Behavioural adaptations of brown and spotted hyaenas in the southern Kalahari

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The brown hyaena, Hyaena brunnea, *lives at over twice the density of the spotted hyaena,* Crocuta crocuta, *in the arid southern Kalahari. This is achieved mainly through the more diverse diet of the brown hyaena, many of the components of which are small and scattered. The spotted hyaena tends to specialise on large and medium-sized mammals. Spotted hyaena territories are three times the area of those of brown hyaenas. Moreover, the social group sizes of the brown hyaena appear to be more responsive to increases in food availability than those of brown hyaenas. Both species employ a hinterland method of scent marking rather than border marking. Solitary foraging brown hyaenas also appear to use scent marking to communicate to other group members where they have recently foraged. Spotted hyaenas are the dominant species and may influence brown hyaena numbers where they occur at high densities.*

In die droë Suider-Kalahari is die bevolkingsdigtheid van die bruin hiëna, Hyaena brunnea, *minstens twee keer dié van die gevlekte hiëna,* Crocuta crocuta. *Dit word hoofsaaklik bereik deurdat die eersgenoemde se dieet baie afwisseling vertoon en deurdat die bestanddele daarvan klein is en wyd versprei voorkom. Die gevlekte hiëna is egter geneig om van groot en middelslagsoogdiere te leef. Gevlekte hiënas se gebiede is drie keer so groot as die bruines s'n, en bowendien lyk dit asof die grootte van die gevlekte tipe se sosiale groepe ook meer met die beskikbaarheid van kos verband hou as in die geval van bruin hiënas. By albei spesies is 'n hinterlandmetode van reukmerking gebruiklik, eerder as grensmerking. Skynbaar pas bruin hiënas wat alleen kos soek ook reukmerking toe om ander lede van hul groep te laat weet waar hulle onlangs kos gesoek het. Die gevlekte hiëna is die dominante spesie en kan, waar hul bevolkingsdigtheid groot is, 'n uitwerking op die getal bruin hiënas hê.*

'The origins of most questions about adaptation lie in comparisons between species.'[1] In this review I discuss and compare some of the behavioural adaptations of the brown hyaena, *Hyaena brunnea*, and the spotted hyaena, *Crocuta crocuta*, to the arid southern Kalahari. I show how these two closely related species are able to co-exist by tapping different food resources and analyse the effect this has had on aspects of their social organization and behaviour. I then discuss how these factors affect the populations of the two species in the area.

The data presented here and the techniques used to obtain them either have been published or are in press. For simplicity the relevant references are quoted only where conclusions have been drawn without data being presented. A full list of the relevant publications with the original data and analyses can be found in refs 2 and 3.

The study area

The southern Kalahari comprises the adjoining Kalahari Gemsbok (South Africa) and Gemsbok (Botswana) national parks. It is an arid region with an irregular rainfall and experiences large temperature fluctuations both daily and seasonally. The area falls mostly between the 200 mm and 300 mm rainfall isohyets; rainfall is erratic and falls mainly in late summer.[4] Naturally occurring free-standing water lasts only for short periods at pans or along river beds after heavy rains, but water from boreholes has been provided in the Kalahari Gemsbok National Park, particularly along the river beds.

The area is largely covered with a layer of red wind-blown sand piled into dunes, which are broken by two large dry river beds and numerous pans. The river beds and environs support higher densities of all ungulates except steenbok, *Raphicerus campestris*, than the dunes (Table 1). Ungulate abundance along the river beds is variable. During periods of high rainfall large concentrations are present, whereas during the extended dry periods most ungulates disperse into the dunes, leaving remnant populations of springbok (*Antidorcas marsupialis*) and blue wildebeest (*Connochaetes taurinus*).[5] Smaller animals such as small canids, Cape hares (*Lepus capensis*) and springhares (*Pedetes capensis*) tend to be more evenly distributed in both habitats. Korhaans (ground nesting birds) are particularly common in the dunes and usually absent from the river beds. Important wild fruits such as the tsama melon (*Citrullus lanatus*) and the gemsbok cucumber (*Acanthosicyos naudianus*) are almost entirely confined to the dunes, where they are patchily distributed and their densities fluctuate markedly from year to year.[3]

Density

Estimates of brown hyaena densities were made by extrapolating mean figures for group and territory size and making allowance for itenerants in the population. Density estimates for the spotted hyaena were calculated by documenting all the clans in the Kalahari Gemsbok National Park and estimating the number of individuals in each by direct observations.[3] There are estimated to be 1,8 brown hyaenas and 0,8 spotted hyaenas per 100 km^2.

Feeding habits

Brown hyaenas feed on a wide range of food, from large carcasses to small animals, pieces of bone, wild fruits, birds' eggs and insects, whereas spotted hyaenas have a more specialized diet, consuming mainly large and medium-sized mammals (Fig. 1). Two-thirds of the food items they fed on were either gemsbok (*Oryx gazella*) or wildebeest. These data are in agreement with those from studies of these species in other areas.[6-9]

Table 1. Mean number and standard error of ungulates counted per 100 km driven in river bed and dune habitats.

	River bed	Dunes
Springbok	1213 ± 265	5 ± 4
Gemsbok	80 ± 19	41 ± 9
Hartebeest	61 ± 20	13 ± 7
Wildebeest	175 ± 83	7 ± 8
Eland	0	11 ± 9
Steenbok	2 ± 1	19 ± 6

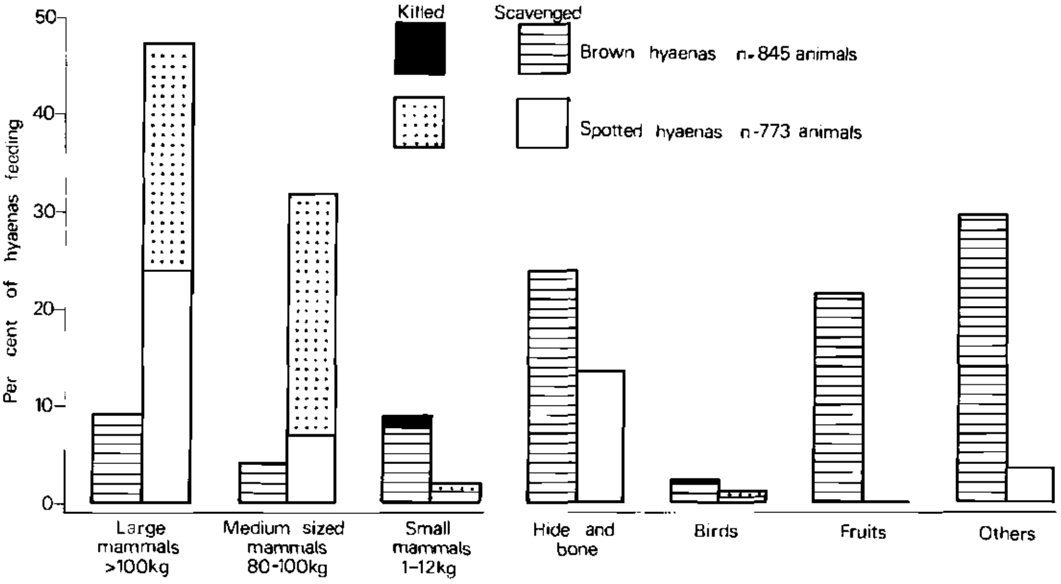

Fig. 1. The diets of the brown hyaena and the spotted hyaena in the southern Kalahari as determined from direct observations. The number of hyaenas observed feeding on each food item is expressed as the percentage of the total number of hyaenas of each species observed feeding. The data for mammals have been analysed on a mass rather than a species basis, e.g. gemsbok and wildebeest calves under one year old have been recorded as medium-sized mammals, whereas those over one year old are represented as large mammals. The proportions killed or scavenged are the percentages of the number of each species observed feeding on each food item. The heading 'Others' mainly includes insects, but also reptiles, birds' eggs and other small unidentifiable pieces of food (from ref. 2).

The two species also differ markedly in the manner in which they procure their food. Brown hyaena are predominantly scavengers and forage alone. Kills formed only 5,8% of the biomass of their food and comprised small animals such as springhares and korhaans. Spotted hyaenas on the other hand are active predators often foraging in groups. These foraging groups varied in size from one to 12 with a mean (± s.e.m.) of 3,0 ± 0,1. Kills accounted for 72,6% of the biomass of their food. Gemsbok calves up to one year of age made up 43% of their kills, followed by wildebeest of all ages (15%) and gemsbok adults (10%).

Both species can apparently survive without free-standing drinking water. Water is conserved through their being active mainly at night; only 6,2% and 10,6% of the time that brown hyaenas and spotted hyaenas respectively were active was in daylight. Furthermore, brown hyaenas obtain moisture from fruits such as the tsama and gemsbok cucumber, and spotted hyaenas drink the blood of their prey.

Social organization

Although they are solitary foragers, most brown hyaenas live in small social groups, the members of which share and defend a common territory, feed together on large food items and cooperate in feeding young by carrying food back to the den.[10,11] The number of adult and subadult brown hyaenas in a group varied from one to nine depending on the quality of the food in the territory at the time. For example, where the food available consisted mainly of small scattered pieces of bone and wild fruits, an adult female and her litter of three cubs were the only brown hyaena inhabitants. In another territory where wildebeest were dying because of drought there were nine adult and subadult brown hyaenas and four cubs. The coefficient of variation in the number of adults and subadults each year in an intensively studied brown hyaena clan over a six-year period was 42%.

The number of adults and subadults in spotted hyaena clans in the southern Kalahari varied between three and 12 individuals, although mostly there were between nine and 11. These groups are far smaller than those of 50 to 80 individuals observed in East Africa.[6,12] Differences in the quality of food resources in the two areas are responsible for the large differences in clan size. Spotted hyaena clans appear to fluctuate less than those of the brown hyaena in the southern Kalahari. The coefficient of variation of an intensively studied spotted hyaena clan over a six-year period was only 13%.

The mean territory size of six clans was 330 ± 41 km^2 for brown hyaenas and 1 095 ± 177 km^2 for spotted hyaenas. In both species there was a significant positive correlation between territory size and the average distance moved between food items (excluding small incidental ones) (for brown hyaenas, r_s = 1,0; $P<0,05$; for spotted hyaenas, r_s = 1,0; $P<0,01$). These findings suggest that territory size is influenced by the way in which food is distributed within it. Furthermore, the average distance travelled between food items was 32,7 km for spotted hyaenas and only 9,2 km for brown hyaenas. Spotted hyaenas need to travel longer distances to find food because of their more specialised feeding habits.

The social system of the brown hyaena is flexible enough for it to be able to take advantage of changes in food availability. The solitary-living individual can become social, sharing a territory with conspecifics and cooperating in raising the young (see also ref. 8). Although spotted hyaenas have a flexible social system[6] and can survive and breed in small groups, if not solitarily, their more specialised feeding habits in the southern Kalahari demand a relatively large territory. This accords with the prediction of Gittleman and Harvey[13] that carnivores with a large proportion of flesh in their diets have particularly large home ranges. Changes in food availability for spotted hyaenas in this area are unlikely ever to be as great as they may become for brown hyaenas. Large concentrations of ungulates are unlikely ever to become sedentary.[5,14] The territories and particularly the group sizes of spotted hyaenas are therefore unlikely to fluctuate to the extent that they do for the brown hyaena.

The two principal habitats of the southern Kalahari, the dunes and river beds and environs, influence the movements of the two species in different ways, mainly through their influence on the dispersion of the hyaenas' food. For spotted hyaenas the distribution of the large and medium-sized ungulates can be expected to be the prime factor influencing their movements, whereas for brown hyaenas circumstances such as the availability of wild fruits and certain small animals may be important. The larger ungulates are mainly distributed along the river beds (Table 1); wild fruits and many small mammals are more common in the dunes.[3] Consequently, spotted hyaenas spent significantly more time foraging in riverine habitats (55,2% of the total distance they were followed) than did brown hyaenas (42,2%) ($\chi^2 = 56,99$; d.f. = 1; $P<0,001$). River beds and their environs make up less than 10% of the area.

Scent marking

Both species scent-mark their territories by pasting strong-smelling anal gland secretions on to grass stalks and by defaecating at latrines. When pasting, each species produces a long-lasting lipid-rich secretion; the brown hyaena produces an additional watery, short-lived component.[15] In addition, brown hyaenas paste at a far higher frequency (2,64 pastings per km moved) than spotted hyaenas (0,13 pastings per km). The main function of the long-lasting secretion appears to be territorial defence. The purpose of the short-lived component is thought to be to inform other group members where a brown hyaena has recently been foraging, so that they do not waste time and energy searching in areas that are likely to be unproductive. This may be important as so much of the brown hyaena's food consists of small items with a slow renewal rate. Defaecation at latrines, which is often accompanied by pasting, may enhance the territorial defence function of pasting.

Both species employ a hinterland method of marking in the Kalahari, depositing their marks (both pastings and latrines) throughout the territory,[15,16] rather than the border method used, for example, by spotted hyaenas in Ngorongoro Crater.[6] Border marking gives the earliest warning of trespass, but involves a single line of defence only, which must be maintained intact and renewed regularly. To keep a dense, fresh line of scent marks along a border requires a supply related to the length of perimeter to be marked. This is possible in the case of spotted hyaenas at the Ngorongoro where large groups share small territories and the length of border to be marked by each individual is relatively short. But in a limited time and with a finite supply of scent, it becomes impossible to visit and mark the borders of the large Kalahari territories with the frequency necessary to maintain the continuity of the line of scent marks. Hinterland marking therefore becomes the strategy.

Despite the vast area over which marks are dispersed by Kalahari hyaenas, computer simulations of these animals entering a territory indicated that the scent marks were distributed in such a way that potential intruders would rapidly encounter these chemical signals as they moved into the area. The simulations suggest that any time a brown hyaena would be within 250 m of a scent mark over most of the territory, and a spotted hyaena within 1 – 2 km. Given the acute sense of smell of hyaenas (they can detect carrion from at least 4 km downwind), it is likely they would be able to detect a scent mark from even 2 km if they were downwind from it.

Scent-marking strategies of both species, therefore, are adapted to large territories and ensure optimum rates of encounter by intruders. These strategies are not species-specific, but are determined by the ecological pressures acting on particular populations. Differences in the pastings, however, are species-specific. The solitary foraging brown hyaena secretes a second paste which is possibly aimed at communicating to fellow group members the areas that may not be productive to forage in. The social feeding spotted hyaena does not need to do this.

Relations between the two hyaena species

Brown hyaenas and spotted hyaenas compete for food mainly when they are scavenging from the carcasses of large mammals. This is particularly important for brown hyaenas as they stand to lose a significant amount of food should they lose such a carcass, either directly or indirectly, to spotted hyaenas. This in fact happened in a part of the study area well frequented by spotted hyaenas. This is illustrated in Table 2, which shows the frequencies with which hyaenas of both species were the first to find carcasses in two adjacent areas. A large spotted hyaena clan denned in the Kousaunt area where spotted hyaenas ate most of the carcasses, whereas spotted hyaenas rarely visited the Kwang area where most carcasses became available to brown hyaenas.

Table 2. Relative frequencies with which brown hyaenas and spotted hyaenas were first to locate a carcass in two areas and the number of occasions that brown hyaenas were displaced by spotted hyaenas (from ref 3).

	Kwang area	Kousaunt area	χ^2
Carcass found by brown hyaena first	22	5	15,17 d.f. = 1; $P<0{,}001$
Carcass found by spotted hyaena first	4	16	
Brown hyaena displaced by spotted hyaena	4	5	8,8*; d.f = 1; $P<0{,}01$

*With Yates' correction.

Table 3. Number of brown hyaenas and spotted hyaenas counted at night in two area (from ref. 3).

	Kwang area ($n = 1\ 053$ km)	Kousaunt area ($n = 1\ 166$ km)	χ^2
Brown hyaenas	20	6	26,40; d.f. = 1; $P<0{,}001$
Spotted hyaenas	10	50	

Away from food, spotted hyaenas are also dominant to brown hyaenas. When the two species meet, spotted hyaenas usually harass the other. They chase it and should they catch up with the brown hyaena they may attack by grabbing the side of the neck and vigorously shaking it. These clashes may even lead to the death of the brown hyaena.

Although brown hyaenas are the more numerous in the southern Kalahari they avoid the comparatively high numbers of spotted hyaenas around Kousaunt. Night counts in the Kousaunt and Kwang areas showed differences in the proportions of the two species even though the habitat was similar (Table 3). Observations of brown hyaenas being absent from an area frequented by spotted hyaena have also been recorded by Skinner and Van Aarde[17] in the Namib desert.

Concluding remarks

The southern Kalahari is a harsh environment. Temperatures are extreme, water is scarce and food resources are thinly and erratically distributed. Of the two hyaena species, the brown hyaena is better adapted to this region than the spotted hyaena. This is borne out by differences in density. The main reason for this is that the brown hyaena has a far more diverse diet than the spotted hyaena and is able to subsist on small, widely scattered food items.

Although the brown hyaena outnumbers the spotted in the southern Kalahari and the latter live at a low density in this region (0,8 animals per 100 km^2), in favourable habitats such as the Ngorongoro Crater there can be as many as 170 hyaenas per 100 km^2 (ref. 6). In areas within the range of the brown hyaena and where spotted hyaenas reach higher densities than in the southern Kalahari, the former species appears to become less common. This is probably due to both interference and exploitation competition with spotted hyaenas. In one such area, the Kruger National Park, the spotted hyaena exploits a far wider niche than in the southern Kalahari, taking on a scavenging role similar to the brown hyaena, as well as hunting large and medium-sized mammals (J.R. Henschel, personal observations).

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1. Clutton-Brock T.H. and Harvey P.H. (1984). Comparative approaches to investigating adaptation. In *Behavioural Ecology an Evolutionary Approach*, edit. J.R. Krebs and N.B. Davies, 2nd edn, pp. 7 – 29. Blackwell, Oxford.
2. Mills M.G.L. (1984). The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe* **27** (suppl.), 237 – 247.
3. Mills M.G.L. (in press). *Kalahari Hyaenas: The Comparative Behavioural Ecology of Two Species*. Allen and Unwin, London.

4. Anon. (1986). *Climate of South Africa: Climate Statistics up to 1984.* Weather Bureau, Pretoria.
5. Mills M.G.L. and Retief P.F. (1984). The response of ungulates to rainfall along the riverbeds of the southern Kalahari. *Koedoe* **27** (Suppl.), 129 – 141.
6. Kruuk H. (1972). *The Spotted Hyena.* University of Chicago Press, Chicago.
7. Skinner J.D. (1976). Ecology of the brown hyaena *Hyaena brunnea* in the Transvaal with a distribution map for southern Africa. *S. Afr. J. Sci.* **72**, 262 – 269.
8. Owens M.J. and Owens D.D. (1978). Feeding ecology and its influence on social organisation in brown hyaenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *E. Afr. Wildl. J.* **16**, 113 – 136.
9. Henschel J.R. (1986). *The socio-ecology of a spotted hyaena* Crocua crocuta *clan in the Kruger National Park.* DSc thesis, University of Pretoria.
10. Mills M.G.L. (1982). The mating system of the brown hyaena, *Hyaena brunnea* in the southern Kalahari. *Behav. Ecol. Sociobiol.* **10**, 131 – 136.
11. Mills M.G.L. (1983). Behavioural mechanisms in territory and group maintenance of the brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *Anim. Behav.* **31**, 503 – 510.
12. Frank L.G. (1986). Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. *Anim. Behav.* **35**, 1500 – 1509.
13. Gittleman J.L. and Harvey P.H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* **10**, 57 – 63.
14. Mills M.G.L. and Refiet P.F. (1984). The effect of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe* **27** (suppl.), 107 – 118.
15. Gorman M.L. and Mills M.G.L. (1984). Scent marking strategies in hyaenas (Mammalia). *J. Zool., (Lond.)* **202**, 535 – 547.
16. Mills M.G.L. and Gorman M.L. (1987). The scent marking behaviour of the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *J. Zool., (Lond.)* **212**, 483-497
17. Skinner J.D. and van Aarde R.J. (1981). The distribution and ecology of the brown hyaena *Hyaen brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert. *Madoqua* **12**, 231 – 239.

Selective brain cooling and survival

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Temporary body heat storage is a useful survival strategy for 10 – 500 kg mammals, when faced with combined heat and dehydration stress. Some mammals in this mass range, as well as some birds and reptiles, protect the thermally vulnerable brain during such storage, by cooling the brain below arterial blood temperature. We review the mechanisms and control of selective brain cooling. Our own studies confirmed the effectiveness of selective brain cooling in sheep (with a carotid rete) and pigeons (with an ophthalmic rete). Whether animals without a rete, including man, are capable of effective brain cooling remains controversial. We discuss the physiological cost of selective brain cooling with respect to dehydration and to the neural control of body temperature.

Die tydelike opberging van liggaamshitte is 'n nuttige oorlewingstrategie by soogdiere met 'n massa van 10 tot 500 kg indien hulle met gelyktydige hitte- en dehidrasiespanning te doen kry. Sommige soogdiere in dié massabestek, asook sommige voëls en reptiele, beskerm hul hittekwesbare brein tydens hitteopberging deur die brein tot onderkant die temperatuur van slagaarbloed af te koel. 'n Oorsig word oor die meganismes van en beheer oor selektiewe breinkoeling gegee. Die outeurs se eie ondersoek het die doeltreffendheid van selektiewe breinkoeling by skape (met 'n karotisnetwerk) en duiwe (met 'n oognetwerk) bevestig. Dit bly steeds 'n omstrede vraag of diere (soos die mens) wat nie so 'n netwerk het nie ook tot breinkoeling in staat is. Die fisiologiese prys van selektiewe breinkoeling teenoor dehidrasie en teenoor senubeheer van die liggaamstemperatuur word bespreek.

Selective brain cooling, that is the cooling of the brain below body core temperature, is a physiological solution to a problem encountered by animals exposed to concurrent heat stress and water shortage. Potentially dangerous heat loads may be imposed on animals by environmental heat, particularly solar radiation, or by the metabolic heat of exercise, and especially by a combination of the two. If lethal rises in tissue temperature are to be avoided, the heat load must be dissipated to the environment. Evaporation of water from the integument or respiratory tract is the most potent means of dissipating the heat, and indeed the only means when ambient temperature approaches body temperature. Evaporative cooling depletes body water, however, and especially in animals that do not have ready access to water; the consequent dehydration compromises physiological function[1] and can be fatal.[2]

Evaporative dissipation of metabolic heat induces greater dehydration in small animals than in large.[3] Taylor[4] has presented a regression equation relating rate of metabolic heat production to body mass and running speed in terrestrial quadrupeds. By dividing his predicted heat production by the latent heat of evaporation of water, we calculated the rate of evaporation necessary to dissipate all the metabolic heat generated by the exercise. The results are shown in Fig. 1, which demonstrates that, if an exercising animal uses evaporation alone to dissipate metabolic heat, the speed at which it can run, or (since both axes are expressed per unit time) the distance it can run at a particular speed, is limited by the concomitant dehydration. One expects that, where the dehydration could become life-threatening, the animal's behaviour will be adjusted so that the need to dissipate metabolic heat by evaporative means is contained. As the figure shows, the nature of the adjustment necessarily depends on body size. For small animals, for example, gerbils (Gerbillinae, approximately 50 g), the rate of dehydration is so high that the animal cannot afford to use evaporation alone to dissipate metabolic heat. Exercise in a hot environment therefore is precluded; where such animals do run, for example to forage, one would expect them to do so at night, when heat can be lost by convection and radiation in addition to evaporation. Indeed this is the case: most small mammals living in hot arid regions are nocturnal. Very large animals, for example eland (*Taurotragus oryx*, approximately 500 kg), on the other hand, dehydrate comparatively slowly even when running at near maximum speed. Also, their relatively low area-to-mass ratio and large thermal inertia reduce the thermal consequences of radiant heat loads, so the very large antelope and the mega-herbivores, for example elephant and rhinoceros, are at no great risk of hyperthermia, even during exercise in hot environments.

Animals in the intermediate mass range, needing to dissipate radiant and metabolic heat loads in warm environments, have their activity limited by the consequences of dehydration. Their activity could be extended if strategies, in addition to evaporation, were employed to cope with the metabolic heat. One such strategy is temporary body heat storage; the animal uses its ther-