T_b $30\text{--}40^\circ\text{C}$, Q_{10} were similar in most species, but differed in dunnarts and lizards (Tukey's, $p < 0.05$). In all species, the Q_{10} was higher at T_b $20\text{--}30^\circ\text{C}$ in comparison with the Q_{10} at T_b $30\text{--}40^\circ\text{C}$ and did not differ among the marsupials. However, the Q_{10} of kalutas and dunnarts at T_b $20\text{--}30^\circ\text{C}$ were greater than those of the lizards (Tukey's, $p < 0.05$), whereas planigales and lizards were indistinguishable.

4. DISCUSSION

Our study provides the first quantitative data on locomotor performance at low T_b in mammals. We show that heterothermic mammals can move directionally while torpid at T_b as low as 14.8°C . The thermal response of locomotor performance we observed was qualitatively similar in marsupials and lizard, following sigmoid curves as in ectothermic organisms in general [18].

The maximum steepness of these sigmoid curves, with Q_{10} well beyond the generally accepted range for thermal dependence of biological functions (i.e. Q_{10} approx. 2–3), shows that running speed is not simply owing to temperature effects on generic biochemical reactions, but rather a complex interaction of neurological, muscular, metabolic and other functions affected differently by

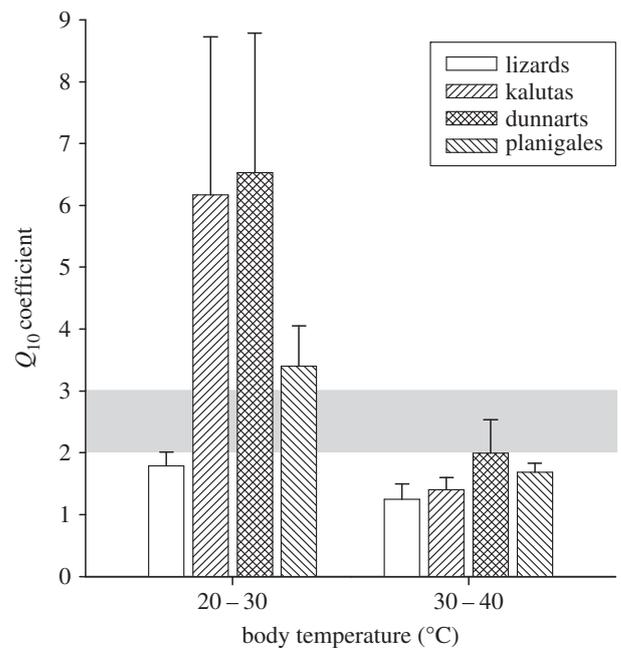


Figure 2. Q_{10} coefficients of running speed (mean \pm s.d.) at T_b $20\text{--}30^\circ\text{C}$ and T_b $30\text{--}40^\circ\text{C}$ for planigales, kalutas, dunnarts and lizards. Shaded area corresponds to $Q_{10} = 2\text{--}3$.

temperature [19]. The Q_{10} of maximum shortening velocity and maximum power output ranged between 1.7–2.4 in isolated mouse muscle between 20°C and 30°C [20], well below values we observed for running speed in our study. With regard to muscle performance of intact animals, important in the context of our study, temperature affects tetanic tension and neural transmission [21], but also affects muscle power output, thus limiting limb cycling frequency [22].

Although the temperature-dependence of locomotion in reptiles and mammals and maximum running speed was similar, functional differences were apparent. Running speeds of the mammals at T_b 20°C were similar to those of the lizards at T_b 10°C . Overall, running speed was less affected by T_b in the lizard ($Q_{10} \leq 2$) than in mammals (Q_{10} 1.8–6.5), and the lizard could move at lower T_b . This is likely related to the extent aerobic/anaerobic metabolism is used. Reptiles have high capacities for anaerobic metabolism enabling them to run at comparable speeds to mammals, but reptiles have less stamina [18]. By contrast, mammals rely heavily on aerobic metabolism and muscle activity is therefore dependent on a continuous blood supply. As cardiac function is strongly reduced at low T_b in heterothermic mammals [23], aerobic metabolism and running speed will be impaired.

Planigales were able to move at the lowest T_b measured, and running speed was less affected by T_b than in the other mammals, reflecting the lowest recorded T_b of 13.8°C observed in the species during basking [16]. To our knowledge, this is the lowest T_b at which purposeful and directional movement has been observed in any mammal in the wild. The difference in the minimum T_b at which movement was observed in the heterothermic mammals reflects different species-specific T_b minima that are metabolically defended during torpor [4,7]; in the lizard, it was the lowest T_b at which movement was recorded.

Reptiles must function effectively at low T_b to avoid predators and capture prey [24]. The main function of the ability by torpid mammals to move from shelters to the surface and seek sun exposure appears to be energy conservation, because small marsupials can save up to 80 per cent of arousal costs by basking [13]. Although basking potentially exposes animals to predators, these cool mammals do not, however, move far from their burrows or rock crevices and often stay motionless while basking [11,14]. They also remain highly alert and capable of astonishing mobility, including the ability to scale vertical cliffs [11,16] and therefore can escape from predators even at relatively low speed. Some other heterothermic mammals, such as bats, echidnas or bears forage even in the open at low T_b [6,25–27]. However, these species can avoid predation because they can either fly, have sharp spines or simply are fierce and large. Thus, it appears that movement at low T_b fulfils important functions in many heterothermic mammals, but its use is adjusted according to the predation pressure experienced in the wild.

The study was approved by the Animal Ethics Committee at the University of New England.

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