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Effect of low-quality diet on torpor frequency and depth in the pichi *Zaedyus pichiy* (Xenarthra, Dasypodidae), a South American armadillo

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ABSTRACT

Daily torpor is a physiological adaptation that allows mammals to cope with energetic challenges associated with unpredictable periods of food shortage. We experimentally tested whether food quality influences torpor frequency and depth in the pichi (*Zaedyus pichiy*), a small, opportunistically omnivorous armadillo endemic to arid and semi-arid habitats of southern South America. We recorded body temperature (T_{sc}) changes in 10 semi-captive, adult female pichis using dataloggers implanted subcutaneously during periods of 21 days. All individuals entered spontaneous daily torpor, but those receiving a low-quality diet had significantly lower daily mean and minimum T_{sc} , spent more time at T_{sc} below their individual lower limit of normothermia, and had a higher Heterothermy Index than controls. Five individuals entered prolonged torpor bouts lasting more than 24 h, two of them repeatedly. Nine out of ten prolonged torpor bouts occurred in individuals feeding on a low-quality diet, suggesting that pichis are able to enter prolonged periods of torpor during severe environmental stress. In combination with their ability to hibernate and to respond to a reduced insect abundance by ingesting other food items, this physiological adaptation allows pichis to better cope with food shortages and a more extreme climate than other armadillos. It may explain why *Z. pichiy* naturally occurs farther south than any other armadillo species.

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1. Introduction

Hypometabolism is a physiological mechanism that is widely used by endotherms to temporarily reduce energy requirements in fluctuating environments (Heldmaier et al., 2004). Hibernation and/or daily torpor have been observed in all basal mammals and in almost all orders that include small mammals (Lovegrove, 2011), lending support to the hypothesis that adaptive heterothermy is a plesiomorphic trait (Grigg et al., 2004; Heldmaier et al., 2004; Lovegrove, 2011; but see Geiser, 2008).

Daily torpor, defined as an opportunistic hypometabolic state lasting less than 24 h, seems to be especially important to balance the energy of mammals inhabiting arid environments, where rainfall is unpredictable and productivity is low (Geiser, 2004).

Abbreviations: HI, Heterothermy Index; LQ, Low-quality diet; SEM, standard error of the mean; T_a , ambient temperature 1 m above ground; $T_{a\max}$, maximum ambient temperature 1 m above ground; $T_{a\text{mean}}$, mean ambient temperature 1 m above ground; $T_{a\min}$, minimum ambient temperature 1 m above ground; T_b , body (rectal) temperature; T_{sc} , subcutaneous temperature; $T_{sc\max}$, maximum subcutaneous temperature; $T_{sc\text{mean}}$, mean subcutaneous temperature; $T_{sc\min}$, minimum subcutaneous temperature; $T_{sc} < \text{norm}$, number of hours during which T_{sc} is below the individual lower limit of normothermia.

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Pichis (*Zaedyus pichiy*; Xenarthra, Dasypodidae) are diurnal armadillos of approximately 1 kg body mass (Superina, 2008; Superina et al., 2009a). These opportunistic omnivores with a preference for insects (Superina et al., 2009a) “probably eat whatever they can whenever they can” (Redford, 1985, p. 431). They are endemic to arid and semi-arid habitats of central and southern Argentina and Chile (Superina, 2008; Wetzel, 1985). Like other armadillos, pichis appear to be poorly equipped to cope with cold ambient temperatures (T_a), having low rates of heat production, a high thermal conductance resulting from a relatively thin fur limited mostly to their ventral surface, and body temperatures that are low, variable, and highly sensitive to changes in ambient temperature (McNab, 1980; Roig, 1971).

Pichis dig and inhabit burrows that can be several meters long and vary in depth between 30 cm (in summer) and up to 1.5 m (in winter); they seal the burrow as they excavate (Superina, 2008). They are capable of entering hibernation during the cold season, when T_a decreases and food availability becomes unpredictable (Superina and Boily, 2007). Prior to hibernation, they build up a subcutaneous fat layer of up to 1.5 cm thick (Superina, 2008).

It is, however, not clear how pichis cope with energetic challenges associated with unpredictable periods of food shortage, such as extended drought periods. Superina and Boily (2007) observed irregular drops in subcutaneous temperature (T_{sc}) of a few hours after the hibernation season, suggesting that pichis may also enter daily torpor. This fact, in combination with reduced field

sightings during extended drought periods (Superina, 2007), led us to hypothesize that pichis use daily torpor to reduce their energetic requirements during periods of environmental stress, and that food quality influences torpor frequency and depth.

The aim of this work was to experimentally test whether a reduction in food quality leads to deeper and/or more frequent torpor in pichis maintained in a semi-natural environment. The majority of studies on the thermoregulation of mammals and birds have been performed in controlled laboratory environments, although it has been shown that some species, such as tawny frogmouths *Podargys strigoides*, may not enter torpor in captivity (McNab and Bonaccorso, 1995) but do so in their natural habitat (Körtner et al., 2001). Körtner et al. (2001) suggested that this discrepancy occurs more frequently in birds than mammals and may be related to captivity-induced stress. Although pichis and armadillos in general are highly susceptible to stress (Superina et al., 2008), the present study was carried out with individuals kept in outdoor enclosures and with access to natural substrate where they could dig. These conditions resembled their natural environment as much as possible and were thought to reduce stress and avoid potential behavioral changes due to confinement in laboratory conditions.

Considering that *Z. pichiy* represents a phylogenetically basal group of placental mammals (i.e., Xenarthra; Delsuc et al., 2002), results presented herein may provide a better understanding of the origin of hypometabolism in endotherms.

2. Methods

2.1. Experimental design

Experiments were performed in March–April 2010 and March–April 2011. Pichis were kept in individual outdoor pens within their natural range in Luján de Cuyo, Mendoza Province, Argentina (33.0 °S, 68.9 °W), where they were exposed to natural light cycles varying between 12 h 34 min and 10 h 59 min over the course of the study period. The pens were made of wire mesh and sheet metal, of 2 m × 1.5 m × 2.5 m each; soil to a depth of 2 m provided a natural substrate for digging burrows. For the duration of the experimental period, food was offered once daily around 10 AM, when most pichis had emerged from their burrows; water was provided ad libitum.

To reduce potential errors related to age or gender, only adult, captive-born female pichis (except one wild-born female that had been in captive conditions for >5 yr) were used. Different females were used in 2010 and 2011 to avoid pseudoreplication. The founders of the captive colony all originated from Malargüe department in southern Mendoza Province, Argentina (36 °S, 69 °W), and the individuals had been kept at the study site since they were born or, in the case of the wild-born female, since its capture.

The individuals were weighed with a spring scale (Pesola AG, Baar, Switzerland) at the beginning and the end of each experimental period.

The subcutaneous temperature (T_{sc}) of the individuals was registered using temperature data loggers (Thermochron iButton DS1921L-F52, resolution 0.5 °C, accuracy 1 °C; Maxim Integrated Products Inc., Sunnyvale, CA) implanted into subcutaneous tissue under the carapace border posterior to the front leg. Data loggers were programmed to register temperature once per hour. Individuals were anesthetized with 15 mg/kg tiletamin/zolazepam (Zelazol, Fort Dodge Sanidad Animal S.A., La Plata, Argentina) and 1 mg/kg xylazine (Sedomin, Laboratorios König S.A., Avellaneda, Argentina) in 2010, and with 1 mg/kg xylazine, 20 mg/kg ketamin and 0.8 mg/kg midazolam (Keta-mid, Holliday–Scott S.A., Beccar, Argentina) in 2011. The implantation site was infiltrated with lidocaine (Procaina-Novo, Chinfeld S.A., Munro, Argentina) prior to incision, the sterilized data logger

introduced at least 1 cm into the subcutaneous tissue, parallel to the carapace border, and the skin sutured. Data loggers were implanted two to three weeks prior to the experiment and extracted surgically at least two weeks after conclusion of the study. In addition, a data logger was placed 1 m above ground near the enclosures to register above ground ambient temperature (T_a) once per hour for the duration of the study.

Experimental and control groups consisted of three individuals each. Group 1 was fed 80–90 g pumpkin (*Cucurbita moschata*; low-quality food, LQ) once daily during three weeks, while Group 2 received 40–50 g dry cat food (Whiskas Beef, Masterfoods Argentina Ltd., Mercedes, Argentina; Control). These food items were selected because the aim was to simulate the change in food quality occurring during a period of environmental stress, where a reduction in insect abundance (Ahearn, 1971; Ruggiero et al., 2009) forces pichis to feed on other food items having a reduced caloric as well as a lower nutrient content. A balanced formula containing animal protein, vitamins, and minerals (e.g., dry cat food; 28% crude proteins, 9% lipids, 4% crude fiber, 8.5% minerals; 360 kcal per 100 g according to the manufacturer) is expected to provide pichis with sufficient nutrients for growth and maintenance. On the other hand, a diet consisting only of pumpkin lacks, or is very poor in, animal protein and lipids, among other components (1% protein, 0.1% lipids, 2% total dietary fiber, 0.5% minerals; 45 kcal per 100 g; USDA, 2012), being therefore of lower quality for an omnivorous species.

Both groups received the same diet for one week, consisting of a varying mix of fruits, vegetables, hard-boiled eggs, and beef. The quantity, however, varied to compensate the weight loss of the experimental group and weight gain of the control group (see 3. Results). This period of seven days was sufficient for all individuals to return to their initial body mass. The groups were then inverted to increase sample size: Group 1 received 40–50 g cat food, while Group 2 now ate 80–90 g pumpkin per day during three weeks.

We are aware that a higher number of individuals per study group would have provided more solid results. However, this was not possible because *Z. pichiy* is a threatened species that is only rarely kept and bred in captive conditions.

2.2. Data analysis

It was difficult to define the limit between normothermia and hypothermia due to the significant daily fluctuations in the T_{sc} of pichis and their use of spontaneous torpor (see 3. Results). Many studies determine torpor entrance as a reduction in body temperature (T_b) during resting below a specific threshold temperature, which is often arbitrarily set at 30 °C (Barclay et al., 2001). Alternatively, the lowest limit of daily normothermic minimum T_b (Lovegrove et al., 2001) or lowest T_b recorded from active individuals (Barclay et al., 2001) is used as a threshold. Rectal temperatures measured in 58 wild, non-torpid individuals varied between 32.2 and 38.3 °C (Superina, 2008), and even in the week prior to the experiment, when all individuals received a food mixture consisting of animal protein, fruit, vegetables, and vitamin-mineral supplements, daily minimum T_{sc} was as low as 26.5 °C (data not shown), making it difficult to determine the minimum T_{sc} during normothermia. We therefore followed the method described by McKechnie et al. (2007) to determine the lower limit of normothermic T_{sc} . We identified the daily modal value for each individual during the period in which it received the control diet and calculated the mean and standard deviation. We excluded daily modal values ≤ 27 °C from this calculation because they indicated the individuals did not reach normothermia on that day. We set the lower limit for the normothermic T_{sc} for each individual as its mean modal value minus two standard deviations.

Boyles et al. (2011) proposed the Heterothermy Index (HI) as a metric to describe the magnitude of a heterothermic response of

an animal and avoid the use of arbitrary threshold temperatures. It was calculated here by using the modal T_{sc} as a proxy for the optimal body temperature for performance, as the latter is not known for *pichis*. As for the lower limit of normothermia, the modal T_{sc} and the corresponding HI values were calculated individually for the experimental periods of March and April.

Thus, the formula used was $HI = \sqrt{\sum(T_{scmod} - T_{sc-i})^2 / (n-1)}$, where T_{scmod} is the modal T_{sc} , T_{sc-i} is the T_{sc} measurement at time i , and n is the number of times T_{sc} is sampled.

As the same individuals were fed both types of diet, repeated measures two-way ANOVA with Bonferroni post-hoc tests were performed to compare daily maximum, minimum, and mean T_{sc} (T_{scmax} , T_{scmin} , T_{scmean}), as well as the number of hours the armadillos spent below their individual lower limit of normothermia ($T_{sc} < \text{norm}$) and the HI of individuals in the experimental and control groups.

Prolonged torpor bouts were defined as periods during which T_{sc} departed from T_{scmax} , steadily declined to a T_{scmin} , and gradually returned to T_{scmax} in an interval of more than 24 h. They were quantified for each experimental period and per animal by manually screening the temperature data.

Linear regression models were used to test whether maximum or minimum T_a (T_{amax} , T_{amin}) may influence T_{scmax} or T_{scmin} , respectively.

Statistical analyses were performed using GraphPad Prism (Version 3.0a for Macintosh and Version 4.0 for Windows, GraphPad Software Inc., San Diego, CA, USA). Unless otherwise stated, values are presented as mean $\pm$ SEM. p -Values below 0.05 were considered statistically significant.

3. Results

A total of 12 individuals were implanted with iButtons. One of the dataloggers implanted in 2010 into an animal of Group 1 failed

due to unknown reasons and did not contain any data. In 2011, one of the individuals of Group 2 acquired a severe skin infection unrelated to datalogger implantation that required prolonged treatment and its exclusion from the experiment. Hence, data were obtained from a total of 10 animals (5 in 2010 and 5 in 2011), each one having received the control and experimental diet during 21 days.

Although the ingested food mass was not quantified, it was notorious that armadillos receiving the control diet always ate all offered food, while individuals feeding on LQ often left behind some of the pumpkin. The latter was probably related to physical satiation.

3.1. Ambient temperature

During the study period of 2010, T_a ranged from -0.5 to 35.0 °C. Overall mean T_a ($T_{a,mean}$) was 16.8 °C, and mean daily $T_{a,min}$ and $T_{a,max}$ were 9.5 and 27.1 °C, respectively.

The range of T_a was similar in the study period of 2011, -0.5 to 33.5 °C. Overall $T_{a,mean}$ was 14.9 °C, and mean daily $T_{a,min}$ and $T_{a,max}$ were 7.4 and 27.2 °C, respectively.

3.2. Body mass

Taking both years together, mean body mass $\pm$ SD at the beginning of the experimental period was 849 ± 47 g for the control group and 865 ± 77 g for the experimental group. On average, *pichis* in the control group gained 115 ± 68 g, or about 14% of body mass, during the 3-week period, while those in the experimental group lost 86 ± 23 g (approximately 10% of body mass). This difference was expected due to the relatively high fat content (9%) of the control diet.

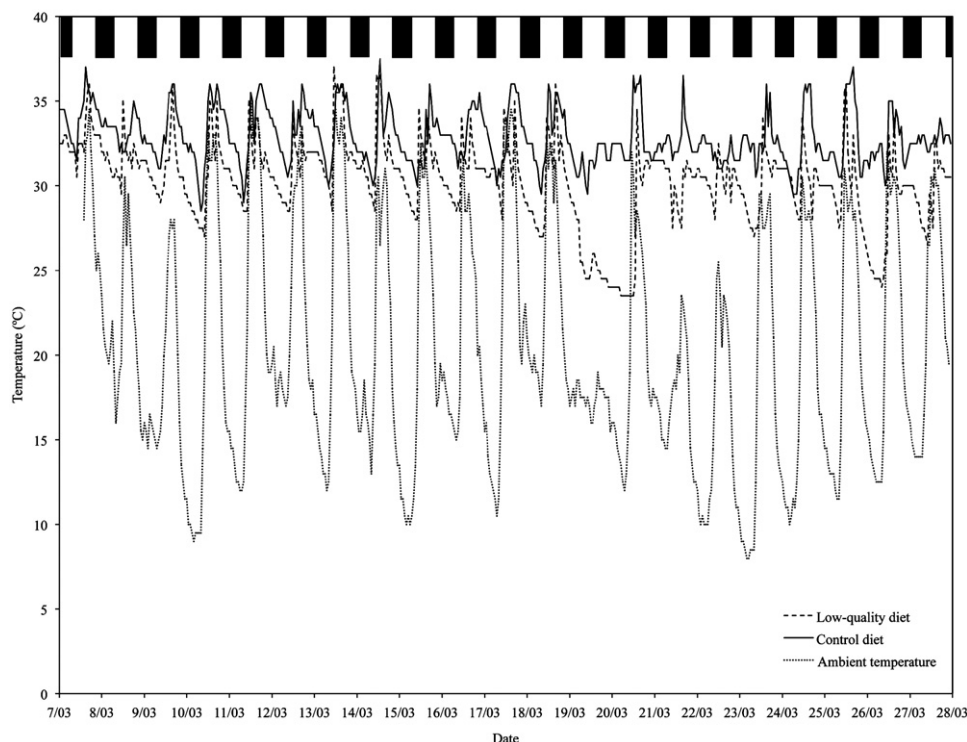


Fig. 1. Typical daily subcutaneous temperature (T_{sc}) changes of two *pichis* (*Zaedyus pichiy*) fed with a low-quality experimental diet or a high-quality control diet, respectively, in March 2010. Black bars mark the scotophase.

3.3. Body temperature

Previous studies showed that in pichis, rectal temperature measurements are approximately 1.0 °C higher than T_{sc} measured with the implants (Superina and Boily, 2007). Thus, the T_{sc} reported here is a biased estimate of T_b .

A total of 10,080 temperature measurements were recorded. In all individuals, T_{sc} showed considerable variation over the course of the day (Fig. 1). Overall mean $T_{sc,max}$ and $T_{sc,min}$ were 34.2 ± 0.1 °C and 27.7 ± 0.1 °C, respectively. The highest and lowest recorded T_{sc} were 38.0 °C and 20.5 °C, respectively, and daily amplitudes varied between 0.5 °C (in a female that was in prolonged torpor, see below) and 14.5 °C (mean 6.2 ± 0.1 °C). Daily $T_{sc,min}$ was most frequently measured between 8 AM and 11 AM (63.8% of daily $T_{sc,min}$ records), while daily $T_{sc,max}$ was usually registered between 1 PM and 4 PM (57.6% of daily $T_{sc,max}$ records; Fig. 2). Mean HI values were 1.8 ± 0.1 (range 0.5–6.7) in the control group, and 2.5 ± 0.1 (range 0.6–10.2) in the experimental group.

A total of ten prolonged torpor bouts (> 24 h) occurred during the experimental periods: one in the second half of March, two in the first half of April, and two in the second half of April of 2010; and one in the first half of April and four in the second half of April of 2011. Of the individuals feeding on LQ, one entered prolonged torpor four and one three times, while two females did so only once. One individual of the control group entered prolonged torpor once. The duration of prolonged torpor bouts varied between 25 h and 84 h (mean 36.3 ± 6.8 h). In addition, one torpor bout of 20 h was recorded at the end of March 2010 and one of 23 h at the end of March 2011.

Fig. 3 shows the fluctuations in $T_{sc,min}$, $T_{sc,mean}$, and $T_{sc,max}$ during the 21-day experimental period. Diet significantly affected $T_{sc,min}$ ($F=98.82$, $DFn=1$, $DFd=189$, $p<0.0001$) and $T_{sc,mean}$ ($F=50.45$, $DFn=1$, $DFd=189$, $p<0.0001$), much more than it influenced $T_{sc,max}$ ($F=6.326$, $DFn=1$, $DFd=189$, $p=0.0127$) (Fig. 3a, b, c). In all cases, T_{sc} was lower in individuals feeding on LQ. $T_{sc,min}$ and $T_{sc,mean}$ varied over time during the course of the experiment ($F=1.811$, $DFn=20$, $DFd=189$, $p=0.0219$ and $F=1.819$, $DFn=20$, $DFd=189$, $p=0.0211$, respectively), while time had no effect on $T_{sc,max}$ ($F=1.27$, $DFn=20$, $DFd=189$, $p=0.20$). Post-hoc Bonferroni tests revealed significant differences in $T_{sc,max}$ only on day 6 of the experiment, while differences in $T_{sc,min}$ were significant on days 2–4, 7–8, 10–16, 18, and 20–21; $T_{sc,mean}$ was significantly different on days 2–4 and 6–7.

Individuals in the experimental group spent, on average, 5.52 ± 0.42 h below their individual lower limit of normothermia ($T_{sc} < \text{norm}$) while the control group did so during 1.46 ± 0.22 h.

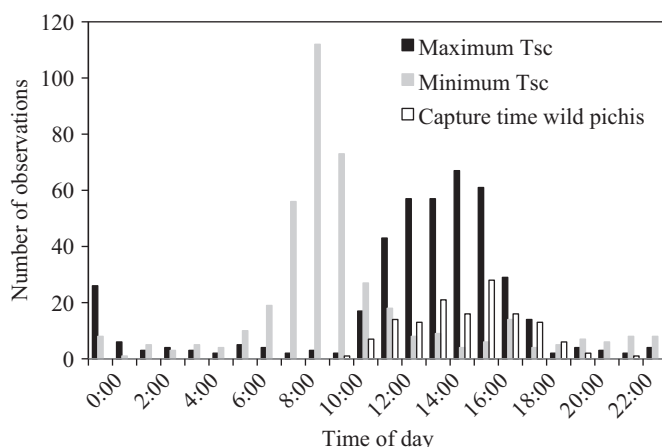


Fig. 2. Timing of maximum and minimum subcutaneous temperature (T_{sc}) of captive pichis (*Zaedyus pichiy*), and time of capture of wild pichis. Note that the shown Argentina Time (UTC/GMT–3 h) is shifted approximately +1:40 h from real solar time.

Differences between experimental and control groups were highly significant ($F=86.66$, $DFn=1$, $DFd=189$, $p<0.0001$). When analyzing the differences on a day per day basis with Bonferroni post-hoc test, we found significant differences on days 2–4, 6, 7, 10, and 13–20 (Fig. 3d). Time spent below $T_{sc} < \text{norm}$ did not significantly vary over the course of the experiment ($F=1.513$, $DFn=20$, $DFd=189$, $p=0.08$).

Higher HI values reflect lower minimum body temperatures and longer, more frequent torpor bouts (Boyles et al., 2011). The HI was consistently higher in individuals receiving LQ (Fig. 4). It was significantly different between the control and the experimental group ($F=48.04$, $DFn=1$, $DFd=360$, $p<0.0001$) and over time ($F=1.734$, $DFn=20$, $DFd=360$, $p=0.0311$). Bonferroni post-hoc test indicated a significant difference between diets ($p<0.05$) on days 2, 3, 14–16, and 19–21.

Although T_{sc} tended to vary with T_a in both groups with very shallow slopes that deviated significantly from 0 ($p<0.001$ for both groups), the fit to a linear regression was not significant ($R^2=0.1519$ and $R^2=0.1052$, respectively). The intercepts of $T_{sc,min}$ were significantly lower in the experimental group ($F=75.9662$, $DFn=1$, $DFd=407$, $p<0.0001$), while they were similar in both groups for $T_{sc,max}$ ($F=0.990953$, $DFn=1$, $DFd=403$, $p=0.3201$).

4. Discussion

The present findings confirm previous reports that pichis can enter facultative daily torpor outside the hibernation season (Superina and Boily, 2007) and suggest that they are capable of adjusting the length and depth of torpor bouts in response to changes in food availability.

All studied individuals entered torpor irrespective of the food type they received. Our analyses based on T_{sc} and $T_{sc} < \text{norm}$, as well as on the HI all lead to the general conclusion that pichis fed a low-quality diet show a stronger heterothermic response. The differences were, however, much clearer in the individual analyses of T_{sc} and $T_{sc} < \text{norm}$ than in the HI analysis. We therefore agree with Brigham et al. (2011), who pointed out several weaknesses of the HI in its current form, and suggest to use it as a complement, but not as a replacement of the use of temperature thresholds.

Our results are in agreement with previous studies that showed that more frequent and/or deeper daily torpor could be induced in several mammal species by limiting either food quantity or quality (Bozinovic et al., 2007; Génin and Perret, 2003; Giroud et al., 2008; Kelm and von Helversen, 2007; Wojciechowski et al., 2007). The effect of diet was considerably stronger on $T_{sc,min}$ and $T_{sc,mean}$ than on $T_{sc,max}$. This finding was not unexpected, as T_b (or, here, T_{sc}) is lower during rest phases and torpor allows animals to reduce energy expenditure while they are inactive, thus further lowering the minimum T_b (Körtner and Geiser, 2000). On the other hand, a relatively high T_b is necessary while the animals are active to ensure optimal enzyme activity (Heinrich, 1977). The decrease in $T_{sc,max}$ in response to a lower food quality was significant in only one day; it was probably an effect of low sample size, as one female receiving LQ was in prolonged torpor on that day and thus had a $T_{sc,max}$ that was 3.5–9.5 °C lower than the other individuals in its group.

The individuals were living in an artificial environment, which may have modified their behavior and, thus, their daily body temperature cycles. However, the timing of $T_{sc,max}$ recorded in this study was in agreement with the times of capture of wild pichis performed over the course of 12 years (Fig. 2). All but one out of 138 captures in the wild occurred after 11 AM, while 111 (80%) of them occurred between 1 PM and 7 PM, i.e., within the timeframe we measured 78% of all daily $T_{sc,max}$ during the experiment.

The considerable daily T_{sc} amplitudes (up to 14.5 °C) were in accordance with previous measurements performed on *Z. pichiy*

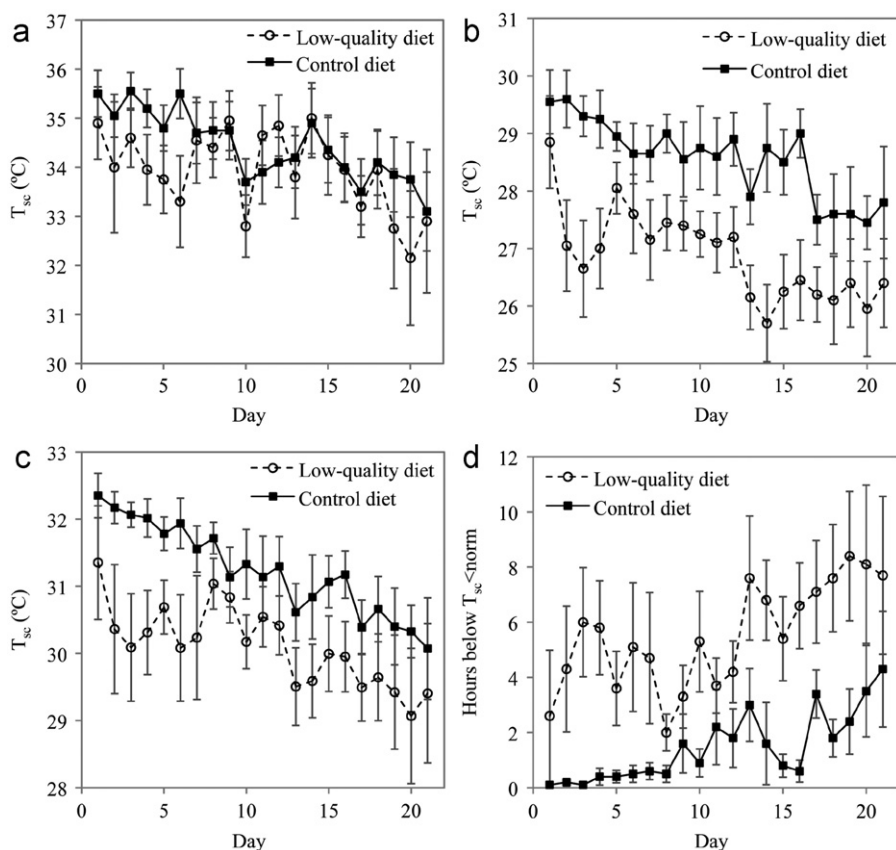


Fig. 3. Changes in (a) maximum, (b) minimum, (c) mean subcutaneous temperature (T_{sc}), and (d) number of hours spent at T_{sc} below the individual lower limit of normothermia ($T_{sc} < \text{norm}$), of pichis (*Zaedyus pichiy*) fed a low-quality experimental diet or a high-quality control diet, respectively. Values are expressed as mean $\pm$ SEM.

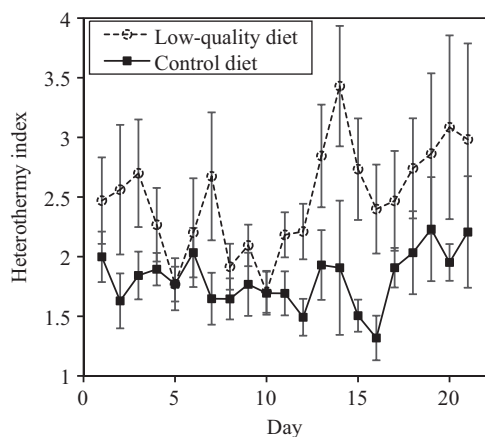


Fig. 4. Heterothermy index of pichis (*Zaedyus pichiy*) fed a low-quality experimental diet or a high-quality control diet, respectively. Values are expressed as mean $\pm$ SEM.

by Roig (1971), who observed variations in rectal temperature between 22 and 36 °C under laboratory conditions.

Previous reports stated that T_b of some armadillo species varies with T_a (Eisenbraut, 1932; McNab, 1985), and Abba et al. (2011a; 2011b) observed a positive correlation between T_a and T_b of wild *Dasypus hybridus* and *Chaetophractus vellerosus*. However, in this study neither $T_{sc\text{max}}$ nor $T_{sc\text{min}}$ could be correlated with T_a . Similarly, Superina et al. (2009b) did not find any correlation between T_a and T_b of 89 wild-caught pichis. Nevertheless, it cannot be denied that T_{sc} of the individuals studied here followed a pattern similar to changes in T_a

(Fig. 1). For instance, $T_{a\text{max}}$ was considerably lower on March 19 and 20, 2010 than the day before or after this period (Fig. 1). The pichi in the control group remained normothermic, but its $T_{sc\text{max}}$ during this period was only 32.5 °C, i.e., 3.5 °C lower than on March 18. At the same time, the animal feeding on LQ entered a prolonged torpor bout during which its T_{sc} dropped as low as 23.5 °C, suggesting that T_a influences T_{sc} at least to a certain degree.

Several individuals entered prolonged torpor during the study period. These torpor bouts would classify as hibernation in the strict sense because they lasted more than 24 h, but we do not consider this term appropriate here for reasons similar to those exposed by Mzilikazi and Lovegrove (2004). Our observations and those of Mzilikazi and Lovegrove (2004) suggest that there are exceptions to the general rule established by Geiser and Ruf (1995), which states that a clear gap exists between the duration of torpor bouts of daily heterotherms and hibernators.

The fact that nine of the ten prolonged torpor bouts occurred in individuals receiving LQ strongly suggests that this was related to food quality. Wild pichis would, thus, be able to enter prolonged periods of torpor during severe environmental stress periods. This could explain the extremely low encounter rates during a nine month drought period affecting Mendoza Province in 2003 reported by Superina (2007).

Environmental stress, such as prolonged droughts, can reduce insect abundance in desert environments (Ahearn, 1971; Ruggiero et al., 2009) and, thus, the availability of the predominant food item of wild pichis (Superina et al., 2009a). Pichis can respond to food shortages by ingesting other food items, such as plant matter. As shown here, they may adjust their energetic balance within a very short period of time by entering deeper or longer torpor. Furthermore, they are the only xenarthrans that are known to hibernate (Superina and Boily, 2007). These physiological

adaptations allow pichis to better cope with food shortages and a more extreme climate than other armadillo species with predominantly insectivorous feeding habits (Redford, 1985), and may explain why this species naturally occurs farther south than any other armadillo (Abba and Superina, 2010; Wetzel, 1985). It would be interesting to study whether other armadillo species inhabiting extreme habitats, such as *Chaetophractus nationi*, *Chaetophractus vellerosus* or *Chlamyphorus truncatus*, also use torpor.

Daily torpor has been reported from a wide latitudinal range, from the tropics to high latitudes, with almost half of the species that employ summer torpor being desert species (Lovegrove, 2000). Lovegrove (2000) suggested that daily torpor is likely to be common in desert species because they are exposed to unpredictable changes in climate and food availability. Geiser and Drury (2003) further developed this idea by proposing that selective pressures may have led to daily heterothermy in desert species not only because they experience unpredictable food shortages, but also because they are exposed to substantial amounts of solar radiation and/or high daily T_a amplitudes that allow passive rewarming. Our results further substantiate Geiser and Drury's (2003) hypothesis given the high solar radiation and daily T_a amplitudes in pichi habitat.

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