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Body Temperatures and Activity Patterns of Tasmanian Devils (*Sarcophilus harrisi*) and Eastern Quolls (*Dasyurus viverrinus*) through a Subalpine Winter

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ABSTRACT

During a field study of carnivorous dasyurid marsupials in subalpine Tasmania, the trapping success for Tasmanian devils (*Sarcophilus harrisi*), but not for spotted-tailed quolls (*Dasyurus maculatus*) or eastern quolls (*Dasyurus viverrinus*), was significantly lower when winter weather conditions turned to sleet or snow or when deep snow lay on the ground. This field study was instigated to determine if devils and eastern quolls spend more time in burrows in severe weather conditions and if they enter torpor. Torpor is known to occur in eutherian mammals as large as devils and in a similar-sized congeneric marsupial, the western quoll (*Dasyurus geoffroyi*). Using radiotelemetry, body temperatures of Tasmanian devils and eastern quolls ranging freely in their natural habitat were monitored throughout winter. Neither species was observed in torpor, even under prolonged severe weather conditions, and the number of hours spent active did not differ between summer and winter or between moderate and severe winter weather conditions. Body temperatures averaged 36.5°C (SD = 0.079, range of 33.5–38.6°C) for the three male eastern quolls and 35.7°C (SD = 0.575, range of 31.3–37.5°C) for the four (male and female) devils. A diel cycle in body temperature occurred in both species; temperatures rose each evening when animals became active, remained high throughout the night despite ambient temperatures falling to the diel minima, and were lower during the day when the individuals were inactive in dens. The amplitude of this

cycle was greater in eastern quolls (1.1°C, SD = 0.142) than in devils (0.6°C, SD = 0.252).

Introduction

Three species of medium-sized dasyurid marsupials occur sympatrically in Tasmania: the Tasmanian devil (*Sarcophilus harrisi*), the eastern quoll (*Dasyurus viverrinus*), and the spotted-tailed quoll (*Dasyurus maculatus*). All have populations in subalpine habitat, and all are solitary, nocturnal carnivores that rest during the day in underground burrows. In an ecological study in a subalpine area, one of us (Jones 1995) noted that, whereas trapping success of both quoll species was not reduced in adverse weather, devils were trapped less frequently when winter weather conditions turned to sleet or snow or when deep snow covered the ground. Lack of devil tracks in the snow around traps in winter, when quoll tracks were common, confirmed the perception that devils may be less active in winter.

These observations raised questions about whether Tasmanian devils may enter short- or long-term torpor in winter. The possibility that torpor also occurs in eastern and spotted-tailed quolls could not be discounted, because Arnold and Shield (1970) and Arnold (1976) reported torpor in the western quoll (*Dasyurus geoffroyi*) under laboratory conditions.

The possibility of torpor and/or hibernation in the Tasmanian devil or the quolls is not unlikely on taxonomic grounds. Periods of daily or longer torpor are known to occur in all three groups of mammals, and at least three distinct patterns have been identified (Hudson 1978; Wang 1989; Geiser 1994). Shallow daily torpor, in which body temperature drops to values between 11° and 28°C for several hours, is well documented in eutherians and is known to occur in four families of marsupials, including the Dasyuridae, and in the short-beaked echidna (*Tachyglossus aculeatus*), but not in the platypus (*Ornithorhynchus anatinus*), among the monotremes (Lyman 1982*b*; Grigg et al. 1992*a*, 1992*b*; Geiser 1994). Shallow torpor may also last for longer periods (Harlow 1981). Deep, prolonged torpor or hibernation, involving a drop in body temperature to 1°–5°C for many days, is known from three families of eutherians and marsupials, not including the dasyurids, and in echidnas (Lyman 1982*b*; Grigg et al. 1989, 1992*a*; Geiser 1994).

Another possible constraint on the ability of devils to enter torpor may be body size, for most hibernators and torpidators are small. However, devils (to 11 kg) are not very different in body size from marmots (*Marmota* spp., the largest eutherian hibernators; to 8 kg), the echidna (a hibernating monotreme; to 7 kg), or New World badgers (*Taxidea taxus*; 10 kg), which exhibit shallow daily torpor (Harlow 1981; MacDonald 1984; Grigg et al. 1989, 1992a; Jones 1995). Although the largest marsupial in which torpor has been reported so far is the western quoll (0.9–1.5 kg; Arnold and Shield 1970; Arnold 1976), there seems to be no reason why body size per se would prohibit the occurrence of torpor in any of these three species of Tasmanian dasyurids.

Accordingly, we decided to monitor body temperatures of Tasmanian devils and eastern quolls throughout a complete seasonal cycle to determine whether periods of torpor or hibernation were a feature of the ecology of either species and, perhaps, might account for the observed lower winter trapping success in devils. Spotted-tailed quolls occur only in low numbers and were not included in the study. All previous studies of the thermal relations of devils and eastern quolls have been on animals in captivity and have focussed on single measurements made at random or on description of daily patterns of temperature change (Martin 1903; Brown 1909; Morrison 1965; MacMillen and Nelson 1969; Guiler and Hedde 1974; Nicol and Maskrey 1980; Nicol 1982). None of these studies reported the occurrence of torpor. However, captivity significantly affects normal behaviour patterns and, in the echidna at least, is known to obscure patterns of torpor and hibernation (Grigg et al. 1989). We chose, therefore, to use radiotelemetry so that we could monitor the body temperatures of individual animals ranging free in their familiar surroundings.

Material and Methods

The study was conducted in a 20-km² area at the northern end of the Cradle Mountain/Lake St. Clair National Park in Tasmania (145°56' E, 41°36' S, elevation 760–1,080 m) between February 1992 and February 1993. This area experiences cool summers (mean summer maximum, 16.0°C) and cold, wet winters (mean winter minimum, 0.7°C) with frosts and frequent snow between June and November. Deep snowfalls (> 30 cm) occur several times during most winters, and snow may lie on the ground for 3–4 wk. Weather records were available from the Cradle Mountain Visitor Centre (Department of Parks, Wildlife, and Heritage).

Animals were captured at night in specially designed large wire cage traps (Jones 1995) baited with beef liver. Only frequently caught individuals from the study population were chosen for telemetry. Calibrated temperature-sensitive radio-transmitters (Sirtrack Electronics) were implanted in the peritoneal cavity under sterile conditions at the field hut, under halothane anaesthesia, following guidelines approved by the

University of Queensland Animal Ethics Committee. Animals were retained in traps in the dark until fully recovered from the anaesthetic and were released at their point of capture after nightfall. Three male and three female devils and three male eastern quolls, all adults, had transmitters implanted in February 1992. No animals showed any postoperative complications on frequent retrapping during the ensuing months.

Radio signals were monitored with a Telonics TR-2 very high frequency receiver. A handheld receiver and directional antenna were used to locate animals in dens and out of range of their dens at night. Most of the data were collected with an omnidirectional whip antenna strung high in a tree within receiver range of the animal's den (or several dens, when possible) and connected to a weatherproof box containing a battery-operated receiver-scanner system and tape recorder switched on and off at predetermined intervals by a specially designed electronic timer (Grigg et al. 1990). Receiver range varied from 50 m to 1 km depending on the topography. Ambient temperatures at the recording site were also collected automatically with additional transmitters placed in a sheltered and shaded spot in the vicinity of the den. Data were transcribed from tapes by replaying them on the same tape recorder used to make the recordings to eliminate the possibility of idiosyncratic tape transport speeds. The pulse interval of the signal was measured with a stopwatch or, when the signal-to-noise ratio allowed, with a digital processor (Telonics TDP-2). The pulse interval was converted to body temperature with calibration curves developed for each transmitter. Calibration involved recording pulse intervals from transmitters submerged in a water bath at temperatures ranging from –3.3° to 37.8°C. The system is accurate to within 0.2°C, with a precision of ±0.1°C. Variable signal strengths, resulting from changes in the orientation of the transmitter's loop antenna, are known to be indicative of movement (Grigg et al. 1992b). The signal strength was recorded as stable or variable for each body temperature record, which suggested that the animal was stationary or moving (active).

Monthly field trips of alternately 12 d and 5 d were conducted. Readings were taken hourly or half-hourly during field trips, intervals frequent enough to detect shallow, daily torpor. The two sets of automatic receiving equipment were set up early in the morning near occupied dens and left for up to 76 h. They were checked early each morning, and if the individual being monitored was not in the den that day, the equipment was moved. An attempt was made to maximize the number of individuals that were monitored for at least 24 h on each field trip. Three nights per trip were dedicated to collecting body temperature data from active animals ranging away from their dens. The automatic timer was set to take readings at 4- or 6-h intervals in the weeks between field trips. At this frequency of readings, the batteries lasted the 2–3 wk between field trips, maximizing the chance of detecting a major period of torpor.

Results

All three female devils bred in March–April, 1 mo after the telemeters were implanted, and two of them raised young successfully during the year (the third was killed by a car). We take this to mean that the data recorded are representative of healthy, normal animals, unaffected by the implanted radio transmitters. Three devils, two females (nos. 29, 79) and one male (no. 4), and two eastern quolls (nos. 18, 27) provided enough data for statistical comparisons of summer and winter. Data from these individuals plus one male eastern quoll (no. 48) and one male devil (no. 59) were analysed for comparison of species differences in body temperature (Table 1).

Body Temperature

No devils or eastern quolls were recorded in torpor, that is, with a body temperature less than 28°C. Repeated-measures ANOVA on 24-h profiles of consecutive data (hourly readings) for summer and winter indicated no differences in the mean ($F_{1,3} = 6.1, P > 0.05$) or amplitude ($F_{1,3} = 6.0, P > 0.05$) body temperature of species or individuals between seasons. Accordingly, all the data from each season were pooled for each animal (Figs. 1, 2). Examination of plots of all the data combined (hourly, every 6 h, and spot temperatures) indicated an uneven representation of data points at different times of day, with fewer data points between 2100 and 0400 hours for some individuals. During this time when they were actively roaming out of range of automatic receiving stations, some body temperature records were collected with handheld receivers, but not as many as were collected automatically at other times of day. This uneven representation would bias estimates of the mean. As all individuals demonstrated a daily cyclical pattern in body temperature as expected (Figs. 1–3), the most appropriate model, sine curves of the form $y = a + b \cos(cx)$, was fitted to the pooled data for each individual. These values

are presented in Table 2. Estimates of the mean and daily amplitude in body temperature and comparison of means and amplitudes between species are based on these parameter estimates from the sine curve.

Body temperatures averaged 36.5°C (SD = 0.079) for the three male eastern quolls and 35.7°C (SD = 0.575) for the four (male and female) devils, not quite significantly different (separate variances, $t = 2.771, df = 3.1, P = 0.06$). The overall minimum and maximum temperatures were 33.5° and 38.6°C for eastern quolls and 31.3° and 37.5°C for devils, respectively (Table 2).

Body temperatures of both species rose each evening when the animals commenced activity, remained high throughout the night despite ambient temperatures falling to the diel minima, and declined during the day when the individuals were inactive in dens (Figs. 1–3). The amplitude of diel cycles in body temperature was greater in eastern quolls, with a daily cycle of 1.1°C (SD = 0.142), than in devils, whose daily cycle was only 0.6°C (SD = 0.252; separate variances, $t = 3.317, df = 4.8, P = 0.022$). Plots of body temperature for female devil 29 and male devil 4 do not show as strong a diel cycle as other individuals and show more variation (Table 2), but the minimum nocturnal values are always higher than the minimum diurnal values (Fig. 2). The small amounts of data obtained from eastern quoll 48 and devil 59 are in agreement with these patterns. The data for the three individual devils for which large amounts of data were obtained suggest that the larger male may have had a lower body temperature with a smaller diel amplitude than the females (Table 2).

Activity and Burrow Use

Diel patterns of activity were surprisingly stable throughout the year in both species. Consequences of automatic data collection were that individuals moved out of range of the receiver near the den for hours during the night, and it could not be distin-

Table 1: Weight, sex, period of observation, and number of records of body temperature for each individual

Species and Identification Number	Sex	Weight (kg)	Period of Observation	N
Eastern quoll 18	Male	1.0	2/7–7/25/92 (167 d)	214
Eastern quoll 27	Male	1.2	2/7–6/6/92 (120 d)	194
Eastern quoll 48	Male	1.1	2/7–3/13/92 (35 d)	45
Devil 2	Female	7.5	2/5–5/10/92 (95 d)	6
Devil 4	Male	7.6	2/5–8/12/92 (189 d)	511
Devil 29	Female	5.2	2/7/92–1/14/93 (342 d)	342
Devil 59	Male	8.7	2/6–6/18/92 (133 d)	15
Devil 75	Male	6.9	2/7/92	0
Devil 79	Female	5.4	2/6/92–2/24/93 (384 d)	237

Note. Devil no. 2 was killed by a car. No records of body temperature were made for devil no. 75. N, number of records.

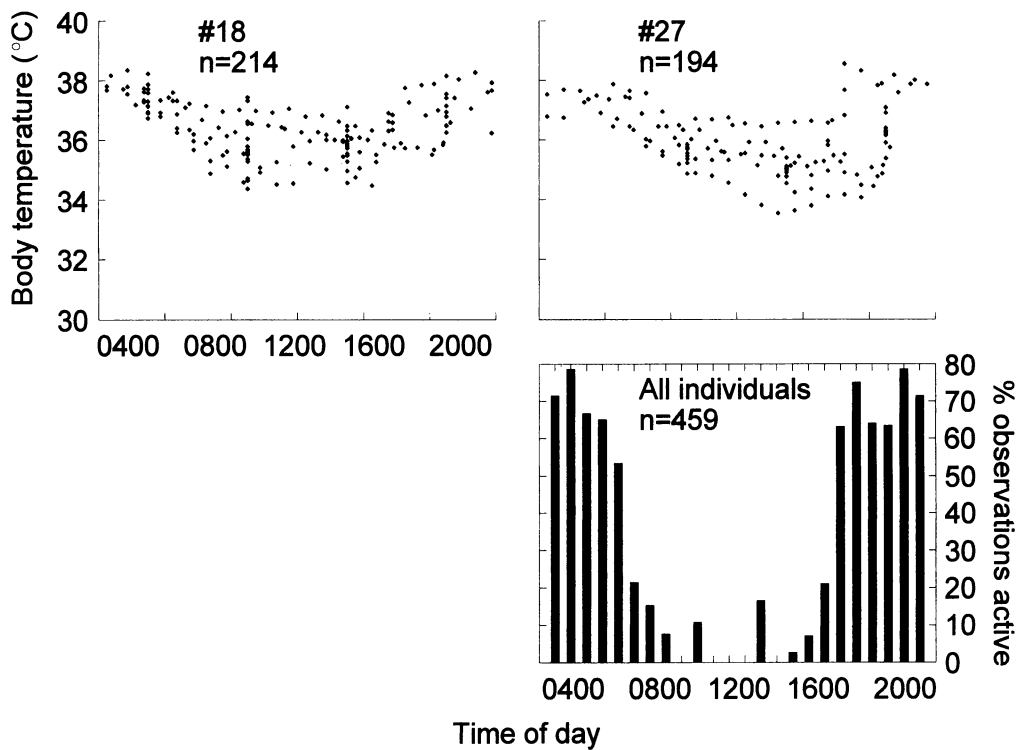


Figure 1. Body temperature of eastern quolls for which enough data for statistical analysis was obtained and activity of all eastern quolls plotted against time of day; n , number of records.

guished whether active individuals within range of the receiver were in the den or outside it but nearby. Therefore, devils and quolls were deemed to be active if they were within range of the receiver and the signal was variable or if they had moved out of range of the receiver (i.e., no signal) but returned to the same den later that night to rest the following day. Activity data were analysed as the number of hourly records in a consecutive 24-h period in which the individual was within range of the automatic receiving system near the den and signal strength was variable or was outside receiving range (total activity period) and as the number of hours in a 24-h period in which the individual was outside the receiving range.

By ANOVA and Student's t -test, no differences (P values always greater than 0.05, mostly greater than 0.2) emerge in total activity period or time spent away from the den between species (devils and eastern quolls), between summer and winter (despite the difference in night length, 8 h in midsummer and 15 h in midwinter) or between severe (sleet, snow, or subzero temperatures with snow on the ground) and moderate weather in winter (only devils analysed; Figs. 1 [lower panel], 2 [lower right panel]). The number of active hours for the one full 24-h profile for an eastern quoll in severe weather lie within the range of active hours for moderate winter weather. Backing up these interpretations of recorded data, both eastern quolls and devils were commonly located out of their dens and were

active at night during snowstorms and on clear nights with 50 cm of snow on the ground and air temperatures of -8°C (eastern quoll) and -5°C (devils). When all data for both seasons and all weather conditions are pooled, devils spent a mean total of 7.92 h (SEM = 0.87, $n = 13$) active at night and eastern quolls a mean total of 8.00 h (SEM = 0.83, $n = 9$) active. The number of hours spent active away from the den (out of receiver range) were less, 5.23 h (SEM = 0.62, $n = 13$) for devils and 6.11 h (SEM = 0.89, $n = 9$) for eastern quolls (Figs. 1 [lower panel], 2 [lower right panel]).

The number of hours of activity at night and the number of hours away from the den did not differ for female devil 29 when she had large (7-mo-old) cubs in a den compared with all other records, made when she was not responsible for denned cubs.

As with the total number of hours spent active, the timing of the onset and cessation of the active period did not vary between species, between summer and winter, or between severe and moderate winter weather. On the average, eastern quolls became active at 2055 hours (SEM = 0.81, $n = 10$) and settled in their dens for the day at 0243 hours (SEM = 0.43, $n = 11$). In a remarkably similar pattern, devils became active at 2105 hours (SEM = 0.96, $n = 11$) and settled for the day at 0205 hours (SEM = 0.76, $n = 11$; Figs. 1 [lower panel], 2 [lower right panel]).

Discussion

Both devils and eastern quolls remained homeothermic and maintained the same activity patterns year-round, including

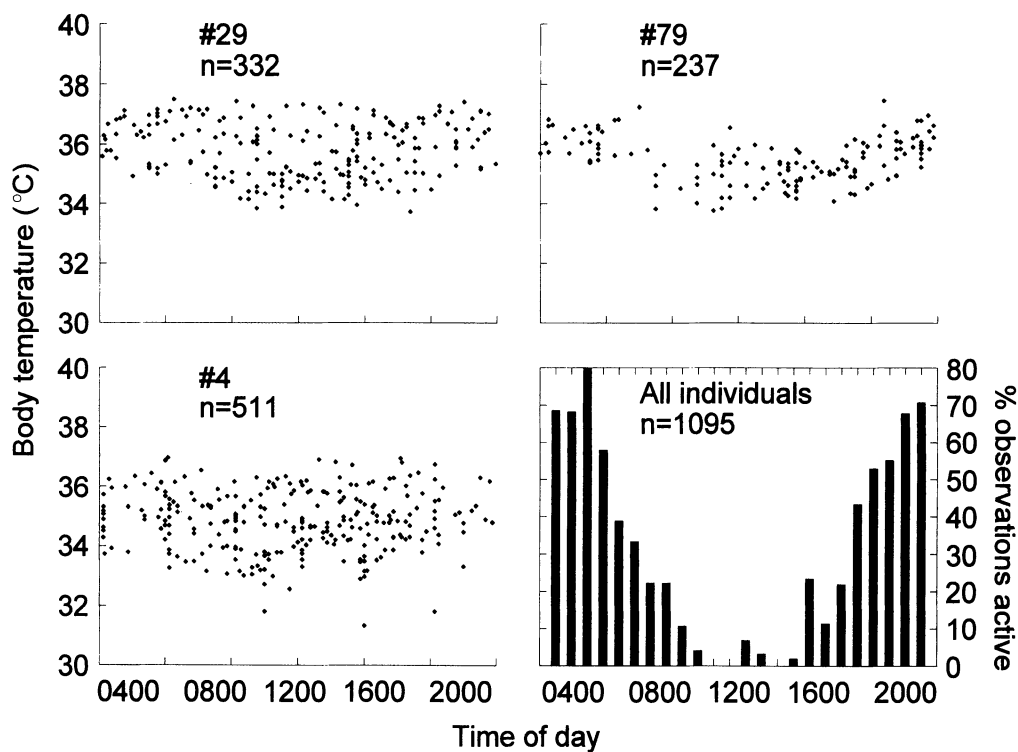


Figure 2. Body temperature of Tasmanian devils for which enough data for statistical analysis was obtained and activity of all Tasmanian devils plotted against time of day; n , number of records.

during the most severe winter weather conditions that they would encounter in their distributional range. There was no tendency shown by either species to enter even shallow torpor at any stage. They are shown to be effective thermoregulators at low temperatures (-8°C at night is the lowest ambient temperature recorded during the study) and in cold, wet conditions of sleet and snow. The similar patterns of activity in both species in all weather conditions are somewhat surprising, as neither has special adaptations for the cold. The foot pads are naked of fur, and the pelage is not very thick (M. E. Jones, personal observation). Indeed, many older devils have sarcoptic mange and go through the winter with naked rumps. However, the conditions in subalpine Tasmania are not as cold as those experienced by arctic animals, such as wolverines, which have special adaptations. So why are trapping success and activity around traps (as assessed by tracks in the snow) reduced on nights of severe weather in winter? Perhaps individuals reduce the scope of their ranging on these nights and restrict their activity to known good foraging areas. This would mean that animals may not range widely enough to find traps or carcasses put out for experimental purposes. Incidental support is provided for this hypothesis by the observation that just as many devils turn up to scavenge at the Cradle Mountain Lodge feeding platform, which is a predictable food supply, in adverse weather as at other times (M. E. Jones, personal observation).

Reduction in trapping success in severe winter weather conditions was recorded in devils but not in spotted-tailed or eastern quolls. This may relate to the body mass, anatomy, and behaviour of the three species. Devils are heavy, with a robust build; short, straight legs; and small, round feet. They fall into deep snow (M. E. Jones, personal observation). Spotted-tailed quolls and eastern quolls both have angled limbs with widely splayed front feet. Eastern quolls are light and move easily across snow. Spotted-tailed quolls have been observed to have difficulty moving in deep snow (M. E. Jones, personal observation); however, this species moves extensively above the ground along logs (Jones 1995) and could avoid some of the deep snow.

The data suggest that the amplitude of the diel cycle is longer in quolls than in devils, which is perhaps related to body size, as devils are substantially larger than eastern quolls. MacMillen and Nelson (1969), however, found no clear trends in a plot of body temperature against body mass for the family Dasyuridae, ranging from 7-g animals to 5.5-kg animals, although there was a clear relationship between body mass and basal metabolic rate, which decreased with increasing body mass.

Relatively few studies of body temperatures or thermal relations of devils (four studies) or eastern quolls (one study) have been published, and all have been on captive, though wild-caught, animals. Sample sizes are small in all cases: only one devil (Morrison 1965; MacMillen and Nelson 1969), three devils (Guiler and Heddle 1974; Nicol and Maskrey 1980; Nicol 1982), and two female eastern quolls (MacMillen and Nelson 1969). Our study represents not only the first field research but also the first study to examine body temperature over the

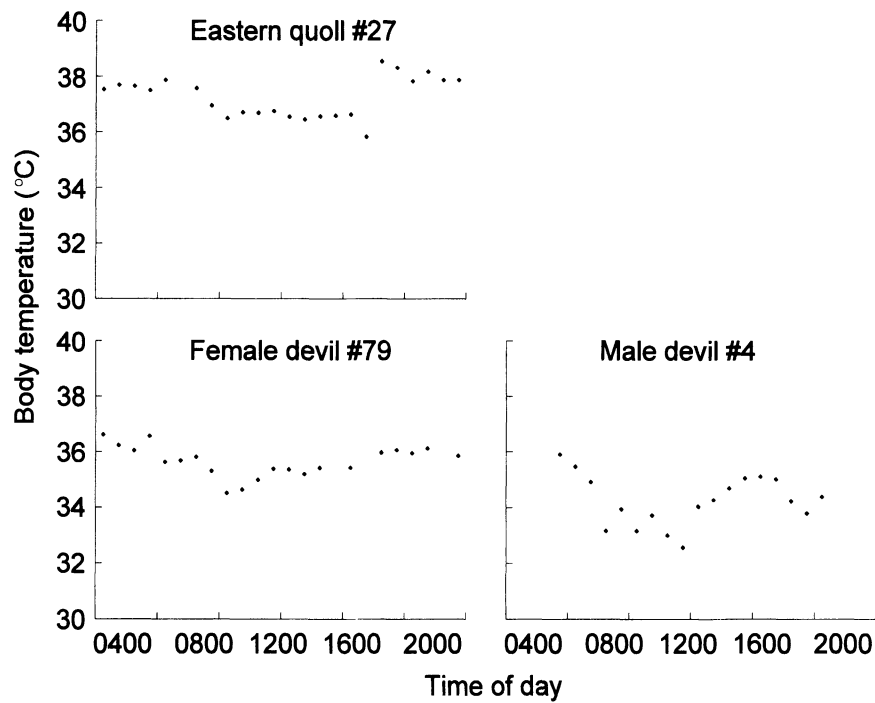


Figure 3. The 24-h profiles of consecutive hourly readings of body temperature from one male eastern quoll, one female devil, and one male devil from a representative day.

whole diel cycle and through seasons and to link this with the activity state of the individual. Our sample sizes are comparable to those in published reports. Body temperatures reported in this study (devils: mean of 35.7°C and range of 31.3–37.5°C; eastern quolls: mean of 36.5°C and range of 33.5–38.6°C) are within the range of those reported in the literature (devils: 31.0–37.9°C; eastern quolls: mean of 36.7°C). Overall ranges for each individual are also comparable (published information is available only for devils). Spotted-tailed quolls, the third dasyurid carnivore at Cradle Mountain and the species inter-

mediate in size between eastern quolls and devils, were not examined in this study because this species is rare. Values in the literature, based on small sample sizes from captive individuals (means of 36.9° and 35.1°C and ranges of 32.1–34.2°C and 36.5–39.9°C; Martin 1903; Brown 1909; MacMillen and Nelson 1969), with the exception of 39.9°C (Martin 1903) are within the range of those found in devils and eastern quolls.

Our study suggests that a circadian rhythm in body temperature occurs in both devils and eastern quolls and that the cycle is stronger in the quolls. No published reports have specifically examined activity in relation to diel patterns in body temperature for devils or eastern quolls. Guiler and Heddle (1974), in the only study to examine body temperature of devils through

Table 2: Estimates of mean and amplitude (with 95% confidence intervals) of diel cycle of body temperature for each individual from the parameters of fitted sine curves and absolute maximum and minimum temperatures from raw data

Species and Identification Number	Sex	Mean Body Temperature (°C)	Amplitude (°C)	Adjusted r^2	Range (°C)
Eastern quoll 18	Male	36.6 (36.43–36.67)	1.0 (.79–1.13)	.44	34.4–38.4
Eastern quoll 27	Male	36.4 (36.24–36.54)	1.2 (1.02–1.46)	.38	33.5–38.6
Eastern quoll 48	Male	36.5 (36.25–36.64)	1.1 (.81–1.42)	.71	35.2–37.3
Devil 4	Male	34.9 (34.78–34.98)	.3 (.13–.39)	.03	31.3–37.0
Devil 29	Female	35.9 (35.84–36.05)	.6 (.47–.73)	.17	33.7–38.6
Devil 59	Male	36.2 (35.63–36.78)	.8 (.20–1.45)	.54	34.7–36.9
Devil 79	Female	35.6 (35.44–35.73)	.7 (.58–.91)	.38	33.8–37.5

Note. Uneven distribution of data points precluded estimates from the raw data. Adjusted coefficients of determination are provided for each curve.

24 h of the day, noted that highest temperatures were associated with activity at night. A rise in body temperature resulting from sustained activity was also reported by Nicol and Maskrey (1980) and Nicol (1982). They also found that, albeit poorly defined, cyclic changes in body temperature accompanied variations in metabolic rate at low temperatures. Below 12°C, metabolic rate and temperature increased. Between 12° and 28°C, body temperature varied passively. These researchers were unable to find spontaneous diurnal variations in body temperature in devils maintained for 7 h at constant temperatures. Our study indicates that this was probably not long enough to detect changes. A strong daily cycle in body temperature related to diurnal inactive and nocturnal active periods, with a change in mean values at ambient temperatures of 10°, 15°, 20°, and 30°C, ranging from 2.2° to 3.8°C, has, however, been demonstrated in a congeneric quoll of body weight and morphology very similar to the eastern quoll, the chuditch (*Dasyurus goeffroyi*; Arnold and Shield 1970; Arnold 1976). Our study is the first report of diel cycles in body temperature for either devils or eastern quolls. This is not incompatible with previous reports on thermal relations of devils, nor with what might be expected for eastern quolls from comparison with similar congeners. Nicol (1982) suggested that decline in body temperature may be an energy-conserving mechanism in devils, but a daily cycle in body temperature, correlating with the activity period, is not at all uncommon among endotherms. How much the elevated body temperatures at night result from activity, as both species are nocturnally active, or from metabolic rates increased to cope with the cold temperatures at night outside burrows at subalpine Cradle Mountain is not known.

This study was inspired by a desire to find out why the trapping success of devils, but not eastern or spotted-tailed quolls, declines in severe winter weather conditions at subalpine Cradle Mountain. It was specifically designed to look for evidence of torpor. Whether either species would exhibit torpor under a different set of environmental conditions, such as food restriction at intermediate temperatures (the typical pattern for small mammals, according to Hudson [1978]), is unknown. However, we found no evidence to suggest that entry to either short- or long-term torpor is a routine event in these dasyurid marsupials.

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