

Are day-active small mammals rare and small birds abundant in Australian desert environments because small mammals are inferior thermoregulators?

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Abstract Small desert birds are typically diurnal and highly mobile (hence conspicuous) whereas small non-volant mammals are generally nocturnal and less mobile (hence inconspicuous). Birds are more mobile than terrestrial mammals on a local and geographic scale, and most desert birds are not endemic but simply move to avoid the extremes of desert conditions. Many small desert mammals are relatively sedentary and regularly use physiological adjustments to cope with their desert environment (*e.g.* aestivation or hibernation). It seems likely that prey activity patterns and reduced conspicuousness to predators have reinforced nocturnality in small desert mammals. Differences such as nocturnality and mobility simply reflect differing life-history traits of birds and mammals rather than being a direct result of their differences in physiological capacity for tolerating daytime desert conditions.

Australian desert mammals and birds

Small birds are much more conspicuous in Australian desert environments than small mammals, partly because most birds are diurnal, whereas most mammals are nocturnal. Despite birds having over twice the number of species as mammals (ca. 9600 vs. 4500 species, respectively), the number of bird species confined to desert regions is relatively small, and their speciation and endemism are generally low (Wiens 1991). In contrast, desert endemism is relatively high for mammals (Kelt *et al.* 1996).

In Australia there are 522 species of small birds and 163 species of small mammals (≤ 600 grams). The mammals are distributed evenly amongst the marsupials (52), rodents (54), and bats (57). The relative species distribution of Australian small mammals and birds

in relation to arid, semi-arid and mesic geographic climate zones varies tremendously (Table 1). A substantial percentage of marsupials and rodents are found only in the arid and semi-arid zones (> 20%), compared to less than 4% for bats and birds. There is no difference in frequencies for marsupial and rodent species in semi-arid/arid zones compared to the mesic zone (Fisher exact $P = 0.658$), but there is a difference for marsupials/rodents compared with bats ($P = 0.002$), and there is a difference between non-volant mammals and birds ($P < 0.001$) but not between bats and birds ($P = 0.402$). Thus the climatic distribution of bats is more similar to birds than to non-volant marsupials and rodents. With few exceptions, bird and bat species exploit arid habitats on an ephemeral basis, escaping to more mesic environments when local conditions become extreme. By contrast, a much greater proportion of non-volant mammals reside permanently in arid to semi-arid habitats. Adaptations for persistent living under hot, dry conditions are therefore more likely to be found in arid zone marsupials and rodents than in birds and bats.

Desert environments

Deserts have high ambient temperatures, low annual rainfall and low humidity. They are also characterized by limited free water, low primary productivity, and sporadic food availability for small mammals and birds. The dry desert atmosphere is very transparent to solar and thermal radiation so solar irradiance is high by day and radiation heat loss is rapid at night. In the arid interior of Australia, daytime air temperatures often exceed 35 °C in summer, but usually drop to below 20 °C by night (Australian Bureau of Meteorology 2003, www.bom.gov.au).

Air temperature (T_a), however, does not accurately represent the thermal conditions experienced by terrestrial animals. The effective environmental temperature for an upright terrestrial animal is a balance between convective and radiative heat exchanges, both of

which depend on properties of both the animal and the environment (Bakken 1976). At ground level, air temperature can be 40 °C warmer than air just 2 cm higher (Fig. 1), due to the effect of the boundary layer of still air near the ground surface. Soil temperatures can be even higher (Lowry 1970; Walsberg 2000). For small, day-active desert mammals that are confined to ground-level locations, their environmental temperature will exceed their body temperature (T_b) for much of the day. The exceedingly high temperatures at ground level will also restrict the activity of arthropod prey (and therefore limit daytime foraging). Small, day-active terrestrial mammals will therefore need either superior thermoregulatory abilities or unusual life-history traits compared to small birds.

Do patterns of thermoregulation differ for small mammals and birds?

Body Temperature

Most small mammals have a T_b of 36-39 °C (Hart 1971), whereas small birds typically have T_b s between 40 and 43 °C, regardless if from arid or mesic environments (Dawson and Hudson 1970; Prinzinger *et al.* 1991). Many birds and mammals can tolerate an increase in T_b of about 4 °C when heat-stressed, which aids in tolerating dry heat exposure (Maclean 1996). Hyperthermia promotes water savings because the elevated T_b maintains a larger temperature gradient for non-evaporative heat loss when T_b exceeds T_a , and reduces environmental heat gain when T_a exceeds T_b (Dawson and Bartholomew 1968). This saves considerable water because of the reduced requirement for evaporative cooling (Tieleman and Williams 1999; Walsberg 2000). The higher T_b of birds and their similar extent of hyperthermia suggests that birds should cope better at high temperature than mammals, although hyperthermia does increase water and energy requirements in all animals. But we just said that hypothermia saves water ????????

Aestivation (summer torpor) occurs in many small desert mammals. Their reduction in T_b and metabolic rate provides considerable energy and water savings, and helps them survive short periods of food and/or water deprivation (MacMillan 1965; Withers *et al.* 1980). In Australia, torpor appears to be a general dasyurid (but not rodent) characteristic, and may pre-adapt them to desert conditions. In contrast, small desert birds rarely aestivate. The desert poorwill (*Phalaenoptilus nuttallii*) and white-throated swift (*Aeronautes saxotilis*) do (Bartholomew *et al.* 1962), but other than caprimulgids (nightjars, tawny frogmouth) that readily use hypothermia, if not torpor (Kortner *et al.* 2001), there are only anecdotal reports of torpor for a few Australian birds (Ives 1973; Serventy and Raymond 1973).

Metabolism and Thermal Conductance

Birds, particularly passerine species, have a higher basal metabolic rate (BMR) than mammals. Desert birds tend to have a lower BMR than non-desert species (Schleucher and Withers 2002; Tieleman *et al.* 2002), and desert rodents tend to have a lower BMR than non-desert species (Hart 1971; Bradley and Yousef 1972). Because field metabolic rate (FMR) of free-living species correlates with their BMR, mammals have lower FMRs than birds and desert-adapted endotherms should have lower FMRs than mesic counterparts (see Cooper *et al.* 2003a). Reduced energy needs and metabolic heat production are advantageous attributes for arid-zone endotherms.

In general, mammals have a higher thermal conductance than birds (see Schleucher and Withers 2001), presumably as feathers provide better insulation than fur. Small desert mammals have a higher than expected thermal conductance (Lovegrove & Heldmaier 1994), but habitat-related conductance is uncertain in birds (McNab 2000; Schleucher and Withers 2002).

Evaporative Heat Loss

Some desert birds and mammals have lower evaporative water loss (EWL), hence evaporative heat loss (EHL), than non-desert species, which conserves water (MacMillan and Hinds 1998; Tieleman and Williams 1999, 2000, 2002). Small species do not increase EHL until the upper critical temperature is exceeded, which conserves water. EHL is enhanced by panting and/or sweating at high T_{as} in mammals. Birds usually increase EHL by panting, and/or gular fluttering. Although birds lack sweat glands, cutaneous EHL is enhanced in some desert species (see Marder *et al.* 2003).

Behavioural Thermoregulation

Small desert birds and mammals display a variety of behaviours that benefit their desert survival. When hot, simple postural changes can augment conductive and convective heat losses up to 4 fold. Other important behavioural adjustments include seeking shade or shelter amongst foliage or in rock crevices, reducing activity, climbing or perching in trees to escape high ground surface temperatures, or soaring to high altitude (birds) to exploit cooler air.

Many small desert mammals use underground burrows, which provide stable and favourable thermal and hygric characteristics. Other refugia (rock crevices, tree hollows, nests) confer similar microclimatic advantages. In contrast, very few desert birds are fossorial, although the North American burrowing owl *Speotyto cunicularia* is, and the elf owl *Micrathene whitneyi*, gila woodpeckers *Melanerpes uropygialis* and rock wrens *Salpinctes obsoletus* make use of thermal refugia.

When cold, some mammals and birds exploit solar radiation in desert environments to reduce thermoregulatory costs. This involves orientation to the incident solar radiation

and microhabitat selection. The structure, colour, spectral properties and skin colour of some animals facilitate solar heat gain, although at the expense of thermal insulation (Walsberg and Schmidt 1989; Cooper *et al.* 2003b). Sunbasking is an important energy-saving behaviour for re-warming from hypothermia or torpor (Geiser and Drury 2003).

Comparison of Small Australian Desert Mammals and Birds

It is surprisingly difficult to compare the thermal limits of small Australian mammals and birds. A valid exploration of thermoregulatory capacity would require that animals be allowed an adequate period of acclimatisation followed by exposure to high temperatures at very low humidities. While birds have featured in such studies (e.g. Weathers 1981), small mammals are presumed to be heat intolerant and are seldom examined in this context. Despite limitations in extent of temperatures examined, some insight is gained by comparing the thermoregulatory responses of the similar-sized sandy inland mouse *Pseudomys hermansbergensis* (12.2 g) and the spinifex bird *Eremiornis carteri* (10-13 g). Body temperature is more constant for *P. hermansbergensis* than *E. carteri* but is, somewhat surprisingly, equivalent near TNZ at about 37.5 °C (Fig. 2). T_b increases as T_a increases and reaches 40 °C for the mouse and over 43 °C for the bird. Metabolic rate is generally higher for the bird than the mouse near TNZ, as expected, but is more similar at low T_{as} , reflecting the better insulation of the bird. EWL is generally higher for the bird and increases dramatically above 35 °C. The proportionately greater increase in C_{dry} in the mouse than in the bird at high T_{as} should give them better water economy at high ambient temperatures. As for the other physiological variables, it is unclear what would happen to the mouse at equivalently high T_{as} (40 °C) as the bird.

From the limited information available and, we thus conclude that differences in thermoregulatory ability do not fully account for the paucity of small diurnal mammals in

Australian deserts, so we examine other factors that may account for the observed differences in diurnality of small birds and mammals.

Water Balance

Water balance is maintained if intake from drinking, preformed water in the food and metabolic water production balance or exceed evaporative and excretory water losses. Generally both birds and mammals from arid habitats have a lower rate of overall water flux than non-desert species (Tieleman and Williams 2000; Cooper *et al.* 2003a). But do birds and mammals differ in their ability to maintain water balance and might this contribute to their difference in extent of diurnality?

Drinking

The limited mobility of small, non-volant mammals restricts their reliance on drinking. They can exploit locally available water after rain or fog, but can't travel long distances to ephemeral or permanent waterholes to drink. Therefore, preformed and metabolic water are more important components of water gain than drinking for small mammals.

Flight facilitates accessing free water, which makes drinking a major component of avian water balance (*e.g.* Fisher *et al.* 1972). Some birds are water dependent and must drink daily. Others may drink when water is available, but do not need water when fresh seed and insects are available. Some species rarely drink, relying on preformed and metabolic water to maintain water balance.

Preformed Water

The fauna of Australian deserts differ from those of North American and Africa by being dominated by small insectivorous mammals (mainly dasyurids) and birds. Insect or

meat-eating mammals and birds seldom need to drink as they obtain adequate water (preformed) from their diet. In contrast, granivores have a diet low in preformed water and so additional water needs to be provided by drinking or metabolic water production. Many desert rodents are specialist granivores (*e.g.* heteromyids of North America and gerbillids of North Africa and south-western Asia), and Australian rodents are presumed to be “granivores” (Morton 1979) although they can have a quite varied diet (Murray and Dickman 1994).

Metabolic Water Production

Some birds and mammals can survive on a diet of air-dried seed without access to drinking water, *e.g.* budgerigar (*Melopsittacus undulatus*), Bourke’s parrot (*Neophema bourkii*), zebra finch (*Taeniopygia guttata*), heteromyid rodents, spinifex hopping mouse (*Notomys alexis*), and some Namib desert rodents (Cade and Dybas 1962; MacMillen and Lee 1967; Withers *et al.* 1980). Their rate of metabolic water production (MWP) is sufficient to balance evaporative and excretory water losses. A high mass-specific metabolic rate and its associated high rate of MWP may be advantageous for small desert birds and mammals. *Taeniopygia guttata* is capable of tolerating saline drinking water (up to 0.8 mol l^{-1}) as its high MWP (31.3 % of the daily water flux) dilutes the saline water that is drunk (Skadhauge and Bradshaw 1974).

Evaporative Water Loss

Many desert mammals and birds have a lower rate of EWL than non-desert species (Withers *et al.* 1980; Hinds and MacMillen 1985, 1986; Tieleman and Williams 1999, 2000, 2002). This may result from a combination of relative hypothermia, or should it be

hypERTHemia ???? low cutaneous evaporation, low BMR, and low respiratory water loss due to countercurrent heat exchange in the nasal passages (Schmidt-Nielsen *et al.* 1970).

At low T_a s, EWL is low and metabolic rate (hence metabolic water production) is high (Fig 2), so the balance of MWP/EWL is favourable. At some critical temperature, the point of relative water economy (PRWE; *e.g.* MacMillan and Baudinette 1993), $EWL = MWP$. The PRWE occurs at a higher T_a in arid compared to non-arid habitat birds and mammals.

Most birds rely on panting to increase EWL when heat stressed rather than cutaneous evaporation (*e.g.* Tieleman and Williams 2002). However, in some birds, most notably columbids and sand grouse, enhanced cutaneous EWL is an important avenue of EHL at high T_a (Larcombe *et al.* 2003; Marder *et al.* 2003). Some small mammals can increase EWL by sweating but others, notably the rodents, lack sweat glands, so rely on enhanced respiratory water loss and salivation.

Excretory Water Loss

Small desert mammals are known to minimise urinary water losses by their exceptional capacity to form highly concentrated urine. The Australian spinifex hopping mouse, for example, can produce urine as concentrated as over 9000 mOsm (MacMillan and Lee, 1969). Granivorous rodents in particular often have superior urine concentrating abilities, which compensates for the low preformed water content of their diet. For insectivorous/carnivorous mammals, the high preformed water content of their food ameliorates the free water shortage in a desert environment. Nevertheless, renal indices of dasyurids are correlated with climate (Brooker and Withers 1994) and water loss is further minimised by low faecal water content and high digestibility of food (Withers 1982).

Urinary water loss is potentially higher for birds as renal characteristics prevent formation of highly concentrated urine. This perhaps relates to their need to prevent precipitation of urates in their nephrons. However, desert birds achieve exceptional excretory water economy by post-ureteral withdrawal of fluid from their excreta (combined urine and faeces) in their hind gut (Goldstein and Skadhauge 2000). Faecal water content can be as low as 50-60% in dehydrated birds (Maclean 1996). Despite this, the ability of birds to survive without drinking is positively correlated with the number and length of the loops of Henle in the kidney (Bartholomew 1972), suggesting that both renal function and hind-gut reabsorption are important in water balance.

Some birds have nasal salt glands that excrete a hyperosmotic NaCl and KCl solution (Goldstein and Skadhauge 2000). They are more important for ion regulation in marine than terrestrial (including desert) species, although ostrich (*Struthio camelus*), sand partridge (*Ammoperdix heyi*), some acciptrid and falconid raptors, and the roadrunner (*Geococcyx californicus*) secrete salts nasally.

In general, birds are inferior to mammals in overall water conservation, which can then have consequences for thermoregulation because of their general reliance on EHL. Being day active and non-fossorial, they are denied two of the major means used by small mammals for reducing thermal exposure and desiccation. This is further exacerbated by their high water turnover rates (reflecting high metabolic rates) and limited urinary concentrating capacity. Nevertheless, the greater mobility and high metabolic water production of small birds ameliorates the potential for water stress in a desert environment, and it is unlikely that differences in water balance requirements favours mammals over birds for desert existence.

Nocturnality/Diurnality, Mobility and Predation

Size imposes several constraints on diurnal activity in small, desert-dwelling mammals. The low thermal inertia associated with their small mass limits the period of time that they can be exposed to solar radiation, particularly on the hot ground surface. The smallest diurnal desert mammals (Golden spiny mouse *Acomys rusattus* and Striped mice *Rhabdomys pumillio*) weigh about 50 g. Because predation pressure is generally inversely related to prey size, small, day-active mammals are highly vulnerable to predation. Consequently, diurnal activity is restricted to highly social small mammals, as intragroup cooperativity helps them detect and avoid predators, especially birds of prey. Australia's small mammals, however, are not social, which further favours their nocturnality. In contrast, most small desert birds are diurnally active, with only a limited tendency to restrict midday activities under very hot conditions. Flight confers much greater mobility, both on a local (*e.g.* moving from the ground to tree tops) and a geographic scale (*e.g.* moving out of desert environments during unfavourable extremes) than is possible for small mammals. In addition to the tremendous advantage that flight affords birds in escaping predators, the social tendencies of birds further protects them from predation.

The increased mobility of birds (and bats) allows them to exploit arid environments under favourable conditions, and to move when resource availability declines. Nomadism is therefore a common characteristic of many desert bird species (Davies 1984). As a consequence, a smaller proportion of bird and bat species are restricted to arid environments compared to non-volant mammal species, although a similar proportion of birds, bats and non-volant mammals occur in arid environments (Table 1).

***Myrmecobius fasciatus* – an exception to the rule**

The numbat (*Myrmecobius fasciatus*) is the only exclusively diurnal Australian mammal. Prior to European settlement numbats were found throughout southern Australia in mesic,

semi-arid and arid habitats, but it now restricted to the south-west of Western Australia (Friend 1990). Does the numbat have any specific physiological and/or behavioural adaptations that enable it to be diurnally active in this arid environment?

Numbats feed only on termites which they extract from shallow sub-surface soil galleries. Termites are more active in soil galleries during the day than at night, so the numbat's exclusively diurnal activity reflects its prey availability (Friend 1986). Numbats are solitary, and their greatest predation risk is from birds of prey.

Like most marsupials, numbats have a body temperature (T_b) of around 37 °C when active, and there is no indication that numbats use hyperthermia when exposed to high T_{as} (Cooper 2003). Like other dasyurids, numbats use mild hypothermia and spontaneous daily torpor, which helps to reduce thermoregulatory costs in winter. This is particularly advantageous as termite abundance is temporally and spatially variable, particularly in arid habitats. The numbat's BMR is not significantly different than that of other (nocturnal) marsupials, despite its arid-habitat distribution and termitivorous diet (Cooper and Withers 2002). Its field metabolic rate (FMR) is also not significantly different than that of other marsupials, and indeed it is very similar to that of other arid-habitat marsupials (Cooper *et al.* 2003a). Thus the numbat shows little evidence of metabolic adaptation to a diurnal habit.

The numbat's rate of evaporative water loss (EWL) is about half of that predicted for marsupials (Cooper and Withers 2002) and may be an adaptation to its diurnality in an arid habitat. However, the numbat's field water turnover rate (FWTR) and kidney morphology are typical of a generalised marsupial (Cooper *et al.* 2003a). Thus the combination of a diet rich in preformed water (Cooper and Withers 2004) and a low rate of EWL permit it to live in the absence of free water.

The biophysical properties of the numbat's pelt enhance, rather than limit, solar heat gain (SHG). The numbat's pelt is sparse, shallow, and has a low reflectivity compared to nocturnal marsupials, being more similar in structure to the pelts of diurnally-active North American ground squirrels (Cooper *et al.* 2003b). SHG can significantly reduce the numbat's thermoregulatory costs at low $T_{a,s}$. Therefore the numbat appears to exploit the high incident solar radiation that characterises arid habitats.

The physiology of the diurnal numbat differs little from that of arid-habitat nocturnal marsupials. Other than a reduced evaporative water loss and a diet with a high water content, the numbat has no apparent physiological specialisations that adapt it to a diurnal lifestyle in an arid environment. Therefore it is likely that Australian marsupials are physiologically capable of diurnal activity in arid habitats, providing their diet satisfies their water needs and predation pressure is not too great.

Conclusions

The major difference between small desert mammals and birds is that birds are highly mobile whereas small non-volant mammals are not. Therefore many desert mammals are endemic, and presumably need to be highly specialised to survive continually in their desert environment. We thus conclude that Australian desert birds and mammals have a variety of physiological and behavioural means for avoiding heat stress, and coping at least on a short-term basis with high environmental temperatures. Likewise, they are generally able to balance their water budget by physiological and behavioural means. Based on the limited information available, we suggest that differences in thermoregulatory ability do not account for the near absence of small, day-active mammals in Australian deserts. Water requirements for them to be day-active at ground level might dictate that they remain near free water sources and/or redirect their foraging to shaded, above-ground locations

such as shrubs and trees. However, given that their mesic relatives have retained nocturnality, it seems more likely that combinations of prey abundance and reduced conspicuousness to predators have reinforced nocturnality in small desert mammals. The general absence of small day-active mammals in Australian deserts (the numbat being the exception) is perhaps not surprising given the complete absence of small day-active mammals for all habitats in Australia.

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Table 1. Numbers and percentages of Australian species of mammals (marsupials, rodents and bats) and birds found only in the arid zone, only in the arid and semi-arid zones, only in the semi-arid zone, only in the semi-arid and mesic zones, only in the mesic zone, and in all zones, and the total numbers/percentages of species. Arid zone is rainfall <250 mm; semi-arid zone is 250<rainfall<500 mm; mesic zone is rainfall >500 mm (Barrett and Dent 1991). Numbers of species estimated from distribution maps for mammals (Strahan 2002) and birds (Simpson and Day 1993).

	Arid only	Arid + Semi- arid	Arid + Semi-arid + Mesic	Semi- arid only	Semi-arid + Mesic	Mesic only	Total
Numbers							
Mammals	14	13	28	6	7	85	163
marsupials	6	6	9	4	1	26	52
rodents	7	6	6	2	2	31	54
bats	1	1	13	0	4	28	57
Birds	12	5	136	31	47	291	522
Percentags							
Mammals	8.6	8.0	17.2	3.7	4.3	52.1	100
marsupials	11.5	11.5	17.3	7.7	1.9	50.0	100
rodents	13.0	11.1	11.1	3.7	3.7	57.4	100
bats	1.8	1.8	22.8	0.0	7.0	66.7	100
Birds	2.3	1.0	26.1	5.9	9.0	55.7	100

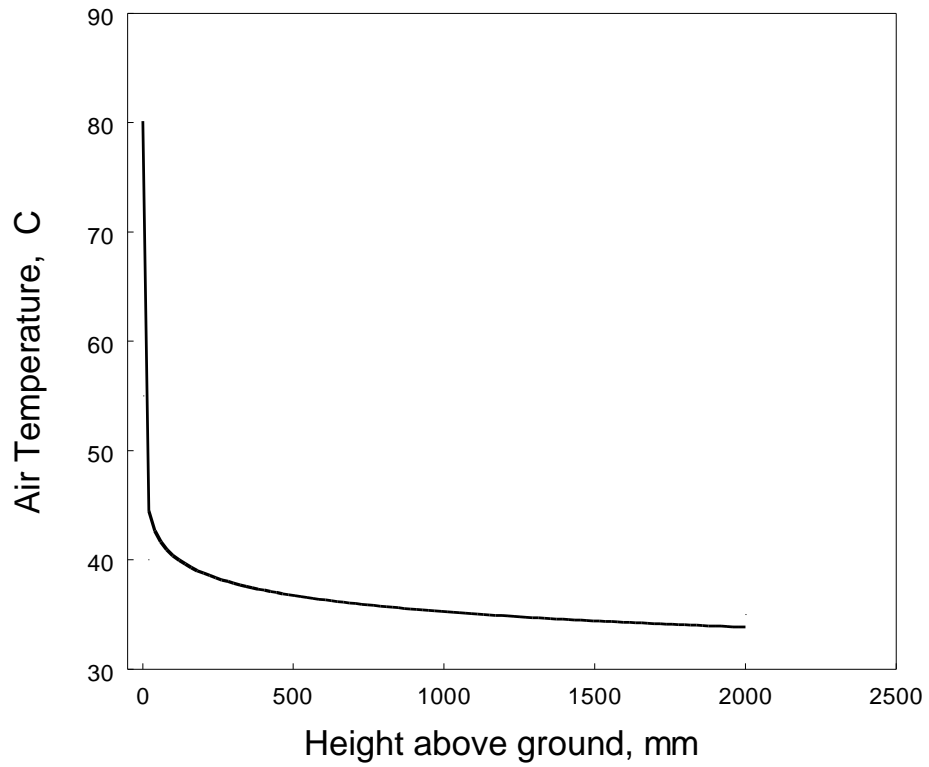


Fig 1. Theoretical relationship between air temperature and height above ground, based on lapse rates associated with an air temperature of 35 °C at 2 metres (after Lowry 1970).

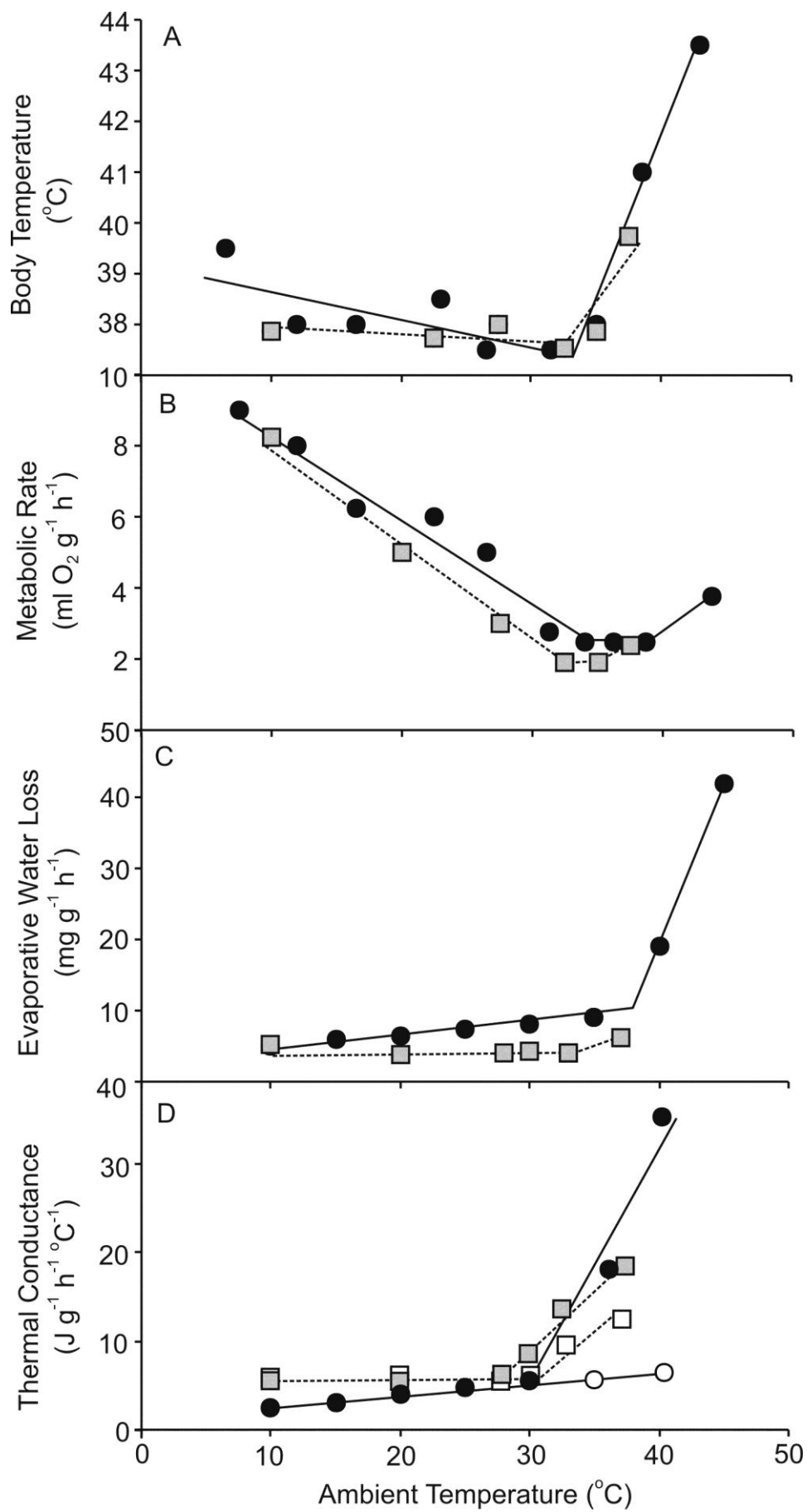


Fig 2. Comparison of thermal and metabolic physiology of a small desert mammal (sandy inland mouse *Pseudomys hermannsbergensis*; squares; MacMillen *et al.* 1969) and the spinifex bird (*Eremiornis carteri*; circles; Ambrose *et al.* 1996); thermal conductance is wet (solid symbols) and dry (open symbols).