J Comp Physiol B (2001) 171: 569–576
DOI 10.1007/s003600100207

ORIGINAL PAPER

F. Geiser · C. Ferguson

Intraspecific differences in behaviour and physiology: effects of captive breeding on patterns of torpor in feathertail gliders

Accepted: 15 May 2001 / Published online: 24 July 2001

Abstract Studies on the physiology of mammals and birds are often conducted using captive-bred individuals and it is commonly assumed that the resulting data are representative of individuals living in the field. To investigate whether these assumptions are justified, we quantified morphological, behavioural, and physiological variables of the small marsupial feathertail glider (*Acrobates pygmaeus*). We compared three populations: (i) individuals from a cool-temperate, montane area, (ii) individuals form a subtropical, coastal area, and (iii) captive-bred individuals. Captive-bred gliders differed from the montane field gliders in morphology (longer tails and snouts), behaviour (longer activity periods) and physiology (less frequent torpor, shorter torpor, shallower torpor, higher metabolic rates during rest and torpor, and slower rates of rewarming). Most of these differences were also apparent between the captive-bred and the coastal field gliders. Unlike both field populations, captive-bred gliders often became hypothermic and were unable to rewarm. In contrast to the other physiological variables, the minimum body temperatures defended during torpor and the corresponding air temperatures differed between the montane and coastal field gliders, but were similar in coastal field and captive-bred gliders. Our study shows that morphology, behaviour and physiology can be strongly affected by breeding in or acclimation to captivity. The poor expression of torpor and thermal performance of the captive-bred gliders raises the question of whether they possess the physiological capability for survival in the wild. Even though captive breeding appears to have only minor effects on some physiological variables, data from captive-bred individuals should only be extrapolated to the field with caution.

Communicated by I.D. Hume

F. Geiser (✉) · C. Ferguson
Zoology, School of Biological Sciences,
University of New England, Armidale 2351, Australia
E-mail: fgeiser@metz.une.edu.au

Keywords Marsupials · Metabolism · Phenotypicplasticity · Selection · Thermoregulation

Abbreviations MR metabolic rate · RMR resting metabolic rate · T_a air temperature · T_b body temperature · TMR torpid metabolic rate · $\dot{V}O_2$ rate of oxygen consumption

Introduction

Capturing mammals or birds in the wild for laboratory experiments can be impractical and expensive and individuals caught in the wild may be difficult to acclimate to captivity. Therefore, many physiological studies have been conducted on captive-bred individuals, including work on the physiology of daily torpor and hibernation (prolonged torpor). Both patterns of torpor are characterised by pronounced reductions of body temperature (T_b) and metabolic rate (MR) and it is widely accepted that energy conservation is the primary function of torpor in the wild (Lyman et al. 1982; Kenagy 1989; Wang 1989; Geiser and Ruf 1995). Nevertheless, the majority of studies on torpor have been conducted in captivity and many of these on captive-bred individuals. For example, in the last three published volumes of International Hibernation Symposia (Carey et al. 1993; Geiser et al. 1996; Heldmaier and Klingenspor 2000), which likely represent current activities in this field, 42% of the 132 papers that concerned some aspect of torpor include or refer to experiments on captive-bred individuals.

Work on captive-bred individuals may, however, be fraught with problems because there is some experimental evidence, which suggests that the use of torpor may differ between wild-caught and captive-bred individuals. For example, mice (*Peromyscus* spp.) caught in the wild frequently entered torpor in captivity, whereas some captive-bred individuals were reluctant to do so (MacMillen 1965; Hill 1975; Vogt and Lynch 1982; Tannenbaum and Pivorun 1984). In *Peromyscus leucopus*, two of three second generation captive-bred

individuals never entered spontaneous torpor (food ad libitum), whereas only one of six wild-caught individuals remained homeothermic (Hill 1975). The marsupial mountain pygmy-possum (*Burramys parvus*) caught in the wild showed substantial pre-hibernation fattening and a pattern of deep and prolonged hibernation in captivity that was similar to that observed in the wild (Geiser et al. 1990; Körtner and Geiser 1998). In contrast, captive-bred mountain pygmy-possums, held under identical environmental conditions did not fatten and never entered torpor (Geiser et al. 1990). Thus, it appears that captive breeding may affect the use of torpor in at least some mammals.

Despite these discrepancies in torpor use between captive-bred and wild-caught individuals, data on the patterns of torpor (e.g. temporal organisation, torpor depth and length) obtained from captive-bred individuals are often used to make predictions about energetics, survival, and even fitness of wild animals. However, to be able to do this, it is important to know whether both the use of torpor as well as the patterns of torpor obtained from captive-bred individuals are accurate assessments of what occurs under natural conditions. Considering that in some species physiological variables of even wild-caught individuals measured in the laboratory differ from those obtained from free-ranging, wild individuals (Augee 1978; Wang 1978; Grigg et al. 1992; Geiser et al. 2000; Körtner et al. 2000) these assumptions may not always be justified.

The aim of the present study was to provide more detailed information on the subject, by investigating whether morphology, behaviour, normothermic MR, and patterns of torpor differ between the same species for wild-caught and captive-bred individuals. We studied feathertail gliders (*Acrobates pygmaeus*, Marsupialia; body mass approximately 12 g), which are among the smallest diprotodont marsupials, eat pollen, seeds, insects and plant exudates (Hume 1999), are nocturnal, and are known to enter deep and prolonged torpor for up to several days at low air temperatures (T_a). Torpor use in this species is not seasonally restricted and can be induced throughout the year (Frey and Fleming 1984; Fleming 1985; Jones and Geiser 1992). The species is well suited for our comparison, because patterns of torpor in heterothermic mammals with weak circannual cycles appear to be most significantly affected by captivity (Körtner and Geiser 2000; Geiser et al. 2000).

Materials and methods

Seven adult *A. pygmaeus* (four females, three males) were collected from nest boxes on the New England Tablelands, near Armidale, New South Wales (30°30′ S; 151°40′ E), at an altitude of about 1000 m (henceforth montane field individuals/gliders). The average T_a range on the New England Tablelands is 0.2–12.6 °C in winter (July) and 13.8–26.7 °C in summer (January) (Bureau of Meteorology).

Four adult *A. pygmaeus* (two females, two males) were obtained from Taronga Park Zoo, Sydney (henceforth captive-bred individuals/gliders). These individuals were fourth or fifth generation captive-bred individuals in the exhibit of the zoo derived from nine individuals (five females, four males) captured at coastal sites between the Sydney area (33°52′ S; 151°12′ E) where average T_a ranges between 7.9–16.0 °C in winter (July) and 18.5–25.7 °C in summer (January), and the Port Macquarie area (31°27′ S; 152°50′ E) where average T_a is 7.4–17.9 °C in winter (July) and 18.5–25.5 °C in summer (January). In the zoo the animals were held under reversed natural photoperiod and the average T_a was 12–16 °C in winter and 15–24 °C in summer.

To ascertain that physiological variables were not entirely a reflection of regional differences, three additional adult *A. pygmaeus* (one female, two males) were caught at low altitude subtropical coastal sites near Port Macquarie (henceforth coastal field individuals/gliders). Only three individuals could be obtained from this area, despite an intensive multi-year capture effort and even these individuals came from three sites approximately 50 km apart.

All *A. pygmaeus* were transferred to the University of New England, Armidale, where they were held individually in cages supplied with sawdust and nesting material. Gliders were fed daily with a mixture containing Heinz high protein cereal, honey, water with supplements of multivitamins and calcium, or Heinz tinned fruits. A piece of apple and water were freely available throughout the study when animals were in their cages. Gliders were acclimated to a photoperiod of L12:D12, lights on from 0600–1800 hours Australian Eastern Standard Time, and T_a 15 °C for a minimum of 3 weeks before measurements began. Physiological measurements were conducted in autumn and winter.

To determine the extent to which gliders used or did not use torpor in their holding facilities, single daily observations for spontaneous torpor (food and water ad libitum) were made either at 0900–1100 hours (*AM*) or at 1300–1630 hours (*PM*). Mean torpor percentage was calculated from the means of total daily observations on individual gliders. *A. pygmaeus* show the typical posture of many mammals in deep torpor, curled into a ball with the tail wrapped over the body (Fig. 1). Sawdust was sprinkled on the animals when observed in torpor at low T_a, but this method was not used at high T_a because it induced arousal. Overnight disappearance of sawdust was considered to mark an arousal episode. If a glider had eaten during the previous night and was in torpor on the following morning or afternoon but ate in the following night, this was classified as a 0.5-day torpor bout. If a glider was observed in torpor on two consecutive mornings and had not aroused between observations, as indicated by untouched food and unaltered position, but was normothermic before and after this torpor episode, this was classified as a 1.5-day torpor bout. Gliders were considered to have undergone multi-day torpor bouts if they were torpid over consecutive days in the same position and had not touched their food. These observations were carried out over 3 weeks at T_as of 15 °C and 20 °C, each, and for 1 week each at T_as

Fig. 1 Typical 'ball' posture of a torpid *Acrobates pygmaeus*. Note the tail is wrapped over the body, the snout is positioned close to the vent, and the ears are folded down

of 8 °C and 12 °C. The coastal field individuals were only investigated at T_as of 12, 15 and 20 °C.

The MR of *A. pygmaeus* acclimated to T_a 15 °C was measured as the rate of oxygen consumption ($\dot{V}O_2$) over a period of approximately 22 h, to determine aerobic metabolism during rest (RMR) and torpor (TMR). $\dot{V}O_2$ was measured with an oxygen analyser (Electrochemistry S-3A). The 0.5-l respirometer vessel was contained in a temperature-controlled cabinet and the T_a in the respirometer was measured to the nearest 0.1 °C using an electronic thermometer with a calibrated thermocouple.

Normothermic animals were placed inside the respirometer at about 1600 hours (i.e. 2 h before lights off) at T_a 5 ± 1 °C. Food or water were not provided during the MR measurements. The flow rate of dry air through the chamber was maintained at 200–400 ml min^{-1} and was measured with a calibrated rotameter or mass flowmeter. Periods of rest occurred before lights off and the animals became active shortly after lights off. At T_a 5 ± 1 °C, *A. pygmaeus* entered torpor during the late night or early morning. Steady-state RMR and TMR values were determined when oxygen consumption was minimal and stable over at least 30 min.

To determine the thermoregulatory set point for T_b in torpid *A. pygmaeus*, the T_a in the respirometer was slowly lowered after gliders were in steady-state torpor at T_a 5 °C in the morning. An increase in TMR and rate of ventilation was assumed to indicate onset of thermoregulation because the animal had reached its set point for T_b that is defended by thermoregulatory heat production (Heller and Hammel 1972; Geiser et al. 1992). The cooling procedure began at about 0900 hours and the T_a in the cabinet was slowly cooled by about 1 °C every 60 min. When the torpid glider began to steadily increase its TMR (at the minimum T_a), it was removed from the chamber and the T_b (minimum T_b) was measured immediately using a 2-cm rectal insertion of a fine (0.5 mm diameter) thermocouple probe calibrated to the nearest 0.1 °C that was read with an electronic thermometer (Omega HH-71 T).

Gliders were weighed before and after the MR measurements to determine the mass lost during the experiment. A linear decrease of body mass was assumed for calculation of mass-specific MR. Gas volumes were corrected to STP and calculated according to Withers (1977). Morphometrics were performed with vernier callipers.

We also used measurements of MR to quantify temporal organisation of torpor and activity patterns of gliders. We determined the time taken for the gliders to become active from a state of rest after lights off (indicated by the abrupt increase in MR) and the length of the activity period (indicated by continuous high MR values) before torpor entry (indicated by an abrupt decrease in MR).

Rates of rewarming were measured at T_a 22 ± 1 °C because most published measurements were conducted near this T_a (Geiser and Baudinette 1990). During the night before rewarming rates were determined, gliders were provided with food and water and kept at T_a 15 °C. In the morning, torpid gliders were removed from the temperature-controlled cabinets and a thermocouple probe was inserted 2 cm into the rectum, held in position with a tape around the tail. The T_b readings (Omega Model HH-71 T) during rewarming were taken each minute until the animal reached a T_b of about 35 °C or when the animal became too active for further measurements. The overall rewarming rate (°C min^{-1}) from the beginning of arousal to normothermia was calculated. The fastest rewarming rate over 10 min was also calculated for T_bs above T_a 22 °C, thus excluding possible effects of passive rewarming.

Means ± 1 SD for the number of individuals '*n*' are shown in the text; '*N*' is the number of observations. Differences between means were tested using an ANOVA (followed by Tukey's test) or a *t*-test where appropriate. Percentage values were arcsine-transformed before testing.

Results

Some morphological traits differed between montane field and captive-bred gliders. Tails (6.2 ± 0.5 cm montane field, 7.0 ± 0.2 cm captive-bred) and snouts (0.53 ± 0.10 cm montane field, 0.65 ± 0.06 cm captive-bred) were shorter (*t*-test; $P < 0.05$) in the montane field than in the captive-bred gliders (not shown). However, body mass did not differ between montane field (12.0 ± 1.0 g), coastal field (11.9 ± 1.3 g) and captive-bred (11.5 ± 0.9 g) gliders (ANOVA; ns, not shown).

The behaviour of field and captive-bred individuals differed during measurements of MR (Fig. 2). The time to onset of activity after lights off in the evening occurred later in coastal field individuals (68.0 ± 27.2 min) than in captive-bred individuals (15.0 ± 5.6 min) (ANOVA $P < 0.02$; Tukey $P < 0.05$; Fig. 2). The time of activity prior to torpor entry also differed among the three groups. The activity period was much shorter in the montane (128 ± 100 min) and coastal field individuals (280 ± 112 min) than in the captive-bred individuals (748 ± 146 min) (ANOVA $P < 0.001$; Tukey $P < 0.05$).

The occurrence of spontaneous torpor (food ad libitum) at T_a 15 °C differed significantly between field and captive-bred gliders (Fig. 3). Torpor in the morning (*AM*) was observed more often in montane field individuals (80.6 ± 14.4%; $n = 7$, $N = 282$) and coastal field individuals (78.5 ± 12.8%; $n = 3$; $N = 35$) than in the captive-bred individuals (26.8 ± 10.2%; $n = 4$; $N = 101$). In the afternoon (*PM*), the occurrence of torpor declined somewhat in all groups, but montane field individuals (80.2 ± 16.7%; $n = 7$, $N = 40$) and coastal field individuals (72.2 ± 25.5%; $n = 3$, $N = 11$) were in torpor much more often (ANOVA $P < 0.001$; Tukey $P < 0.05$) than captive-bred individuals (10.0 ± 11.5%; $n = 4$; $N = 18$; Fig. 3).

Maximum torpor bout duration also differed among the groups. In the montane field gliders, duration of torpor bouts increased from 0.5 days at T_a 20 °C to about 5 days at T_a 8 °C (Fig. 4). Captive-bred gliders did

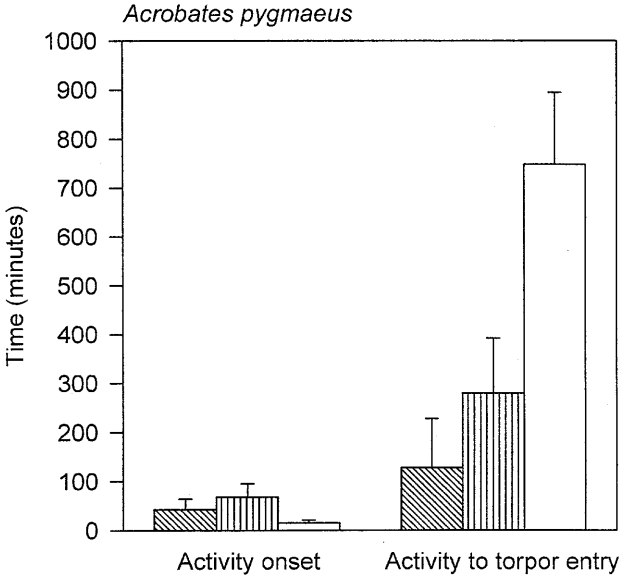

Fig. 2 The time interval (mean ± SD) to activity onset after lights off and the duration of the activity period before torpor entry in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) *A. pygmaeus*

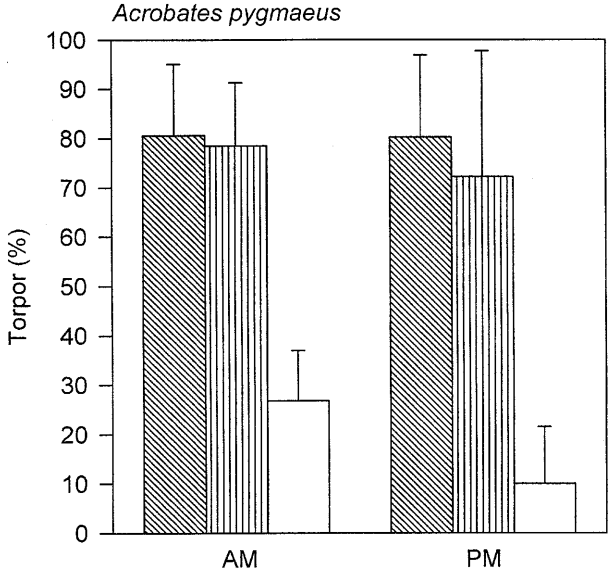

Fig. 3 Percent spontaneous torpor (mean ± SD) observed in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) *A. pygmaeus* in the morning (*AM*: 0900–1000 hours) and afternoon (*PM*: 1500–1630 hours) at air temperature (T_a) 15 °C

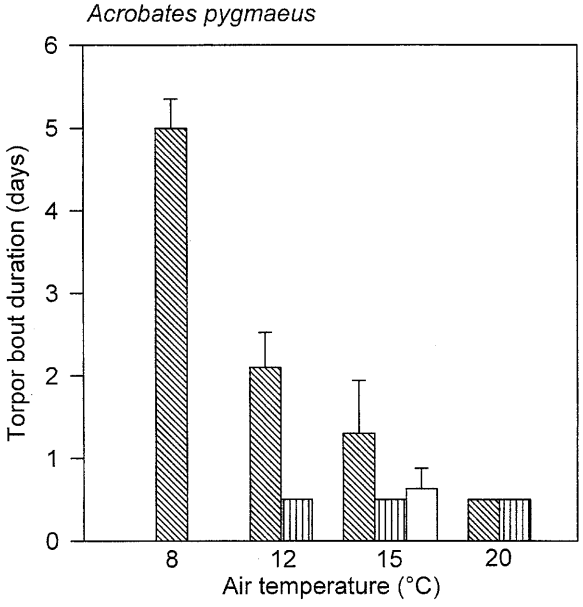

Fig. 4 The maximum duration of torpor bouts (mean ± SD) as a function of T_a in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) *A. pygmaeus*. Captive-bred individuals did not enter torpor at T_a 20 °C and became hypothermic (were unable to rewarm) at T_as 8 °C and 12 °C

not enter torpor at T_a 20 °C. At T_a 15 °C, maximum torpor bout duration in the montane field individuals was 1.3 ± 0.6 days ($n = 7$), which was about twice that in the captive-bred individuals (0.6 ± 0.3 days, $n = 4$; Fig. 4). During prolonged exposure to T_as 8 °C and 12 °C, the captive-bred individuals remained normothermic for a few days and then became hypothermic for up to 4 days. Hypothermic individuals differed in their posture from torpid individuals in that they did not assume a ball shape and failed to wrap their tail around the body. Hypothermic captive-bred individuals were unable to arouse at T_as 8 °C and 12 °C, but survived after they had been rewarmed using an external heat source. Coastal field individuals remained torpid for 0.5 days at T_as 12, 15 and 20 °C, and were never hypothermic.

Presumably reflecting differences in morphology and/or insulation, the RMR of captive-bred gliders at T_a 5 ± 1 °C was somewhat higher (22%; *t*-test $P < 0.05$) than that of the montane field individuals (Fig. 5). The MR during torpor was much lower in the field than in the captive-bred individuals (Fig. 5). The steady-state TMR at T_a 5 °C was 0.066 ± 0.013 ml O_2 g^{-1} h^{-1} in montane field individuals and 0.067 ± 0.028 ml O_2 g^{-1} h^{-1} in coastal field individuals, and both were less than half the TMR in captive-bred individuals of 0.155 ± 0.031 ml O_2 g^{-1} h^{-1} (ANOVA $P < 0.001$; Tukey $P < 0.05$). Further, the reduction of MR during torpor in comparison to RMR was more pronounced in the field than in the captive-bred individuals. The mean TMR at T_a 5 °C was 1.19 ± 0.39% of the RMR in the montane field individuals, 1.06 ± 0.37% in coastal field individuals, and these percentages were significantly smaller than those in the captive-bred individuals (2.17 ± 0.43%; ANOVA $P < 0.01$; Tukey $P < 0.05$).

The shorter activity periods, earlier torpor onset and the lower MRs in field gliders relative to captive-bred gliders were reflected in their loss of body mass (not shown). During the approximately 22 h of MR measurements, mean body mass loss in the montane field individuals (1.3 ± 0.5 g) and the coastal field individuals (1.1 ± 0.4 g) was about 60% of that in the captive-bred individuals (2.0 ± 0.3 g; not shown). However, the means did not differ significantly among the three groups (ANOVA $P = 0.079$).

Slow cooling of torpid individuals revealed further physiological differences among torpid gliders (Fig. 6). The TMR of captive-bred individuals at T_a 3.5–5 °C, at which no physiological thermoregulation (i.e. no thermoregulatory increase of MR) was evident, was more than twice that of montane field individuals. One individual captive-bred glider began to thermoregulate at T_as of between 4 °C and 3.5 °C; this individual is shown separately at T_a 2.5 °C and 3 °C because of its large increase in TMR (Fig. 6). The other captive-bred gliders began to thermoregulate at T_as between 3 °C and 1.5 °C. In contrast, all montane field individuals were thermo-conforming to about T_a 1.5 °C, but showed a thermoregulatory increase of TMR below T_a 1 °C. The minimum TMR for montane field individuals at T_a 1.5–2 °C was 0.042 ± 0.022 ml O_2 g^{-1} h^{-1}.

The mean minimum T_b, minimum T_a, and the corresponding T_b–T_a differential derived from the cooling experiments differed significantly between captive-bred and field gliders (Fig. 7). The minimum T_b was 2.0 ± 0.5 °C (montane field), 4.2 ± 0.8 °C (coastal field),

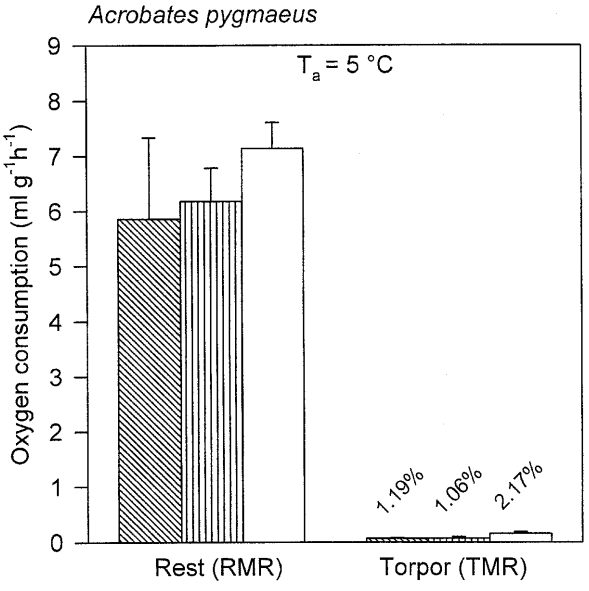

Fig. 5 Mass-specific metabolic rates (mean ± SD) measured as oxygen consumption at T_a 5 °C in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) *A. pygmaeus* during rest (*RMR*) and steady-state torpor (*TMR*). TMR was 1.19% of RMR in montane field individuals, 1.06% of RMR in coastal field individuals, and 2.17% of RMR in captive-bred individuals

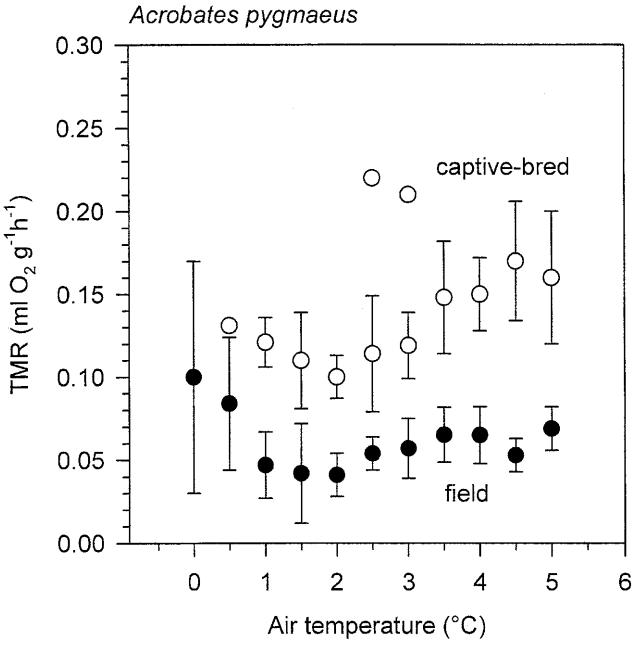

Fig. 6 Mass specific metabolic rates (TMR; mean ± SD) during cooling of torpid montane field and captive-bred *A. pygmaeus*. Montane field individuals (*filled circles*) had lower TMRs and commenced to thermoregulate at lower T_as than captive-bred individuals (*unfilled circles*). One captive-bred individual is shown separately because it began to thermoregulate at a higher T_a than the other captive-bred individuals

and 4.9 ± 1.2 °C (captive-bred). The minimum T_a and minimum T_b differed between the two field populations and between montane field and captive-bred individuals (ANOVA $P < 0.01$; Tukey $P < 0.05$), but not between the coastal field and captive-bred individuals. The T_b–T_a differential was 2.3 ± 1.2 °C in the captive-bred gliders, which was almost twice that of the montane (1.2 ± 0.5 °C) and coastal (1.3 ± 0.6 °C) field individuals. The mean T_b–T_a differential differed between montane field and captive-bred gliders (ANOVA $P < 0.025$; Tukey $P < 0.05$).

Rewarming from torpor was faster in the field than in the captive-bred gliders (Fig. 8). Overall rewarming rates in the montane field individuals were 74% faster (*t*-test; $P < 0.001$) than in the captive-bred individuals. Maximum rewarming rate in the montane field individuals was 0.88 ± 0.09 °C min^{-1} and 0.50 ± 0.05 °C min^{-1} in the captive-bred individuals and these averages differed (*t*-test; $P < 0.001$). One coastal field individual had an overall rewarming rate of 0.73 °C min^{-1} and a maximum rewarming rate of 0.82 °C min^{-1}, which was similar to that of the montane field individuals.

Discussion

Our study shows, that behaviour, morphology, metabolism, as well as most variables of torpor differ substantially between wild-caught and captive-bred *A. pygmaeus*. These findings are of consequence for the interpretation of the physiology of torpor in relation to animal ecology, but also for laboratory based studies on organismal and integrative animal biology in general.

We observed a number of physiological/morphological differences between the glider populations. These were most pronounced between captive-bred and montane field individuals and were observed for tail and snout length, torpor frequency, torpor duration, TMR, reduction of TMR in relation to RMR, minimum T_b, minimum T_a, T_b–T_a differentials, and rates of rewarming. The physiological variables revealed that torpor was more frequent, deeper and longer in the montane field than in the captive-bred individuals. Most of these variables were indistinguishable or at least similar between the montane and coastal field individuals, but differed between both field populations and the captive-bred individuals. As differences were generally observed between both field population and the captive-bred individuals, although the former came from different climates, it is likely that laboratory breeding rather than long-term selection due to different climatic histories is the reason for the observed variability. We do not believe that the physiological differences between wild-caught and captive-bred individuals simply reflect prolonged maintenance in captivity in the latter because even after 1 year in captivity the montane field individuals were capable to enter deep and prolonged torpor at low T_a, similar to the pattern observed soon after capture.

Behavioural differences between field and captive-bred individuals were observed in the temporal organi-

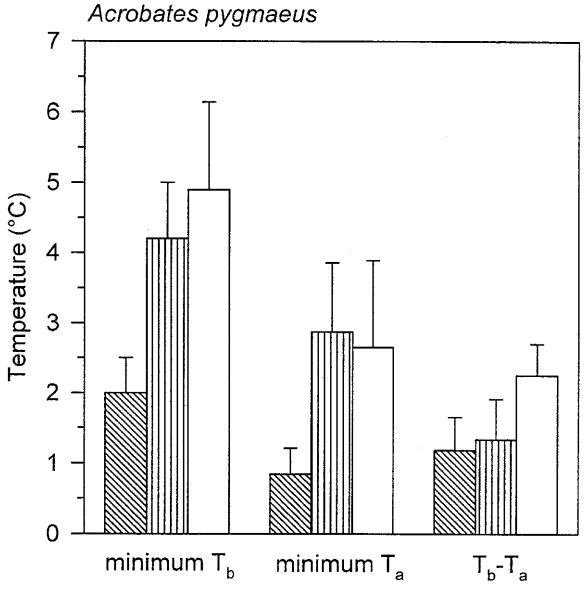

Fig. 7 The minimum body temperature (T_b) at which torpid *A. pygmaeus* commenced thermoregulation and the corresponding minimum air temperature (T_a) and the T_b–T_a differential. Variables are means ± SD in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) individuals

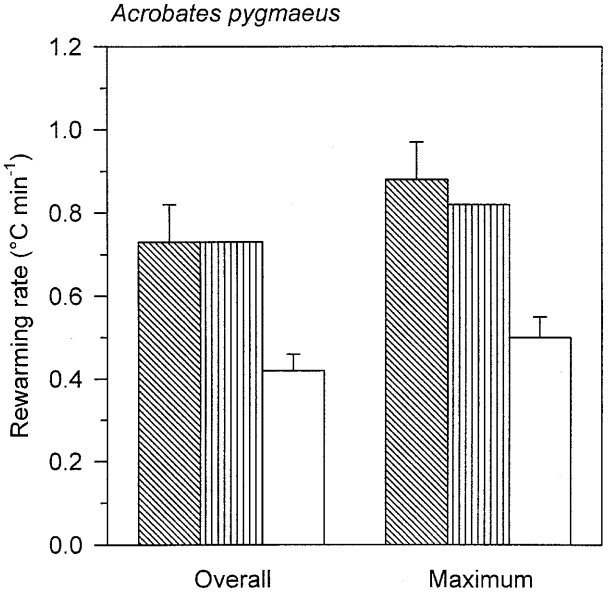

Fig. 8 Rewarming rates from torpor (mean ± SD) measured at T_a 22 °C in montane field (*diagonally-hatched bars*), coastal field (*vertically-hatched bars*), and captive-bred (*clear bars*) *A. pygmaeus*. Both the overall rewarming rates from the beginning to the end of the arousal process and the maximum arousal rates measured over 10 min were faster in the field than in the captive-bred individuals

sation of their daily activity patterns. Captive-bred gliders commenced activity well before field individuals and remained active for longer. The prolonged nocturnal activity in captive-bred individuals may reflect the availability of ad libitum food and relative mild T_a throughout their development and adult life, and consequently a low requirement to use nocturnal torpor for energy conservation. However, the longer activity periods in captive-bred than in field gliders may also be related to predator avoidance. It is possible that gliders from the field minimise foraging time and exposure to potential predators such as owls or arboreal carnivorous mammals in comparison to those bred in captivity, which do not have to be concerned with this aspect of activity.

A further important physiological difference was that, unlike the captive-bred individuals, field individuals from both populations never became hypothermic, and were always able to arouse from torpor. In contrast, the captive-bred individuals frequently became hypothermic during prolonged exposure to low T_a and were unable to rewarm using endogenous heat production. This physiological dysfunction of captive-bred gliders at low T_a is also likely a reflection of low torpor use in captivity and/or a low thermogenic capacity because of exposure to mild T_a throughout life. It is well established that warm-acclimation can reduce the thermal capacity in endotherms substantially (Feist and White 1989) which by itself could result in a reduced heat production for rewarming (Jones and Geiser 1992), especially at low T_a. As the incidence of hypothermia in the captive-bred individuals was very high even under access to ad libitum food and at T_as that are regularly experienced even in coastal areas of eastern Australia, these individuals may not have the physiological capability for survival in the wild. This observation has implications for captive breeding and release of endangered small mammals and birds, as practised by conservation biologists and also raises the question of whether maintenance and breeding of rare species in zoos provides a useful reservoir for endangered populations of small endotherms in the wild.

The decline in the use of torpor displayed after four generations in *A. pygmaeus* is similar to that observed in hamsters (*Mesocricetus auratus*), which exhibited a reduction in torpor frequency after only two generations (Chaffee 1966). These responses could be due to a lack of selection for extensive use of torpor in the laboratory, or simply a reflection of phenotypic plasticity. As captive-bred individuals usually are not exposed to thermal and nutritional stress during development, a greater proportion of young are likely to survive and a limited ability to use of torpor as an energy saving mechanism is unlikely to have serious consequences. Nevertheless, if this scenario were correct, one would predict a large variation among captive-bred individuals, which was not the case. Thus, the more likely explanation may again be that exposure to mild temperatures and access to food throughout development and growth does not trigger appropriate developmental switches that are important for survival in the wild. Lack of torpidity for prolonged periods could, for example, limit the differential expression of gene products that may be important for entry and maintenance of torpor (Boyer and Barnes 1999; Martin et al. 2000). The effects of temperature

cycles during development on the expression of torpor could be experimentally tested.

Captive-breeding did not appear to affect one physiological variable of torpid gliders. Unlike most other physiological variables, the minimum T_b that is defended during torpor and the corresponding T_a differed between montane and coastal field gliders, but were similar between coastal field and captive-bred gliders. Although regional differences in torpor patterns have been observed among different populations of echidnas, *Tachyglossus aculeatus* (Nicol and Andersen 1996), we are not aware of comparable intraspecific data on minimum T_bs in other heterothermic endotherms. However, in closely related mice of the genus *Peromyscus*, the minimum T_b appears to be a function of the climate of their habitat. *Peromyscus maniculatus* from a cold montane region showed lower minimum T_b than *Peromyscus leucopus* and *Peromyscus gossypinus* from a low altitude warmer region (Tannenbaum and Pivorun 1984). Measurements on bats also support the view that the minimum T_b of many bats is climate-related (Kulzer 1965; Bartels et al. 1998; Arlettaz et al. 2000). It appears that the thermoregulatory set point for T_b is not strongly affected by captive-breeding for a few generations or maintenance in captivity of *A. pygmaeus* or other hibernating mammals (Geiser et al. 2000), but is a reflection of climatic differences experienced by populations and consequently long-term natural selection in the wild.

Energy expenditure while in torpor is lowest at T_as close to the minimum T_b (Song et al. 2000). Exposure to T_as below the minimum T_b is associated with a substantial increase in energy expenditure because thermoregulatory heat production and frequency of arousal increase (Geiser and Kenagy 1988; Geiser and Broome 1993; Barnes and Buck 2000). A minimum T_b much above the T_a experienced during prolonged torpor would result in prolonged periods of thermoregulation and thus rapid depletion of energy reserves especially of small species. Therefore it is likely that if the set point for the minimum T_b is not close to or below the T_a experienced during most of the hibernation season, winter mortality would increase (Geiser and Kenagy 1988). As most small mammals enter deep prolonged torpor as sub-adults or adults in winter, the selective pressure to maintain the set point for T_b below the T_a commonly experienced in winter is likely to act on adults rather than on juveniles during development.

We detected enormous differences in some physiological variables between field and captive-bred individuals. Differences in torpor use between laboratory and field individuals were about 300% or greater, those for TMR > 100%, and those for rates of rewarming about 74%. In normothermic individuals differences between captive-bred and field individuals were > 200% for time of activity onset, > 250% for the period of activity and 22% for RMR. These differences are far greater than those often used for interspecific comparative analyses in which great emphasis is placed on the importance of phylogeny in determining physiological variables. The large intraspecific differences between captive-bred and field gliders suggest, however, that many physiological variables are extremely pliable, are not necessarily related to phylogeny, and reflect phenotypic plasticity as expressed during acclimation/acclimatisation to environmental variables. Other physiological variables, such as the minimum T_b, are apparently due to long-term selection, but similarities between unrelated taxa within similar habitats (Geiser and Ruf 1995) and differences within the same species from different habitats (this study) suggest that again ecological factors rather than phylogeny are the important determinants (Westoby et al. 1995).

Our study demonstrates that caution must be used in extrapolating behavioural and physiological data obtained from captive-bred individuals to those living in the wild. It shows that pronounced changes in morphology, behaviour and physiology can be caused by short-term environmental influences and should cause us to question the assumption that physiological differences are always linked to phylogeny.

Acknowledgements We would like to thank Mark Brigham, Gerhard Körtner, Bronwyn McAllan, Xiaowei Song and Craig Willis for help with various aspects of this work. Experiments were approved by the University of New England Animal Ethics Committee. The study was supported by a grant from the Australian Research Council to FG.

References

Arlettaz R, Ruchet C, Aeschimann J, Brun E, Genoud M, Vogel P (2000) Physiological traits affecting the distribution and wintering strategy of the bat, *Tadarida teniotis*. Ecology 81:1004–1014

Augee ML (1978) Monotremes and the evolution of homeothermy. In: Augee ML (ed). Monotreme biology. Royal Zoological Society of New South Wales, Mosman, pp 111–119

Barnes BM, Buck CL (2000) Hibernation in the extreme: burrow and body temperatures, metabolism, and limits to torpor bout length in artic ground squirrels. In: Heldmaier G, Klingenspor M (eds) Life in the cold. Eleventh International Hibernation Symposium. Springer Verlag, Berlin Heidelberg New York, pp 65–72

Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). J Comp Physiol B 168:233–239

Boyer BB, Barnes BM (1999) Molecular and metabolic aspects of mammalian hibernation. BioScience 49:713–724

Carey C, Florant GL, Wunder BA, Horwitz B (eds) (1993) Life in the cold: ecological, physiological, and molecular mechanisms. Westview, Boulder

Chaffee RRJ (1966) On experimental selection for super-hibernating and non-hibernating lines of Syrian hamsters. J Theor Biol 12:151–154

Feist DD, White RG (1989) Terrestrial mammals in cold. In: Wang LC-H (ed) Advances in comparative and environmental physiology, vol 4. Springer, Berlin Heidelberg New York, pp 327–360

Fleming MR (1985) The thermal physiology of the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Burramyidae). Aust J Zool 33:667–681

Frey H, Fleming MR (1984) Torpor and thermoregulatory behaviour in free-ranging feathertail gliders (*Acrobates pygmaeus*) (Marsupialia: Burramyidae) in Victoria. In: Smith AP, Hume

ID (eds) Possums and gliders. Surrey Beatty and Australian Mammal Society, Sydney, pp 393–401
Geiser F, Baudinette RV (1990) The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. J Exp Biol 151:349–359
Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. J Comp Physiol B 163:133–137
Geiser F, Kenagy GJ (1988) Duration of torpor bouts in relation to temperature and energy metabolism in hibernating ground squirrels. Physiol Zool 61:442–449
Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966
Geiser F, Sink HS, Stahl B, Mansergh IM, Broome LS (1990) Differences in the physiological response to cold in wild and laboratory-bred mountain pygmy possums *Burramys parvus* (Marsupialia). Aust Wildl Res 17:535–539
Geiser F, Stahl B, Learmonth RP (1992) The effect of dietary fatty acids on the pattern of torpor in a marsupial. Physiol Zool 65:1236–1245
Geiser F, Hulbert AJ, Nicol SC (eds) (1996) Adaptations to the cold. Tenth International Hibernation Symposium, University of New England Press, Armidale
Geiser F, Holloway JC, Körtner G, Maddocks TA, Turbill T, Brigham MR (2000) Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier G, Klingenspor M (eds) Life in the cold. Eleventh International Hibernation Symposium. Springer, Berlin Heidelberg New York, pp 95–102
Grigg GC, Augee ML, Beard LA (1992) Thermal relations of free-living echidnas during activity and hibernation in a cold climate. In: Augee ML (ed) Platypus and echidnas. Royal Zoological Society of New South Wales, Sydney, pp 160–173
Heldmaier G, Klingenspor M (eds) (2000) Life in the cold. Eleventh International Hibernation Symposium. Springer, Berlin Heidelberg New York
Heller HC, Hammel HT (1972) CNS control of body temperature during hibernation. Comp Biochem Physiol A 41:349–359
Hill RW (1975) Daily torpor in *Peromyscus leucopus* on an adequate diet. Comp Biochem Physiol A 51:413–423
Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge
Jones CJ, Geiser F (1992) Prolonged and daily torpor in the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Acrobatidae). J Zool (Lond) 227:101–108
Kenagy GJ (1989) Daily and seasonal uses of energy stores in torpor and hibernation. In: Malan A, Canguilhem B (eds) Living in the cold II. Libbey Eurotext, London, pp 17–24
Körtner G, Geiser F (1998) Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). Oecologia 113:170–178
Körtner G, Geiser F (2000) The temporal organisation of daily torpor and hibernation: circadian and circannual rhythms. Chronobiol Int 17:103–128
Körtner G, Brigham RM, Geiser F (2000) Winter torpor in a large bird. Nature 407:318
Kulzer E (1965) Temperaturregulation bei Fledermäusen (Chiroptera) aus verschiedenen Klimazonen. Z Vergl Physiol 50: 1–34
Lyman CP, Willis JS, Malan A, Wang LC-H (eds) (1982) Hibernation and torpor in mammals and birds. Academic Press, New York
MacMillen RE (1965) Aestivation in the cactus mouse *Peromyscus eremicus*. Comp Biochem Physiol 16:227–247
Martin S, Epperson E, Breukelen F van (2000) Quantitative and qualitative changes in gene expression during hibernation in golden-mantled ground squirrels. In: Heldmaier G, Klingenspor M (eds) Life in the cold. Eleventh International Hibernation Symposium. Springer, Berlin Heidelberg New York, pp 315–324
Nicol SC, Andersen NA (1996) Hibernation in the echidna: not an adaptation to the cold? In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold. Tenth International Hibernation Symposium. University of New England Press, Armidale, pp 7–12
Song X, Körtner G, Geiser F (2000) Temperature selection and energy expenditure in the marsupial hibernator *Cercartetus nanus*. In: Heldmaier G, Klingenspor M (eds) Life in the cold. Eleventh International Hibernation Symposium. Springer, Berlin Heidelberg New York, pp 119–126
Tannenbaum MG, Pivorun EB (1984) Differences in daily torpor patterns among three southeastern species of *Peromyscus*. J Comp Physiol B 154:233–236
Vogt FD, Lynch GR (1982) Influence of ambient temperature, nest availability, huddling, and daily torpor on energy expenditure in the white-footed mouse *Peromyscus leucopus*. Physiol Zool 55:56–63
Wang LC-H (1978) Energetics and field aspects of mammalian torpor: the Richardson's ground squirrel. In: Wang LC-H, Hudson JW (eds) Strategies in cold. Academic Press, New York, pp 109–145
Wang LC-H (1989) Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In: Wang LC-H (ed) Advances in comparative and environmental physiology, vol 4. Springer, Berlin Heidelberg New York, pp 361–401
Westoby M, Leishman MR, Lord JM (1995) On misinterpreting the 'phylogenetic correction'. J Ecol 83:531–534
Withers PC (1977) Measurements of $\dot{V}O_2$, $\dot{V}CO_2$ and evaporative water loss with a flow-through mask. J Appl Physiol 42:120–123