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SEASONAL DIFFERENCES IN FIELD METABOLISM, WATER REQUIREMENTS, AND FORAGING BEHAVIOR OF FREE-LIVING AARDWOLVES

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Abstract. Aardwolves occur in east-central and southern Africa in regions of arid and semi-arid grasslands. In South Africa, they feed almost exclusively on the termite Trinerivitermes trimenoides during the warmer months of the year, whereas on cold winter nights these insects remain below ground, unavailable to aardwolves. At this time aardwolves shift their foraging efforts to a less abundant termite species, Hodoterme mossambica. This species provides less food for aardwolves, making the wintertime potentially a period of energy stress for them.

In this study, we report the first estimates of field metabolism and water flux as determined by doubly labeled water for a myrmecophagous eutherian mammal. Specifically, we tested the hypotheses that a reduced basal metabolic rate and pulmocutaneous water loss lead to a conservative field metabolic rate (FMR) and water flux in free-living aardwolves during summer and winter. Further, we quantified the activity budget of aardwolves during summer and winter to construct a time-energy budget for them. We used knowledge of water flux in aardwolves and of the water content of their prey to construct a water budget during summer and winter, and to estimate the seasonal consumption of termites by aardwolves.

During summer (November–January), aardwolves that averaged 7768 g in body mass had a CO2 production of 112.5 L CO2/d, equivalent to an energy expenditure of 2891.2 kJ/d. During winter (June–July), when body mass averaged 8543 g, CO2 production averaged 71.8 L CO2/d, which translates to an FMR of 1844.8 kJ/d. Water flux equaled 615 mL/d in summer, but only 292 mL/d in winter, a decrease of 53.1%.

Aardwolves were active for an average of 8.7 h/d in summer, but only 4.05 h/d during winter. A time budget for active periods showed that aardwolves spent a significantly larger proportion of their active time feeding in summer than in winter (26.7 vs. 15.2%). In addition, males and females spent 12.6% of their time in winter in breeding activities such as courtship and copulation. For aardwolves in summer, our model estimated a DEE of 2370.5 kJ/d, whereas during winter it predicted a DEE of 2086 kJ/d. These values deviated from our estimates of FMR by -18% and +13.1%, respectively.

From data on water flux and the water content of termites, we estimated that aardwolves consumed 222,445 Trinerivitermes per night during the summer. Using previously obtained data on foraging, we predicted that aardwolves consume 833 termites per patch with an intake rate of 33 termites per second while feeding. During winter, aardwolves consumed 5867 Hodoterme and 2515 Trinerivitermes per night. Our estimate of gross energy consumption was 5616 kJ/d in summer and 3022 kJ/d in winter. Assuming an assimilation efficiency of 0.66, metabolizable energy intake would be 3707 kJ/d in summer and 1995 kJ/d in winter. These values exceed FMR measurements by +22% in summer and by +8.1% in winter. It appears that aardwolves were in positive energy balance during our measurements of FMR.

Key words: aardwolf; basal metabolic rate; carnivores; doubly labeled water; energy expenditure; field metabolic rate; myrmecophagous animals; radiotelemetry; termites; time-energy budget; water influx.

INTRODUCTION

Aardwolves (Proteles cristatus) are solitary, nocturnal, medium-sized (7–10 kg) mammals that occur in east-central and southern Africa, typically in regions of arid and semi-arid grasslands, including the Kalahari Desert and some parts of the hyperarid Namib Desert (Skinner and Smithers 1990). Throughout much of their
range they are exposed to seasonal temperature extremes, hot summer days, cold winter nights, and brief pulses of rainfall punctuated by long dry spells. Although their taxonomic status remains controversial (Ewer 1973, Meester et al. 1986, Skinner and Smithers 1990), the consensus is that aardwolves belong to the Hyaenidae (Wayne et al. 1989, Wozencraft 1989), members of which typically have large forelegs, powerful jaw musculature, and well-developed sectorial teeth. One morphological character distinguishes aardwolves from other relatives: they have poorly developed peg-like cheek teeth (Anderson et al. 1992, Anderson 1994), a feature that has prompted some to place them in a separate family, the Proteidae (Skinner and Smithers 1990).

The degeneration of cheek teeth of aardwolves is thought to be an adaption to their diet, one of the most specialized of all the Carnivora. Over their entire range, aardwolves feed on termites, primarily species that belong to the genus _Trinervitermes_, by licking them from the soil surface with their long, spatulate tongue (Kruuk and Sands 1972, Cooper and Skinner 1979, Richardson 1987a). In South Africa, aardwolves feed primarily on _Trinervitermes trinervoides_, a common termite species, active during the warmer months of the year, which lives in dome-shaped mounds in grasslands. Because these insects lack cuticular pigmentation and thus cannot tolerate direct sunlight, they remain confined to their mounds during the day, whereas at night, they emerge on the soil surface to forage, often in dense aggregations numbering in excess of 4000 individuals (Richardson 1987a). About three-fourths of each termite foraging party consists of workers, with the remainder being soldiers that station themselves on the perimeter of the column (Kruuk and Sands 1972). The latter possess enlarged frontal glands capable of projecting sticky, noxious secretions of terpenoids (β-pinene and limonene; Braekman et al. 1984), distasteful chemicals that successfully deter many potential predators (Stuart 1969, Prestwich 1983, Richardson and Levitan 1994). During winter nights when ambient air temperatures drop below 10°C, _T. trinervoides_ remain belowground, inaccessible to aardwolves. Lacking morphological specializations such as long claws that would expedite excavation of mounds, aardwolves switch their foraging efforts to another species of termite during this time, _Hodoterme mossambicus_ (Richardson 1987a).

As a result of its dark pigmentation, _H. mossambicus_ can forage at any time, but is mainly active during the daytime, especially in winter (the dry season). This species of termite does not possess a chemical defense system as does _Trinervitermes_. Soldiers are not present in its colonies, nor does it construct an epigean termite mound (Nel 1968). _H. mossambicus_ provides far less food for aardwolves, in part because its presence on the soil surface is less predictable, apparently because this species stores food underground during the dry season, and in part because when it does forage on the surface, it does so in smaller foraging parties, usually 10–20 individuals. As a consequence of this, and of the fact that aardwolves apparently do not forage for insects other than termites, their food intake is reduced by as much as 80% during the winter months, a period thought to be energetically stressful for them (Richardson 1987a). In support of this idea are the facts that adults can lose up to 20% of their body mass and that juveniles suffer their highest mortality in winter.

McNab (1984) reported that, regardless of their taxonomic affiliation, ant- and termite-eating mammals that weigh >1 kg have a reduced basal metabolic rate (BMR), an example of evolutionary convergence for a physiological character. Such a diminution in basal metabolism gains ecological significance if a diminished BMR translates into a reduced metabolic rate in the field, but this idea has rarely been tested. McNab proposed a number of factors that could have been responsible for the evolution of a reduced BMR in myrmecophagous mammals (i.e., mammals that feed on ants or termites). We favor the idea that because termites are, at times (such as during cold weather) unavailable on the soil surface, aardwolves face periods of prolonged fasting. A reduced BMR would allow them to survive these periods of food deprivation.

In a previous laboratory study, we measured the oxygen consumption and evaporative water loss of aardwolves during both summer and winter at ambient temperatures ranging from 5° to 35°C (Anderson et al. 1997). Basal metabolism during summer and winter averaged 77.6 and 60.7%, respectively, of the values predicted by the Kleiber (1961) equation, whereas estimates of evaporative water loss varied from 55 to 39% of predictions, depending on the season. We concluded that aardwolves have much lower basal metabolic rate and evaporative water loss relative to other eutherian mammals, and that these factors together made significant contributions toward their capacity to endure periods of food deprivation, like those encountered during the wintertime, and toward their successful occupation of arid lands, which have low primary production and scant rainfall.

In this study, we report the first estimates of field metabolism and water flux as determined by doubly labeled water (DLW) for a myrmecophagous eutherian mammal. Moreover, we describe a novel approach to obtaining frequent samples of the body water pool of isotopically labeled animals, which allows serial estimates of energy expenditure and water flux without excessive handling of experimental subjects. Specifically, we tested the hypotheses that reduced basal metabolism and pulmocutaneous water loss, as measured in the laboratory, lead to a conservative field metabolic rate (FMR) and water flux in free-living aardwolves. Further, we quantified the activity budget of aardwolves during summer and winter to construct a time–energy budget for them, thereby examining their seasonal pat-
terns of energy allocation. Lastly, we used our knowledge of the water flux of aardwolves and of the water content of their prey to construct a water budget for aardwolves during both summer and winter, and to estimate their seasonal consumption of termites.

**MATERIALS AND METHODS**

**Study area**

We studied aardwolves for two years, from December 1988 to January 1991, on a 2015-ha study plot on the Benfontein Game Farm (28°50′ S, 24°50′ E), located ~6 km southeast of Kimberley, South Africa. The vegetation of the area was dominated by short perennial grasses, such as *Eragrostis* spp., *Stipagrostis* spp., and Karoo shrubs (Richardson 1985).

**Climate**

Classified as semi-arid, the climate of the Kimberley region is characterized by warm, relatively moist summers, and cold, dry, winters (Schulze and McGee 1978). During the two years of our study, mean maximum air temperatures exceeded 30°C during December and January, but also regularly dropped below 20°C at night during this same season (Anderson 1994). The lowest mean minimum air temperatures occurred during June and July (1.0° and 1.5°C, respectively). Climatic data for the region were obtained from the Kimberley Weather Station at the Kimberley Airport, Kimberley, South Africa, located ~5 km from our study area.

**Study animals**

The natural history of aardwolves has been described by Richardson (1987a), Koehler and Richardson (1990), Skinner and Smithers (1990), Anderson (1994), and Van Jaarsveld et al. (1995). During the nonbreeding season, a male aardwolf along with his mate will occupy a single territory of 1–4 km², containing ~3000 termite mounds. Boundaries are patrolled by both sexes, and are regularly marked with pungent secretions from the animals’ anal glands. Despite joint occupancy of a territory, individuals are solitary at this time and forage alone. Each territory contains several midden, irregularly shaped areas of ~12 m² consisting of loosely packed sandy soil that are used for defecation. During their daily foraging routines, aardwolves typically walk 8–12 km in summer; in winter, distance traveled is highly variable. On some cold winter nights, aardwolves find little food, with the result that they move only short distances, sometimes <3 km, before retiring for the night, whereas during the mating period of this same season (July), males may roam >24 km in search of a mate.

The breeding season begins when females enter estrus, typically the first two weeks of July, when ambient temperatures are low. After a gestation period of ~90 d, two to four cubs are born, usually in October. For ~15 wk following birth, the young are most susceptible to predation, especially from black-backed jackals (*Canis mesomelas*). As a consequence, males spend a considerable portion of their active period guarding the den at this time. Cubs begin foraging for termites at ~3 mo of age, and are independent by ~7 mo. Thereafter they are excluded from the natal territory.

**Den temperatures**

Within each territory, aardwolves construct 5–6 dens, usually by enlarging vacant springhare (*Pedetes capensis*) burrows (Richardson 1987b, Anderson 1994). Occupation of a den significantly affects the temperatures that aardwolves experience. To obtain an idea of the seasonal variation in temperatures that aardwolves encounter while in their den, we measured the air temperature of an unoccupied den at hourly intervals for two consecutive days during midsummer (December) and during midwinter (June) using a KM multi-channel temperature recorder. We inserted a thermistor ~2.5–3.0 m into the burrow, or ~75% of the length of the den (Anderson 1994), to measure the temperature of the air. Additional thermistors were placed on the soil surface near the den entrance, and in the air ~1 m above the soil surface. The latter thermistor was shaded by aluminum foil.

**Body temperature**

To facilitate locating individual aardwolves and to simultaneously monitor body temperature (*Tb*), we implanted a temperature-sensitive radio transmitter into the abdominal cavities of six animals, two males and four females, to which we assigned names (Anderson and Richardson 1992). Surgical procedures followed Mckenzie et al. (1990). The transmitters (IMP/400/L; Telonics, Incorporated, Mesa, Arizona) weighed 120 g, which is 1.2–1.6% of the body mass of aardwolves and less than the maximum 3–5% transmitter mass/body mass ratio recommended by Amlanar and MacDonald (1980). The transmitters were calibrated before implantation, and recalibrated after removal 8–12 mo later to correct for any drift in pulse rate. We allowed animals to recover for 3 wk from our surgical procedures before we began monitoring *Tb* by means of a Yaesu FT290R radio receiver (Yaesu Musen Company, Tokyo, Japan). We recorded *Tb* for each aardwolf (*N* = 6) at hourly intervals over two 24-h periods during both summer (12 d; November–March) and winter (12 d; June–July). Pulses were counted for 2-min intervals and averaged to obtain a mean count at each hourly interval.

**Body mass**

In addition to the data for body mass of aardwolves used in our DLW experiments, we also obtained information on body masses of other aardwolves from several sources. During the course of previous field work we immobilized a number of animals, all of which
were weighed with a 10-kg Pesola scale, or a 25-kg Salter scale (model 235). Additional data were obtained from records of the McGregor Museum, the South African Museum, the National Museum, and the Transvaal Museum, all located in South Africa; from the State Museum, in Windhoek, Namibia; and from records of the Northern Cape Nature Conservation Service. Only individuals older than 7 mo of age were included in the analysis.

Nutritional characteristics of termites

To assess the nutritional characteristics of *T. trinervoides*, we collected monthly samples of these insects during the period of May 1989–April 1990 from an area adjacent to our study area. Each month we broke open three termitaria and collected \( \sim 5–10 \) g of each caste using forceps. Samples were frozen at \(-10^\circ\text{C}\) pending analysis.

The water content of workers and soldiers was determined by drying in an oven at 70\(^\circ\)C to constant mass. Other aspects of the nutritional content of termites, such as their fat content, nitrogen content, and ash content, were determined at the University of Pretoria. For some analyses, samples from two consecutive months were combined to provide sufficient material for each determination. Fat extraction was accomplished by petroleum ether distillation using the Soxhlet technique (Allen et al. 1974). Nitrogen content of samples was determined by the Kjeldahl method (Horwitz 1975). Crude protein was estimated by multiplying nitrogen values by 6.25 (McDonald et al. 1981). Ash content was measured after combustion in a muffle furnace at 500\(^\circ\)C, for \( \sim 5 \) h (Paine 1971).

The energy content of *Trinervitermes* workers and soldiers has been characterized by Adam (1993). He reported that mass-specific energy content did not vary significantly between months within castes, but did differ significantly between castes. Workers, which averaged 1.65 mg dry mass, had an energy content of 17.0 J/mg dry mass, whereas soldiers averaged 0.93 mg and 17.7 J/mg. When feeding on *Hodoter mes mosambicus*, aardwolves consume workers that harvest grasses on the soil surface (Richardson 1987a). These individuals have a average wet mass of 70.95 mg and a dry mass of 30.3 mg (M. C. van der Westhuizen, personal communication). We have assumed that the energy density of *Hodoter mes* is equivalent to that of worker *Trinervitermes*.

Activity patterns

A general accounting of when aardwolves were active during each season was made by noting when radio-tagged animals exited their dens in the afternoon or evening, and when they returned (exit and entrance times were recorded for 2–3 d for each aardwolf each season).

For animals injected with DLW, we partitioned their active time into an activity budget by recording their behavior every 30 s, as indicated by an electronic metronome (Wiens et al. 1970). Aardwolves were accustomed to our vehicle and would allow us to approach within 15–40 m, depending on the animal. Once we located an aardwolf, we observed it through binoculars with the aid of a spotlight attached to our vehicle. We continued recording data into a portable tape-recorder for a maximum of 30 min, or until we lost visual contact (the more usual occurrence). After following an animal for the maximum period, we waited for at least 30 min before beginning another observation session. Behavior was classified as walking, feeding, resting (lying down, usually near the den), scent marking, standing, running or loping, courtship, and other (which included grooming, urination, and defecation). If aardwolves were feeding at the signal, we noted the termite species that they were eating. Determination of prey type was relatively easy because only two species of termite occurred on our study area (Richardson 1985), and because aardwolves characteristically remain stationary for at least 20–30 s when ingesting *T. trinervoides* (Kruk and Sands 1972, Richardson 1985), but only pause for a few seconds while licking up *H. mosambiques*. Additionally, at each signal of the metronome, we recorded the dominant species of the plant community in which aardwolves were foraging (see Richardson 1985 for a complete description of each community), and the distance to the nearest termite mound. The latter measurement was motivated by the idea that during the summer aardwolves forage predominantly on *T. trinervoides*, which forage up to 20 m away from their termitaria (Richardson 1985), but during the winter they sometimes feed solely on *H. mosambiques*. Hence we thought that aardwolves would forage closer to exposed mounds during the summer.

If we suspected that our presence was influencing the behavior of aardwolves, as was the case for several animals, especially the day after injection, we immediately terminated observations until the following evening. This procedure reduced our sample size somewhat for time budgets, but assured that our DLW estimates were representative of a natural situation. We did not obtain adequate data to analyze sexes separately, and hence have combined time-budget data for both sexes.

Calculation of energy budget

We employed a two-part model to estimate energy expenditure from time-activity budgets of aardwolves:

\[
H_{\text{DEE}} = H_{\text{inactive}} + H_{\text{active}}
\]

(1)

where \( H_{\text{DEE}} \) = total daily energy expenditure (in kilojoules per day), and \( H_{\text{inactive}} \) and \( H_{\text{active}} \) represent the energy expended (in kilojoules) in the den and while active, respectively. Energy expenditure while in the den was evaluated as:

\[
H_{\text{inactive}} = (H_{d} + H_{\text{inh}}) + H_{\text{sys}}
\]

(2)
where $H_e$ is the basal metabolic rate (0.734 kJ/min, summer; 0.617 kJ/min, winter; Anderson et al. 1997), $H_{th}$ is the energy expended in digestion ($H_{th} = \text{heat increment of feeding}$), $H_{TR}$ is the energy expended in thermoregulation (in kilojoules per minute) and $t$ is time (in minutes) spent inactive. Based on work on dogs (16.6 kg) and sea otters (18.4 kg; Enhydra lutris), we assumed that postprandial resting metabolism was 50% higher than basal metabolism (Costa and Kooyman 1984, Diamond et al. 1985), and that metabolism remained elevated 5 h after entry into the den in summer. Because of their reduced food intake, we assumed that the heat increment of feeding was important for 2 h in the den in winter (Richardson 1987a).

Energy expenditure while active was estimated as:

$$H_{active} = \sum H_i t_i + H_{TR} t$$

(3)

where $H_i$ is the energy expenditure of the $i$th activity (in kilojoules per minute), $t_i$ is the time (in minutes) spent in the $i$th activity, $H_{TR}$ is the energy expended in thermoregulation (in kilojoules per minute), and $t$ is time (in minutes). We estimated the energy cost of walking from body mass and the average velocity of aardwolves when walking by the equation (Taylor et al. 1982): $V_{CO\text{}} = (\text{milliliters of oxygen per second per kilogram}) = 0.533M_b^{0.319}V_b + 0.300M_b^{0.303}t$, where $M_b$ is body mass in kilograms and $V_b$ is velocity (in meters per second). The average walking speed of an aardwolf is 2.3 km/h or 0.64 m/s (Richardson 1987a). The energy cost of feeding was evaluated as 2.25 times the resting metabolic rate (RMR). It is well known that the metabolism of fed animals during the active period is somewhat higher than basal metabolism (e.g., Karasov 1981). For this analysis, we assumed that RMR equaled 1.7 × BMR (Taylor et al. 1970, King 1974). We based this assessment, in part, on the report of Golightly (1981), who examined the oxygen consumption of postabsorptive kit foxes (Vulpes macrotis) over 24-h periods. He showed that metabolism increased by 60–80% compared to basal levels during periods when foxes were normally active. We assigned a value of 3 × RMR to courtship behavior. Further, we assumed that the energy cost of scent marking equaled 2 × RMR, and that energy expended in the other category could be approximated as 2 × RMR. For energy expenditure while standing, we used the intercept of the Taylor et al. (1982) equation, and for the cost of running we evaluated their equation for a speed of 10 km/h (M. D. Anderson, unpublished manuscript). Energy costs for thermoregulation were estimated by using the appropriate equation for laboratory metabolism evaluated at the average daily minimum air temperature for the time period that animals were labeled (Anderson et al. 1997). We recognize that the latter procedure only crudely estimates the energy cost of thermoregulation. In reality, aardwolves experienced higher ambient temperatures than the minimum for at least part of their active period, which would result in an overestimate of costs, but they were also exposed to significant convective cooling while active, which would cause an underestimate of thermoregulatory costs from laboratory data. These errors are in the opposite direction.

**Field metabolism and water flux**

Estimates of daily energy expenditure and water flux were obtained by means of the DLW technique, in which the rate of decline of an isolate of hydrogen in the body water pool provides a measure of water flux (Nagy and Costa 1980), and the loss rates of both a hydrogen isolate and $^{16}$O yield an estimate of CO$_2$ production (Lifson and McClintock 1966, Nagy 1980). Using appropriately derived conversion factors, energy expenditure can be calculated from CO$_2$ production (Gessaman and Nagy 1988, Weathers and Sullivan 1989). The efficacy of hydrogen isotopes to monitor water flux has been well documented; estimates are typically within ±10% of mean values (Nagy and Costa 1980, Degen et al. 1981, Crum et al. 1985). Additionally, the DLW method has been validated for several species of vertebrates, including reptiles (Congdon et al. 1978), birds (Williams and Nagy 1984, Williams 1985, Gales 1989), and mammals, including man (Mullen 1970, Nagy and Montgomery 1980, Gettinger 1983, Schoeller and Van Santen 1982, Schoeller et al. 1986a,b). Results from these and other studies indicate errors of <10% on average.

Following Anderson and Richardson (1992), we captured aardwolves using a Telinject dartgun (Telinject, Randburg, South Africa) with darts containing a mixture of ketamine hydrochloride (15–20 mg/kg) and acepromazine (15–40 mg/kg). Anesthesia was induced within 5 min after darting. After removing 2 mL blood from a vein in the leg for the determination of background levels of isotopes, we slowly infused 15–20 mL of a solution containing a mixture of tritium and 15% $^{16}$O intraperitoneally into the animal. The volume administered depended on the mass of the aardwolf, such that initial enrichments in injected animals yielded $660$ Bq/10 mL body water for tritium, and 220 µmol/ml above background for $^{16}$O. Animals were kept under light anesthesia for ~2 h while the isotopes equilibrated with body water. From a vein in another leg, we collected 5 mL of blood, weighed the aardwolf, then laid it in front of its den. We watched from our vehicle to assure that the animals recovered. On subsequent days we positioned ourselves near the dens of injected animals around the time we expected them to emerge. As is the case of aardwolves, most animals defecated soon after leaving their den in one of several middens within their territory. With latex gloves on our hands, we collected these feces, being careful to exclude any adhering soil, and placed them in a glass tube sealed with an airtight stopper. In the laboratory, we rendered the stopper-glass tube junction airtight with wax, and then stored the feces at −10°C until we distilled water from them. For a final blood sample,
and for a final body mass, we redated each aardwolf, and collected blood and measured body mass as before.

In the laboratory, we lyophilized blood and fecal samples to obtain pure water (Vaughn and Boling 1961), which was then flame sealed in 2-mL glass ampules and sent to Global Geochemistry Corporation (Los Angeles, California) for determination of the concentrations of $^{18}$O. Concentrations of hydrogen isotopes were determined following Williams (1987) using a Beckman 5800 TS liquid scintillation counter (Fullerton, California).

In theory, any fluid that is in isotopic equilibrium with the body water pool can be sampled for use in the doubly labeled water technique, but samples of blood are almost always employed (Lifson et al. 1955, Nagy 1980, 1983). Because we used a somewhat novel approach in obtaining samples of body water, we deemed it prudent to confirm that the water in feces was in isotopic equilibrium with body water. To do so, we injected a captive aardwolf with tritium (92.5 MBq/animal), and then took blood samples on subsequent days when we observed it to defecate. After 26 h from the time of injection, the difference between tritium levels in blood and feces was 1.2%, and after 44 h, the difference was 1.4%. When we repeatedly pipetted from the same sample ($N = 3$), differences in counts averaged $0.8 \pm 0.3\%$. Further confirmation that water in feces can be used to sample the body water pool comes from a comparison between final blood samples and fecal samples that were obtained shortly before we redated the aardwolf. For Panza during the summer, the difference between $^{18}$O concentrations of fecal water, obtained at 2100 h, and a final blood sample collected 1 h later was 0.2%. We conclude that water in feces is in isotopic equilibrium with the water of the body water pool.

We have used a two-compartment model to calculate CO$_2$ production (Racette et al. 1994):

$$r_{CO_2} = \frac{N}{2.078}(1.007k_a - 1.041k_f) - 0.0246R_{gf}$$

where $N$ is the average total body water (in moles), $k_a$ and $k_f$ are the respective isotope turnover rates, and $R_{gf}$ is the rate of water loss through gaseous routes subject to isotope fractionation. The constants 1.007 and 1.041 adjust for the differences between isotope dilution spaces and total body water (Nagy 1980, Racette et al. 1994).

Our calculation of water flux employed Eq. 15 of Lifson and McClintock (1966), modified to compensate for fractionation as these authors suggested. Their correction factor for fractionation was based on the properties of deuterium; we used tritium, which could have different fractionation properties. However, Karasov et al. (1988) have shown that in vivo fractionation of $^2$H and of $^3$H are not significantly different.

To calculate CO$_2$ production and water flux requires knowledge of the quantity of water in the animal. This information can be estimated from the dilution space of $^{18}$O, provided the exact dosage of the isotope administered is known (Lifson and McClintock 1966, Crum et al. 1985). In animals for which we were confident of the injection volume, total body water averaged 69.0 ± 3.5% in the summer ($N = 3$), and 62.3 ± 4.6% ($N = 3$) during the winter. In cases where we were uncertain as to the precise amount of isotope mixture administered, we used average values. These results are consistent with those of Geffen et al. (1992) for Blanford’s foxes (Vulpes cana), which had a body water content ranging from 62.1 to 73.3% during summer and 63.7 to 66.1% during winter. We assumed that total body water changed linearly during the measurement period. We also assumed that body mass changed linearly over time to calculate body masses for intervals between our initial and final measurements of body mass.

We estimated the relationship between CO$_2$ production and energy expenditure as 25.7 kJ/L CO$_2$, a value empirically derived for a lizard eating early-instar mealworms (Nagy 1983). According to Gessaman and Nagy (1988), the potential errors incurred when using this conversion factor are <5% for carnivorous mammals, even for an individual that does not eat during the measurement interval, but relies completely on body fat for its source of energy.

**CO$_2$ concentration in den air**

If unlabeled CO$_2$ enters the body of an animal that has been injected with DLW (across respiratory surfaces or skin), the turnover of isotopes in that animal will be affected, and this may cause errors in calculated CO$_2$ production (Lifson and McClintock 1966, Nagy 1980). Aardwolves spend a considerable portion of their day confined to a den, and it is known that CO$_2$ concentrations in burrows can rise to levels far above ambient air, at least for small rodents (2–10%; Darden 1972, Arieli 1979, Gettinger 1983). However, if labeled animals are rebreathing their own CO$_2$, then errors are minimized, as would be the case for aardwolves during winter when they slept alone (Nagy 1980). But if labeled animals occupy a confined space with other unlabeled animals, as was the situation with Calypso and Electra, which shared their dens during the summer with two and three cubs, respectively, then the potential exists for elevated CO$_2$ concentrations to significantly influence estimates of CO$_2$ production (Nagy 1980). We measured the CO$_2$ concentration of the air in two aardwolf dens, one occupied by an adult female and her three cubs, the other by an adult male. In both situations, aardwolves had been present in their dens for at least 6 h prior to sampling of air. Using a pump attached to a tygon tube positioned ~3 m into each den, we filled several Douglas air bags with air from the den. In the laboratory, air samples were analyzed for CO$_2$ concentration by means of a LI-COR carbon dioxide analyzer (model LI-6262; LI-COR, Lincoln, Nebraska).
Nebraska). Air from the den with the female and her cubs contained 0.2% CO₂, whereas air from the den with the solitary male contained 0.3% CO₂. Errors introduced by these levels of CO₂ would be small (Schoeller et al. 1986b; see also Covell et al. 1996).

**Statistics**

To test for statistical differences of body temperature between seasons, we used a Mann-Whitney U test (Zar 1984). For evaluation of differences between the composition of termite castes where data were in the form of percentages, we arcsine transformed data before performing independent sample t tests. Our original experimental design consisted of comparing the FMR and water flux of the same six aardwolves during two seasons. Following our first set of measurements (winter), Rapunzel disappeared. Hence, because we had unequal sample sizes for seasons, we tested for differences between seasons for FMR and water influx by a mixed-model random coefficient regression analysis for repeated measures (Crowder and Hand 1993), where season was assigned as a fixed effect and individual aardwolves as a random effect. Computations were performed by SAS Proc Mixed procedure (SAS Institute 1990).

**RESULTS**

**Den temperatures**

In summer (December), temperatures within a den showed only minor fluctuations over a 24-h period and averaged 27.2° ± 0.2°C, even though the ambient surface temperature ranged from 15° to 38°C during this time (Anderson 1994). In winter (June), den temperatures also remained nearly constant throughout the day, though lower than in summer, averaging 12.2° ± 1.2°C (mean ± 1 SD). Soil surface temperature varied from 3° to 30°C during the same interval.

**Body temperature**

Mean Tₘᵦ of six aardwolves averaged 36.6° ± 0.6°C during summer (November–March), significantly higher than the value for winter (June–July), 35.8° ± 1.2°C (Mann–Whitney U test, Z = 8.9, P < 0.01). While aardwolves were active, Tₘᵦ did not differ significantly between seasons, averaging 37.2° ± 0.4°C (N = 79) and 37.3° ± 0.7°C (N = 38) during summer and winter, respectively, but while inactive in their dens, their Tₘᵦ was significantly higher in summer, 36.1° ± 0.3°C (N = 185) vs. 35.5° ± 1.1°C (N = 227) (Mann-Whitney U test, Z = 8.4, P < 0.01).

**Body mass**

Body masses of male and female aardwolves did not differ significantly from each other in either summer (December–February) or winter (June–August), and thus we have combined data for both sexes. For all data combined, including data for both unlabeled and labeled animals, body masses differed between seasons. During the summer months, body mass averaged 9.1 ± 1.0 kg (N = 17 animals), while during the winter months, it averaged 8.3 ± 1.1 kg (N = 60 animals), measures that differ significantly (t = 4.5, df = 9, P < 0.05). The lowest body masses that we recorded occurred in August, when males and females together averaged 7.5 ± 0.9 kg (N = 13). For the aardwolves that we used in our DLW experiments, body mass averaged 7768 ± 638 g and 8543 ± 1215 g during summer and winter, respectively. Body mass was not significantly different between seasons for this group of animals (t = 1.3, df = 9, P > 0.2).

**Nutritional characteristics of termites**

Worker termites contained a significantly higher percentage of water than did soldiers (76.3 vs. 70.9%; t = 6.5, df = 22, P < 0.01), and they were higher in protein content (51.9 vs. 39.1%; t = 4.3, df = 10, P < 0.01). Workers contained a lower percentage of lipids (3.1 vs. 4.9%; t = 4.9, df = 10, P < 0.01) and ash (11.6 vs. 21.9%; t = 3.9, df = 4, P < 0.05) (Table 1).

**Time budgets**

Aardwolves were active for an average of 8.77 ± 1.43 h/d (N = 12) during summer, but only 4.05 ± 3.98 h/d (N = 18) during winter, values that are significantly different (t = 5.2, P < 0.01) (Fig. 1 insert). They emerged from their dens at an average time of 1920 ± 0.5 h (N = 18) and returned to them at 0404 ± 1.52 h (N = 12) at night in summer, but in winter they often initiated their aboveground activity before sunset (1628 ± 0.95 h; N = 23). The time when they returned to their den in winter varied considerably, with the average time of return being 2028 ± 3.97 h (N = 18).

The activity schedules of injected aardwolves differed significantly between seasons (χ² = 107.2, df = 6; P < 0.0001, Fig. 1). In winter, they spent a signif-

| Table 1. Nutritional characteristics of Trinervitermes trinervoides. |
|------------------|---------|---|------|-------|---|---|
| Nutritional characteristic | Workers | | | Soldiers | | |
| | Mean (%) | 1 SD | N | Mean (%) | 1 SD | N | P |
| Water | 76.3 | 2.5 | 24 | 70.9 | 3.2 | 24 | 0.01 |
| Protein | 51.9 | 4.3 | 12 | 39.1 | 3.6 | 12 | 0.01 |
| Lipid | 3.1 | 0.6 | 12 | 4.9 | 1.0 | 12 | 0.05 |
| Ash | 11.6 | 2.3 | 6 | 21.9 | 6.1 | 6 | 0.01 |
significantly larger proportion of their active time eating termites (26.7 vs. 15.2%), even though the total time spent feeding in winter was less because of their relatively short period of activity. In addition, males and females spent ~12.6% of their time in winter in breeding activities such as courtship and copulation.

Prey species varied between seasons, with aardwolves feeding on *Trinervitermes* 65.8% of the time, but they also spent a considerable amount of time feeding on *Hodotermes* (34.1%), an unusual situation during this season (Fig. 2; $\chi^2 = 77.5$, df = 1, $P < 0.0001$; Richardson 1987a). In winter, these percentages were nearly reversed; aardwolves fed on *Trinervitermes* 33.8% of the time and *Hodotermes* 66.2%.

Though the percentage of time spent in different vegetation types differed significantly between seasons, aardwolves foraged most often in plant communities dominated by *Stipagrostis uniplumis* or *Pennisetum incana* during both summer and winter (Fig. 3; $\chi^2 = 49.3$, df = 4; $P < 0.001$). For data from the summer, there existed a correlation between the amount of time aardwolves spent in each vegetation type and the number of termite mounds/ha ($r = 0.70$, df = 8, $P < 0.05$), but for data from winter the relationship was not significant ($r = 0.60$, df = 8, $P = 0.11$).

Aardwolves foraged within 20 m of a *Trinervitermes* mound > 70% of the time regardless of the season, but tended to forage farther from mounds in the winter (Table 2; $\chi^2 = 68.9$, df = 5, $P < 0.001$).

We converted time expenditure into an energy budget from a model that sums energy expenditures for resting in their den, activity outside of the den, thermoregulation, and the heat increment of feeding (Fig. 4). Our model summed to 2370.5 kJ/d for aardwolves in summer, and 2086 kJ/d in winter, values that deviated from our DLW estimates by -18.0% and +13.1%, respectively. A portion of the underestimate of energy expenditure during summer can be attributed to milk production by females. Both Electra (three cubs) and Calypso (two cubs) were feeding cubs during our measurements, although Electra's cubs were nearly independent. Because the energy content of milk and the rate of its production is highly variable, both among species and individuals, it is difficult to estimate the amount of energy devoted to this process by aardwolves. However, estimates of energy output in milk...
Fig. 2. The percentage of time that aardwolves spent feeding on two species of termites. Aardwolves foraged inside *Trinervitermes* mounds only after an aardvark (*Orycteropus afer*) had dug in the mound.

Fig. 3. The percentage of time that aardwolves spent foraging in various plant communities in (A) summer and (B) winter. Each vegetation type is identified by its dominant plant species. (C) The percentage of time that aardwolves spent in plant communities as a function of the number of *Trinervitermes* mounds. The solid line is the regression line for summer data.
Table 2. The percentage of time spent by aardwolves in foraging at various distances from the mounds of *Trimeresurus*.

<table>
<thead>
<tr>
<th>Distance category (m)</th>
<th>Percentage of observations†</th>
<th>Summer</th>
<th>Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–5</td>
<td>34.2</td>
<td>28.3</td>
<td></td>
</tr>
<tr>
<td>6–10</td>
<td>22.2</td>
<td>24.2</td>
<td></td>
</tr>
<tr>
<td>11–15</td>
<td>16.5</td>
<td>18.4</td>
<td></td>
</tr>
<tr>
<td>16–20</td>
<td>17.6</td>
<td>11.0</td>
<td></td>
</tr>
<tr>
<td>&gt;20</td>
<td>9.4</td>
<td>18.4</td>
<td></td>
</tr>
</tbody>
</table>

† Total number of observations for summer = 935, and for winter = 2171.

range from ~418 kJ/d to 1255 kJ/d for mammals similar in size to the aardwolf (Martin 1984, Ofedal 1984).

A seasonal comparison of the allocation of energy to various components of the energy budget showed that more energy is devoted to activity in summer (61.9% of total expenditure), but that only 33.5% was devoted to activity in winter.

**Field metabolism and water flux**

During summer (November–January), aardwolves that averaged 7768 g in body mass had a CO₂ production of 112.5 L/d or 2891.2 kJ/d (Table 3). During winter (June–July), mean body mass was higher than summer values (8543 g), as a consequence of Electra and Joseph weighing ~2.5 and 1.5 kg more, respectively, early in the winter period. Carbon dioxide production during this season averaged only 71.8 L/d, or 1844.8 kJ/d, a substantial reduction from summer values. Summer values for CO₂ production were significantly different from winter values ($F_{season} = 9.9$; df = 1, 15; $P < 0.006$).

Water flux equaled 615 mL/d during summer, but only averaged 292 mL/d during winter, a decrease of 53.1%. When we statistically compared water flux between seasons, differences were significant ($F_{season} = 11.9$; df = 1, 15; $P < 0.001$).

**Discussion**

**Tests of hypotheses**

Among the 4060 species of living mammals (Vaughan 1986), only 18 species, or less than one-half of one percent, have the capability of feeding almost exclusively (>90% of diet) on either ants or termites, insects characterized by a relatively high ash and low fat content compared to many other species of invertebrates (Redford and Dorea 1984, Redford 1987). Dietary specialization on this low-quality food is accompanied by a reduction in basal metabolism, as measured in the laboratory, for most, if not all, of these myrmecophagous species (McNab 1984). However, in view of the fact that BMR makes a variable contribution to total daily energy expenditure, from 45% down to ~27% (Kleiber 1961, Nagy 1987), and that, at least for one mammal, the marmot (*Marmota flaviventris*), a relatively low BMR does not translate into a reduced FMR (Salsbury and Armitage 1994), the coupling between BMR and metabolism in the field remains unclear. As a result, the evolutionary and ecological significance of a diminution in BMR is still an unresolved problem, despite attempts to place variation in basal metabolism into an ecological framework (McNab 1980, 1984, 1986, Bennett 1988).

We report the first measurements of FMR for the aardwolf, which has a markedly reduced BMR—between 68 and 58% of expectation, depending on the season, summer or winter, respectively. Our results support the hypothesis that a reduced BMR results in a lower FMR. Based on DLW studies of 46 eutherian species, the equation of Nagy (1987) predicts a FMR of 4873.3 kJ/d for aardwolves in summer (mean body mass = 7768 g), whereas for these animals in winter (mean body mass = 8543 g), it yielded a value of 5265.0 kJ/d. We have found an average FMR of 2891.2 kJ/d for summer and 1844.8 kJ/d for winter, deviations of ~40.6 and ~65.0%, respectively, from these predictions.

Data for the field metabolism of carnivores that live in the desert are scant; we only found information for the Blanford’s fox (0.8–1.0 kg; *Vulpes cana*), a canid found in the deserts of Israel (Geffen et al. 1992). Foxes had an average FMR of 627 kJ/d in summer and 655 kJ/d in winter. Mass-adjusted FMR, i.e., FMR divided by mass raised to the slope of the allometric equation for desert eutherian mammals, equaled 2.90 kg⁻⁰.⁷₈₆·d⁻¹ and 2.85 kg⁻⁰.⁷₈₆·d⁻¹ for summer and winter foxes, respectively. Comparable values for aardwolves are 2.53 kg⁻⁰.⁷₈₆·d⁻¹ for summer and 1.5 kg⁻⁰.⁷₈₆·d⁻¹ for winter. The FMR of aardwolves is remarkably low, especially in winter, when compared to eutherians in general, or when the comparison is restricted to desert mammals.

Our results may support the hypothesis that a reduced pulmocutaneous water loss leads to a conservative water flux in the field. We have found it methodical to compare the water flux of aardwolves with allometric equations in the literature because conclusions vary depending on the equation one chooses. For example, one might expect that eutherians living in the desert would have one or more adaptations that lead to a more frugal water economy than nondesert species, as appears to be true for many small desert rodents (Nagy and Peterson 1988). However, according to the equations of Nagy and Peterson (1988), a 10-kg desert eutherian is expected to have a higher water flux than an animal of the same body mass in a non-desert situation, suggesting the counterintuitive idea that larger desert forms have higher rates of water turnover than other similar-sized species that do not live in environments where water is in limited supply. We have elected to compare the water flux of aardwolves with other desert eutherians, but suggest that these conclusions are tentative. Measured rates of water influx for aardwolves,
615.0 mL/d (summer) and 292.0 mL/d (winter), are 17.7 and 64.3% lower, respectively, than one would expect of a eutherian mammal living in an arid environment. If we employ the equation for mammals that live in habitats other than deserts, the prediction would be 556.6 mL/d for an aardwolf in summer and 596.8 mL/d for winter. Here, we would conclude that the water flux of an aardwolf is reduced only in winter. Mass-adjusted water flux for the Blansford fox, a desert mammal that relies on its food for water, was 0.42 mL H₂O-(mass)⁻⁰.₈₁₈·d⁻¹ in summer and 0.32 mL H₂O-(mass)⁻⁰.₈₁₈·d⁻¹ in winter, whereas the same values for aardwolves were 0.40 mL H₂O-(mass)⁻⁰.₈₁₈·d⁻¹ and 0.18 mL H₂O-(mass)⁻⁰.₈₁₈·d⁻¹, respectively (Geffen et al. 1992). By most standards the water influx of aardwolves is remarkably low in the wintertime.

**Mechanisms that reduce FMR**

In summer, the FMR of aardwolves (2891.2 kJ/d) is 1982 kJ/d less than expected based on Nagy’s (1987) equation, whereas, in winter their FMR (1844.8 kJ/d) is 3420.2 kJ/d lower than predicted. What factors contribute to such a frugal total energy expenditure in aardwolves? Because their BMR accounts for a considerable proportion of their FMR, 36.6% in summer and 48.2% in winter, adjustments in BMR can significantly impact their total energy expenditure. For example, subtracting BMR for each season from predictions based on the Kleiber (1961) equation suggests an energy savings of 275.0 kJ/d in summer and 543.3 kJ/d in winter. These values represent only 13.9% (summer; 275.0/1982 kJ/d) and 15.9% (winter; 543.3/3420.2 kJ/d) of the apparent reduction in the energy usage, indicating that other components of their energy budget might also be reduced. We suggest that the energy expended on activity by aardwolves is also minimized relative to other carnivores, which potentially have large expenditure for activity because they travel greater distances than other noncarnivorous mammals (Garland 1983, Karasov 1992).

**Patterns of energy allocation**

Evaluation of metabolism under laboratory conditions in combination with estimates of FMR as given...
### Table 3. Body masses, field metabolic rates, and water influx of aardwolves during summer and winter near Kimberley, South Africa.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Body mass (g)</th>
<th>CO₂ production (L/d)</th>
<th>Field metabolism† (kJ/d)</th>
<th>Water influx (mL/d)</th>
<th>Change in body mass (%)</th>
<th>Period (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summer‡</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Electra</td>
<td>7105</td>
<td>65.4</td>
<td>1680.3</td>
<td>717</td>
<td>1.3</td>
<td>1.22</td>
</tr>
<tr>
<td>Electra</td>
<td>7215</td>
<td>126.9</td>
<td>3262.1</td>
<td>310</td>
<td>1.9</td>
<td>0.81</td>
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<tr>
<td>Electra</td>
<td>7225</td>
<td>51.8</td>
<td>1331.9</td>
<td>590</td>
<td>1.6</td>
<td>3.03</td>
</tr>
<tr>
<td>Joseph</td>
<td>8875</td>
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<td>3040.6</td>
<td>1074</td>
<td>-0.6</td>
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<tr>
<td>Joseph</td>
<td>8825</td>
<td>148.9</td>
<td>3827.5</td>
<td>640</td>
<td>-0.5</td>
<td>1.27</td>
</tr>
<tr>
<td>Joseph</td>
<td>8800</td>
<td>114.7</td>
<td>2947.1</td>
<td>326</td>
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<td>1.99</td>
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<tr>
<td>Joseph</td>
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<td>3247.1</td>
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<td>2699.5</td>
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<td>1.05</td>
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<td>7720</td>
<td>85.8</td>
<td>2204.9</td>
<td>1011</td>
<td>0.0</td>
<td>3.99</td>
</tr>
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<td>7720</td>
<td>83.3</td>
<td>4711.2</td>
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<td>Sancho</td>
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<td>113.7</td>
<td>2921.2</td>
<td>83</td>
<td>-4.5</td>
<td>3.78</td>
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<tr>
<td><strong>Mean‖</strong></td>
<td>7768</td>
<td>112.5</td>
<td>2891.2</td>
<td>615</td>
<td>-1.3</td>
<td>1.89</td>
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<td><strong>SD</strong></td>
<td>638</td>
<td>35.0</td>
<td>898.9</td>
<td>375</td>
<td>2.9</td>
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<td><strong>Winter§</strong></td>
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<td>Electra</td>
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<td>111.9</td>
<td>2876.5</td>
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<td>73.0</td>
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<td>1548.9</td>
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<td>8359</td>
<td>86.4</td>
<td>2220.0</td>
<td>551</td>
<td>-1.0</td>
<td>3.07</td>
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<td>2502.7</td>
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<td>-1.2</td>
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<td>Rapunzel</td>
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<td>39.7</td>
<td>1020.5</td>
<td>193</td>
<td>-0.8</td>
<td>1.99</td>
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<td>Rapunzel</td>
<td>8055</td>
<td>71.8</td>
<td>1845.3</td>
<td>711</td>
<td>-0.7</td>
<td>1.10</td>
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<td>Rapunzel</td>
<td>7938</td>
<td>69.5</td>
<td>1786.4</td>
<td>53</td>
<td>-0.7</td>
<td>3.00</td>
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<td>Calypso</td>
<td>7595</td>
<td>89.1</td>
<td>2290.3</td>
<td>453</td>
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<td>Sancho</td>
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<td>867.5</td>
<td>211</td>
<td>3.2</td>
<td>3.50</td>
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<tr>
<td><strong>Mean‖</strong></td>
<td>8543</td>
<td>71.8</td>
<td>1844.8</td>
<td>292</td>
<td>-0.3</td>
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<tr>
<td><strong>SD</strong></td>
<td>1215</td>
<td>23.2</td>
<td>595.2</td>
<td>211</td>
<td>1.20</td>
<td>2.7</td>
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</tbody>
</table>

† CO₂ production was converted to energy use by the relationship 25.7 J/mL CO₂ (Nagy 1983).
‡ For Electra, measurements were made 15–20 June 1990; data for other animals were collected during July 1990.
§ For Calypso, measurements were made 24–29 January 1991; data for other animals were collected during November 1990.
‖ Mean is based on initial and final body masses only.

by DLW provide a useful tool for dissecting total daily energy expenditure into components (McNab 1989). Using this approach, insights can be gained concerning patterns of energy allocation and how these patterns vary with different life histories. Compartmentalization of the energy budget of aardwolves emphasizes major shifts in patterns of their energy allocation between seasons. In summer, transport, primarily walking for termites, and to a lesser extent while patrolling the boundaries of their territory, used the largest amount of energy, 36.3% of DEE. While in their den, presumably sleeping, aardwolves expended an estimated 780.7 kJ, or 32.9% of the total DEE. Because nighttime ambient temperatures can fall below their lower critical temperature (23.2°C; Anderson et al. 1997), thermoregulatory costs were higher than one might expect in the summer, 9.5% of their total. Thermoregulatory costs while in the den were zero during the summer because ambient temperatures consistently remained within their thermal neutral zone. The wintertime pattern of energy expenditure differs markedly from that of summer, with the largest expenditure (57.3%) being energy cost while in their den (which includes energy expenditure for BMR, HIF [heat increment of feeding], and thermoregulation). Thermoregulatory costs while active in winter equaled 9.2% of the total, but this value is probably an overestimate because aardwolves frequently begin foraging in the afternoon during this season, when ambient temperatures are more favorable than the average minimum value that we have used in our calculation.

The cost of transport in free-living animals has ecological significance, especially for carnivores that travel large distances each day in search of food (Garland 1983). Unfortunately, few studies have quantified patterns of energy allocation directly for mammals. From indirect estimates of movement distances, Covell et al. (1996) calculated that locomotion accounted for 21% of total daily energy expenditure for the swift fox (Vulpes velox), the highest proportion so far reported for a mammal. We have found that aardwolves expend...
36.3% of their FMR on locomotion during summer, a much higher proportion than reported for the fox.

**Gross energy consumption**

By counting the heads of soldiers in fecal droppings, and assuming a soldier/worker ratio of 0.32 in the diet, Richardson (1987a) estimated that an aardwolf consumed a total of 309,600 *Trinervitermes* each night during the summer months. An independent assessment of termite consumption, for the summer months when aardwolves typically feed almost exclusively on *Trinervitermes*, can be made with the following equation:

\[ T = (W - m)(aX_1 + bX_2) \]

where \( T \) = the total number of *Trinervitermes* consumed, \( W \) = water influx (milliliters per day), \( m \) is metabolic water production calculated as 0.66 mL, \( \text{H}_2\text{O}/L \), \( \text{CO}_2 \) (Nagy 1983), and \( X_1 \) and \( X_2 \) are the average quantities of water (in grams) in workers and soldiers, respectively. The factors \( a \) (0.758) and \( b \) (0.242) adjust for the proportions of workers and soldiers in the diet (Richardson 1987a). Assuming that each worker weighs 3.63 \( \times \) 10\(^{-3}\) g (wet mass), 76.3% of which is water, whereas each soldier weighs 1.93 \( \times \) 10\(^{-3}\) g, 70.9% of which is water (Anderson 1994), then to obtain 540.7 mL \( \text{H}_2\text{O} \)/d (615 mL \( \text{H}_2\text{O} \) – 74.3 mL metabolic water) would require eating 222,445 *Trinervitermes* in total. If 75.8% of this intake were workers, or 168,613 individuals, then from workers aardwolves would obtain 467.1 mL \( \text{H}_2\text{O} \)/night, whereas from soldiers they would obtain 73.6 mL \( \text{H}_2\text{O} \)/night (53,832 individuals). Our estimate of termite consumption during the summer is 28.2% lower than that of Richardson (1987a). If aardwolves feed on an average of 267 patches of *Trinervitermes* each night (Richardson 1987a), then they consume \(~833\) termites per patch (222,445/267). Assuming they spend \(~25\) s foraging at each patch (Kruuk and Sands 1972, Richardson 1985), then they have an intake rate of 33.3 termites/s while feeding.

Evaluation of termite consumption during the winter is more complicated because the proportions of *Trinervitermes* and of *Hodotermes* in the diet are highly variable depending at least in part on the ambient temperature. Assuming that 70% of their diet is *Hodotermes* (Richardson 1987a, this study), and that the water content of *Hodotermes* is 40.7 \( \times \) 10\(^{-3}\) g/individual (M. C. van der Westhuizen, personal communication), then termite ingestion can be calculated by

\[ T = (W - m)(aX_1 + bX_2 + cY) \]

where \( T \), \( W \), \( m \), \( X_1 \), \( X_2 \), \( a \), and \( b \) are as before, \( c \) is the water content per individual *Hodotermes*, and \( c \) is the proportion of *Hodotermes* workers in the diet. Thus, from this equation, aardwolves consume an average of 8381 termites per winter night, or 5867 \(~:\) *Hodotermes* and 2515 *Trinervitermes*, which provide 239 mL and 6.1 mL \( \text{H}_2\text{O} \), respectively.

Armed with the knowledge of the number of termites consumed and of their energy density, we can estimate gross energy consumption. In summer, 168,613 *Trinervitermes* workers would yield 278.2 g dry matter (168,613 \( \times \) 1.65 \( \times \) 10\(^{-3}\) g dry mass/individual), and soldiers would yield 50.1 g dry matter (53,832 \( \times \) 0.93 \( \times \) 10\(^{-3}\) g dry mass/individual), for a total of 328.3 g dry matter. If the energy density of workers is 17.0 J/mg dry mass and for soldiers is 17.7 J/mg dry mass, then aardwolves have a gross energy intake of 5616 kJ/d in summer. Similar suggest a consumption of 3022 kJ/d in winter, assuming that the energy density of worker *Hodotermes* can be approximated by that of worker *Trinervitermes*. We do not know the assimilation efficiency of aardwolves feeding on termites; we approximate it as 0.66, a value for birds eating insects (Ricklefs 1974). In summer metabolizable energy intake would be 3707 kJ/d, a value 22% higher than our DLW estimate for energy expenditure. In winter, metabolizable energy intake would be 1995 kJ/d, or \(~8.1\) % more than expenditure. During our measurements, aardwolves were apparently in positive energy balance for both seasons.

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