Chapter 3:
Seasonal Differences in Metabolism and Thermoregulation

3.1 Introduction:

The success of a species depends primarily on the ability of that species to survive and cope with its environment. While an environment is rarely stable, there are certain aspects, such as seasonal changes in climate, that may be reasonably predictable. In many parts of the world these seasonal changes can be quite extreme and, particularly for endothermic species, adaptations to thermoregulatory mechanisms are necessary because climate and food availability are invariably linked. Basically, there are three types of response patterns available: 1) alterations to the amount of heat lost; 2) changes to the thermogenic capabilities; and 3) escape the harsh conditions (Wunder 1979). These patterns may be achieved by either physiological, morphological or behavioural approaches, or a combination of the three.

Behavioural modifications in response to climate may involve alteration of activity levels and patterns (Kenagy 1973; Wallis 1982; Stebbins 1984; Frey 1991; Reynolds & Gorman 1994), posture (Wallis 1982), social behaviour and aggregation (Sealander 1952; Morton 1978a; Andrews & Belknap 1986), use of nests, burrows and dens (Kenagy 1973; Frey 1991), basking (Neal & Lustick 1974; Frey 1991) and changes in feeding habits (Smith 1982; Ferron *et al.* 1986; Haim *et al.* 1990). On an extreme scale, animals may migrate to escape severe conditions (Bartholomew 1982; Piersma *et al.* 1995), but this is usually restricted to large mammals or those species that can fly or swim (Tucker 1975; Schmidt-Nielsen 1990).

Physiological and morphological variables that may be altered to adapt to climatic changes include body mass (Haim *et al.* 1991; Boswell *et al.* 1994; McDevitt & Speakman 1996); body size (Hyvärinen 1984; Quay 1984); metabolic rates, including BMR (Heldmaier & Steinlechner 1981; Feist & White 1989; McDevitt & Speakman 1996), and RMR (Merritt 1986; Stephenson & Racey 1994; McDevitt & Andrews 1995); TNZ (Heldmaier & Steinlechner 1981); T_b (Stephenson & Racey 1994); insulation (Sealander 1952; Wunder *et al.* 1977; Heldmaier & Steinlechner 1981; Reynolds & Lavigne 1988); pelage colour (Hoffmann 1973); and thermal capacity (Rosenmann *et al.* 1975; Heldmaier *et al.* 1986). Animals may also utilise daily torpor or hibernation to evade the harsh conditions (Geiser 1994), but this will be covered in a later chapter (Chapter 6).

Problems have been encountered in determining the exact response of animals to seasonal changes in climate due to the use of acclimated animals in the laboratory, rather than seasonally acclimatised ones (Grodzinski & Wunder 1975; Wunder 1979; Yousef 1979). In some instances, acclimation to continuous cold temperatures elicited the opposite response for a particular variable (eg. body mass, RMR) to those animals acclimatised to natural conditions (Hart 1971; Lynch 1973; Yousef 1979; Hyvärinen 1984). In addition, animals acclimated to a constant photoperiod may not undergo any change as some variables may be correlated with rate of change of photoperiod rather than critical photoperiodic length (McAllan & Dickman 1986). Therefore, care needs to be taken in evaluating results obtained from acclimation experiments. However, only a few detailed laboratory studies are available on the thermogenic responses of birds and placental mammals acclimatised to seasonal changes in climate, and limited detailed investigations have been made on Australian marsupials. Although environmental conditions may not be as severe in Australia compared to the northern hemisphere, animals within this country still have to be able to cope with stresses associated with seasonal fluctuations in climate.

While laboratory studies with acclimatised animals are few, there have been some seasonal studies of metabolic rates of free-living marsupials (Morton 1980; Smith *et al.* 1982; Wallis

& Green 1992; Wallis *et al.* 1997), including the sugar glider (Quin 1993). All these studies, apart from one (Wallis *et al.* 1997), indicated that while climatic conditions may have changed, daily field metabolic rates remained the same, and, therefore, adjustment for climatic change may be present. In the one study where a seasonal difference in field metabolic rate was observed, the higher field metabolic rates observed in early spring relative to midsummer in the long-nosed potoroo, *Potorous tridactylus* (Wallis *et al.* 1997), may have been due to a number of factors, eg. differences in lactation energetics or activity patterns, rather than to seasonal change in climate since there was only a 4 °C difference in T_a between the two seasons measured. However, while field metabolic rates may be useful in determining the daily energy budgets for a species, it is impossible from these measurements to differentiate between the various aspects of thermoregulation to determine what specific, if any, changes are occurring. It is for this reason that laboratory studies distinguishing between different physiological states and time of day, using acclimatised animals, are necessary if the variables responsible for such changes are to be identified.

The distribution of the sugar glider includes both tropical and temperate regions of Australia and New Guinea (Suckling 1995). Within the New England Tablelands region, where sugar gliders are common, average maximum T_a range from 12.2 to 27.2 °C during July (winter) and January (summer) respectively, while average minimum T_a range from 0.4 to13.4 °C during the same months (Fig. 3.1; Bureau of Meteorology 1997). Rainfall also tends to be seasonal, falling primarily during the summer months (Fig. 3.1; Bureau of Meteorology 1997). Consequently, in this region, sugar gliders experience relatively pronounced seasonal changes in both T_a and rainfall. Measurements of daily field metabolic rates showed no seasonal change, however, data were extremely limited during autumn and winter (Quin 1993). Therefore, it is unresolved whether this marsupial species does adjust its thermal physiology to cope with these seasonal changes in climate and, if it does, which variables, both physiological and behavioural, are altered.

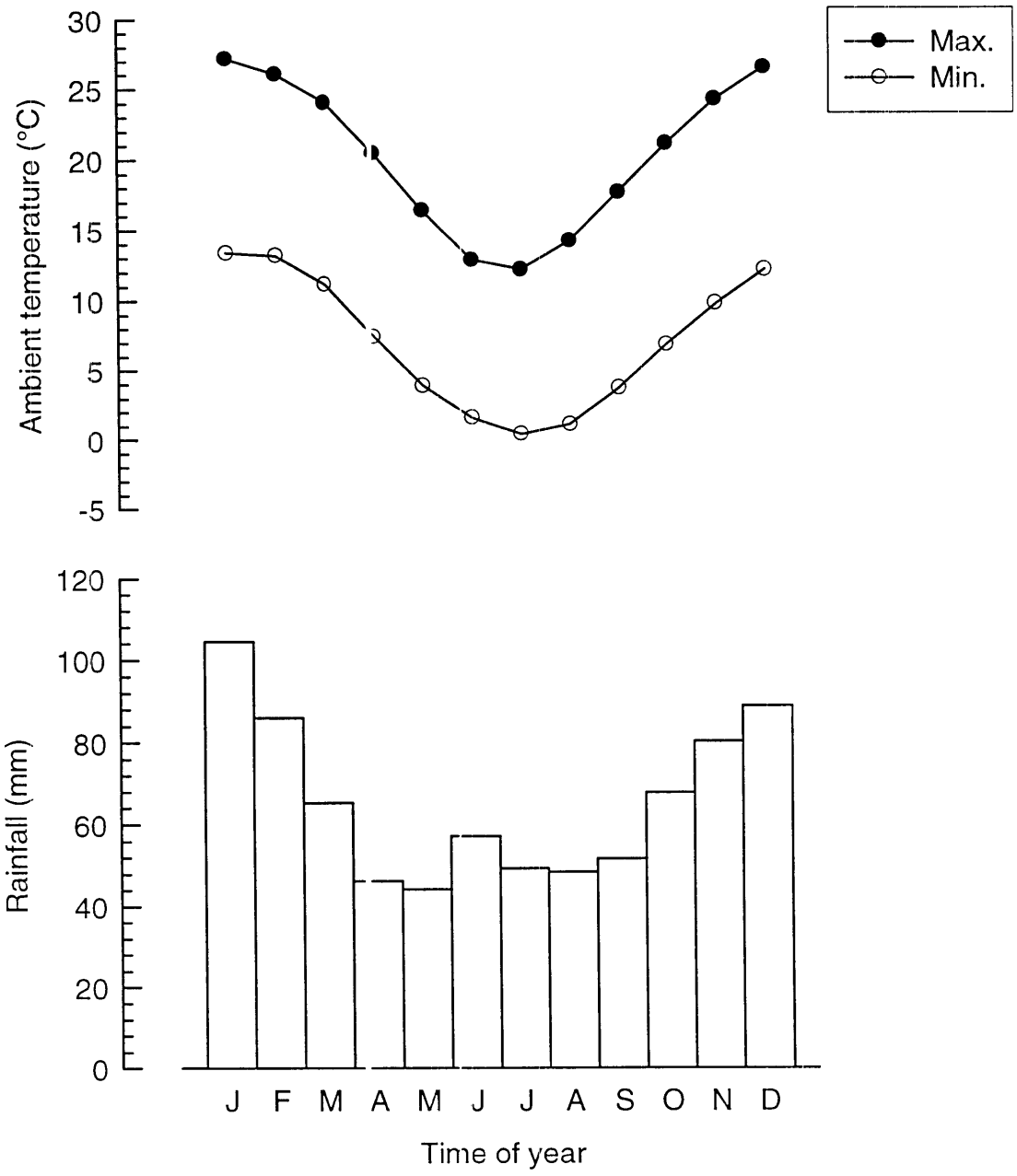


Fig. 3.1. Average monthly minimum and maximum ambient temperatures, and rainfall for Armidale, NSW. Data from the Bureau of Meteorology, Australia, 1997.

3.2 Materials and Methods:

Measurements of body mass, metabolic rates, T_b, conductance, activity and food consumption, and CAT scans were all performed according to the procedures outlined in Chapter 2.

All animals used for the calculation of mass, metabolism, T_b, conductance and CAT scans had obtained an average mass of ≥140 g (males) and ≥115 g (females) and were, therefore, considered to be adults (Suckling 1995). No female was included that was known to be either pregnant or lactating.

It is already known that sugar gliders are sexually dimorphic with regards to their body mass (Suckling 1995), and this was also true for the animals in the present study ($p=0.049$; Fig. 3.2). However, when all other data were analysed for differences due to gender, no significant differences were observed. Therefore, all data were pooled, with the exception of body mass, for the analyses.

3.3 Results:

3.3.1 Body mass:

Body mass of *P. breviceps* displayed distinct seasonal fluctuations, with animals of both sexes displaying the same response to the time of the year (Fig. 3.2). Each year body mass peaked during the months of May and June (June 1995: males 157.5±3.5 g, N=2, females 154.0±18.7 g, N=3; May 1996: males 166.2±7.1 g, N=5, females 150.9±13.7 g, N=7), which was followed by a pronounced decrease to a minimum during August-September (August 1995: males 132.8 g, N=1, females 119.3 ± 5.1 g, N=3; September 1996: males 146.0±14.6 g, N=5, females 133.2± 10.0 g, N=6). As the animals were only included in the

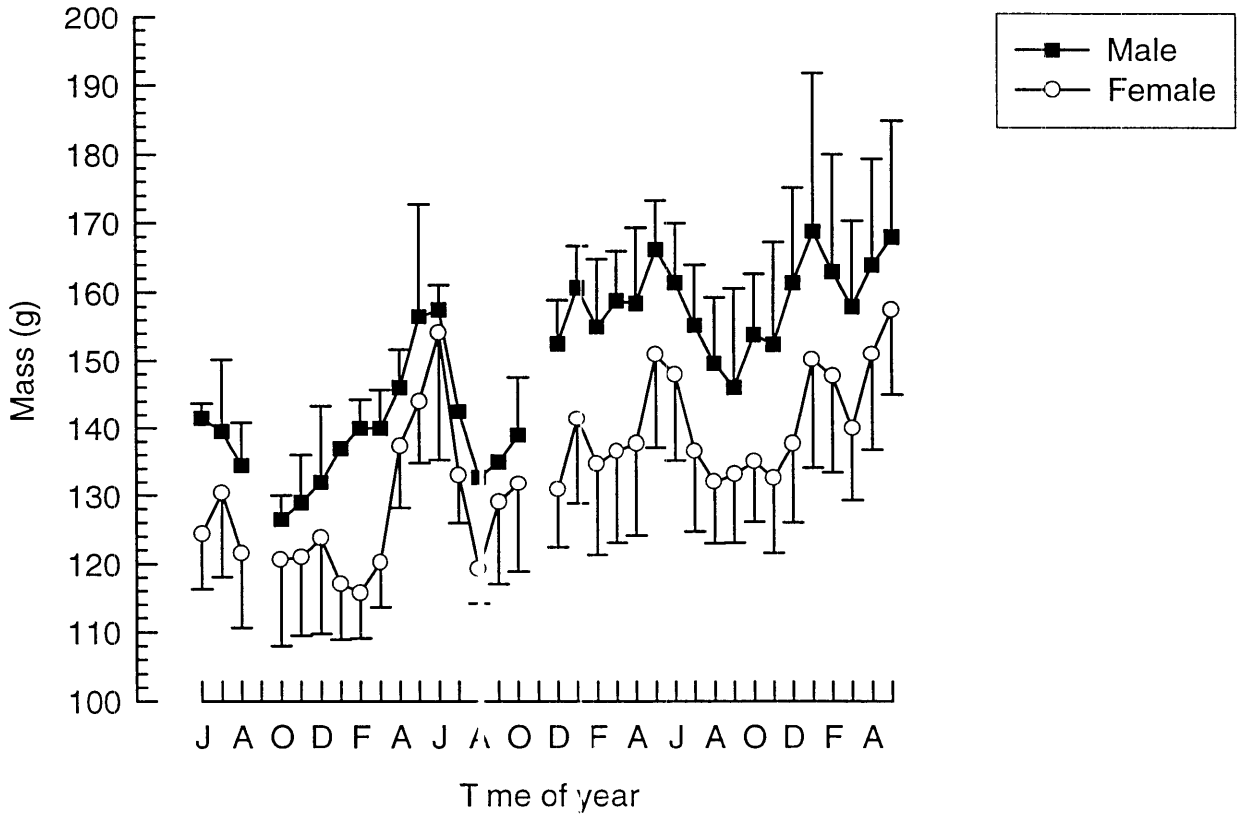


Fig. 3.2. Mean (±SD) body mass of adult male and female *P. breviceps* from June 1994 to May 1997.

estimates of monthly masses after they had attained the average mass for adult gliders, this decrease in mass was not due to the inclusion of smaller, juvenile animals. A smaller increase in mass occurred during early summer, which became more pronounced each consecutive year, followed by a subsequent decrease in February-March. When data were statistically analysed for April 1996-March 1997, the time when continuous data on a large sample size was available, a significant time effect on the body mass of the five male and five female *P. breviceps* over the course of the year was evident (males: $F=4.72$ DF 11, 44 $p<0.001$; females: $F=6.68$ DF 11, 44 $p<0.001$, repeated measures ANOVA). While there was no significant linear effect ($p>0.05$), a significant inverse parabolic effect was observed ($p<0.05$) indicating that the mass of the animals was greater in May/June than at other times of the year.

Although no linear effect was observed from April 96-March 97, it is evident that there was a significant increase in mean body mass during the course of the study. As sugar gliders are predisposed towards obesity when kept in captivity (Dunn 1982), this was most probably due to the effect of feeding these animals *ad lib.*, and not due to continued growth of the animals throughout their lives. The reason for the excess food was twofold: i) to determine if there were any seasonal changes in the amount of food consumed, and, more importantly, ii) to ensure that all animals, especially the subordinates of the groups, obtained a sufficient quantity of food to maintain their body mass. Despite the excess amount of food provided, the mass of a few individuals remained near average and did not display any significant increase. However, others, in particular those caught as juveniles or born in captivity, continued to increase their mass markedly, as is witnessed by the increase in standard deviation throughout the course of the study (Fig. 3.2).

3.3.2 Metabolism:

All individuals that did not enter torpor displayed a similar general metabolic pattern while in the respirometry chamber for approximately one day (Fig. 3.3). After being placed within the chamber in the late afternoon animals usually showed an initial short period of restlessness before they settled down. Once the light switched off the animal became active and metabolic rate displayed a sudden increase with marked fluctuations. Generally, the animal remained active throughout the night, though there could be short periods of rest. Concurrent with the light coming on, the animal ceased its activity, indicated by a sudden decrease in metabolic rate, and once more became settled. In some animals, the metabolic rate in the early morning undershot RMR for a short period of time before increasing to a stable level. RMR of the day following the night of activity were generally lower than those exhibited during the previous afternoon, which were most probably slightly elevated because the animal was still agitated after being handled. Values measured in the morning were, therefore, used to determine the animal's RMR. The animal generally remained at rest for the entire photophase until it was removed from the chamber later that afternoon, though there were sometimes short bursts of activity.

3.3.2.1 Resting metabolism:

3.3.2.1.1 Basal metabolic rate:

Basal metabolic rates (BMR) were obtained in postabsorptive, normothermic adult gliders by gradually altering T_a during the photophase (eg. Fig. 3.4). Metabolism decreased with increasing T_a until it reached a minimum value, whereupon it started to increase. BMR was determined as the minimal metabolic rate during these measurements.

The mean BMR differed among seasons (Fig. 3.5; F=4.00 DF 3, 46 p=0.013, ANOVA). The mean BMR of 0.511±0.068 $ml\ g^{-1}\ h^{-1}$ measured in winter was 15 % less than that in

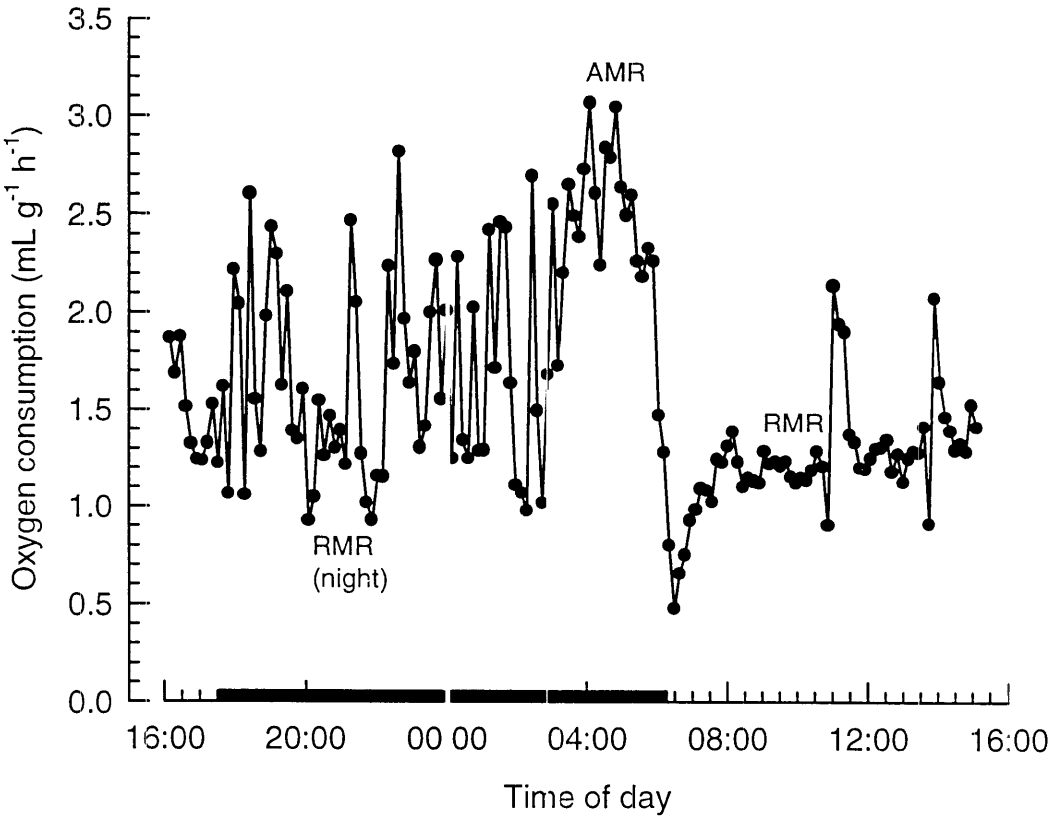


Fig. 3.3. Example of a metabolic trace for an individual *P. breviceps* (Pb15) at ambient temperature (T_a) 10 °C during winter. Food and water were not available. Dark bar indicates night; RMR = resting metabolic rate; AMR = active metabolic rate.

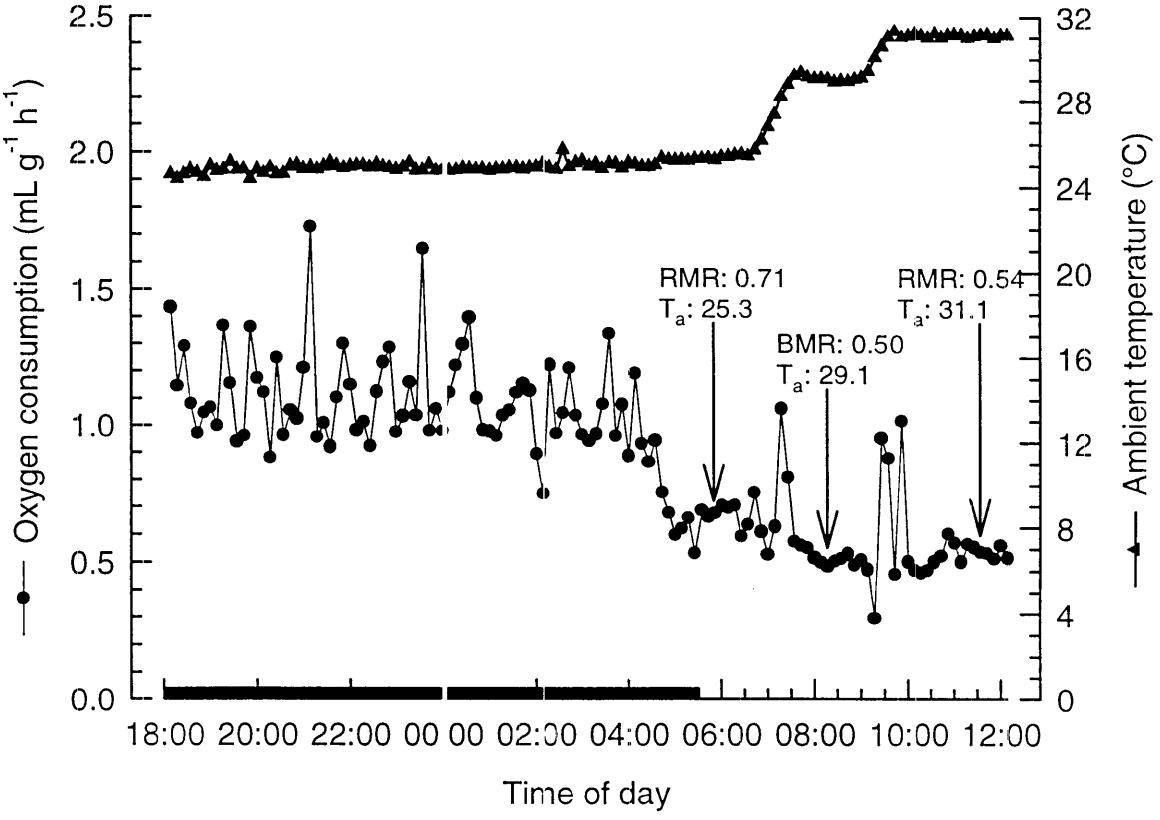


Fig. 3.4. Example of a metabolic trace used to obtain basal metabolic rate (BMR) for an individual *P. breviceps* (Pb4) during spring. Food and water were not available. Dark bar indicates night; RMR = resting metabolic rate.

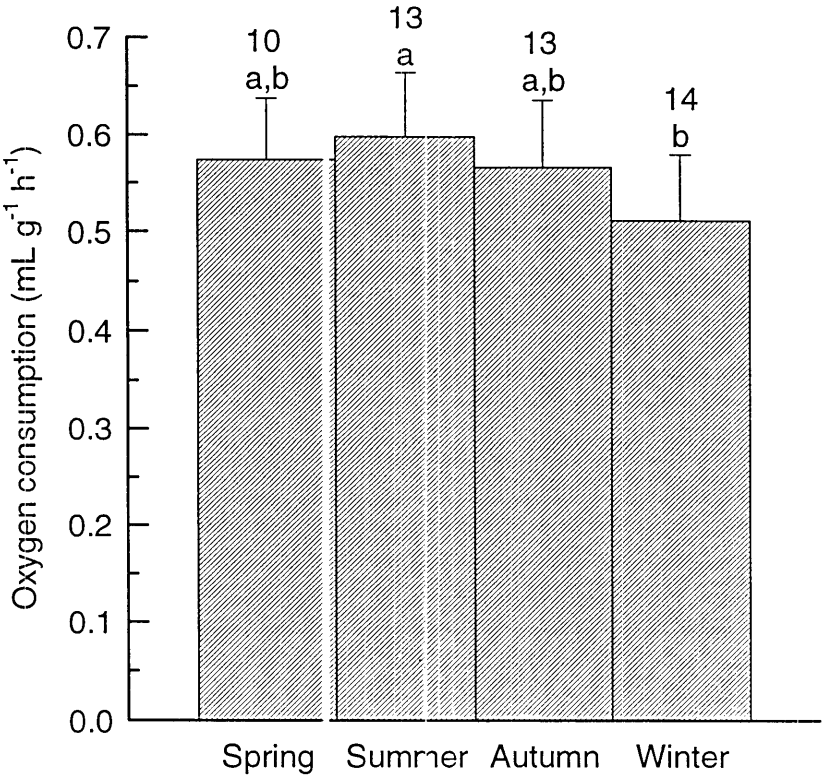


Fig. 3.5. Mean (±SD) basal metabolic rate (BMR) for *P. breviceps* during each season. Numbers indicate number of individuals; different letters indicate significant differences ($p<0.05$) between seasons.

summer (0.598±0.066 mL g^{-1} h^{-1}). This difference was significant ($p<0.01$, Tukey). However, neither winter nor summer BMR were significantly different from the mean BMR during autumn (0.566±0.069 mL g^{-1} h^{-1}) or spring (0.574±0.063 mL g^{-1} h^{-1}).

These seasonal differences in BMR may partially be explained by differences in body mass. Mean body mass of animals used for BMR measurements in each season displayed a more or less inverse change to that of mean BMR in different seasons (Fig. 3.5 *cf.* Fig. 3.6). Whereas the minimum BMR value occurred in winter, which was followed in increasing order by autumn, spring and summer values, the minimum mean body mass occurred in summer (127.7±12.7 g) followed in increasing order by spring (129.9±15.1 g), winter (134.4±17.0 g) and autumn (136.9±13.7 g). However, these mean masses were not significantly different from each other ($F=1.03$ DF 3,46 $p=0.387$, ANOVA), most likely because of the large variability in body mass between individuals.

When all seasons were combined, absolute BMR (mL O_2 h^{-1}) was positively correlated with body mass (Fig. 3.7; $y=27.7+(.349x$, $p<0.001$, $r^2=0.24$). However, the elevations of the regression equations differed when the seasons were treated separately (Fig. 3.7, Table 3.1; $F=3.72$ DF 3, 45 $p=0.018$, ANCOVA). Elevations for winter BMR were significantly lower than the other three seasons ($p<0.05$, Tukey), although both the winter and autumn regressions were not quite significant ($p=0.074$ and $p=0.075$, respectively). The slope and elevation for the regression equations for spring, summer and autumn were indistinguishable ($p>0.05$, Tukey).

The mass-specific BMR (mL O_2 g^{-1} h^{-1}) was inversely related to body mass (Fig. 3.8; $y=0.762-0.0015x$, $p=0.029$, $r^2=0.10$). When seasons were treated separately, however, mass-specific BMR and body mass were no longer correlated (Table 3.2). Once again it is obvious that there is a great deal of variability in the body mass of individuals, as witnessed by the low r^2 values and the large amount of scatter (Figs. 3.7; 3.8). While for each season the body mass during BMR covered the entire range, from approximately 120-160 g, it is

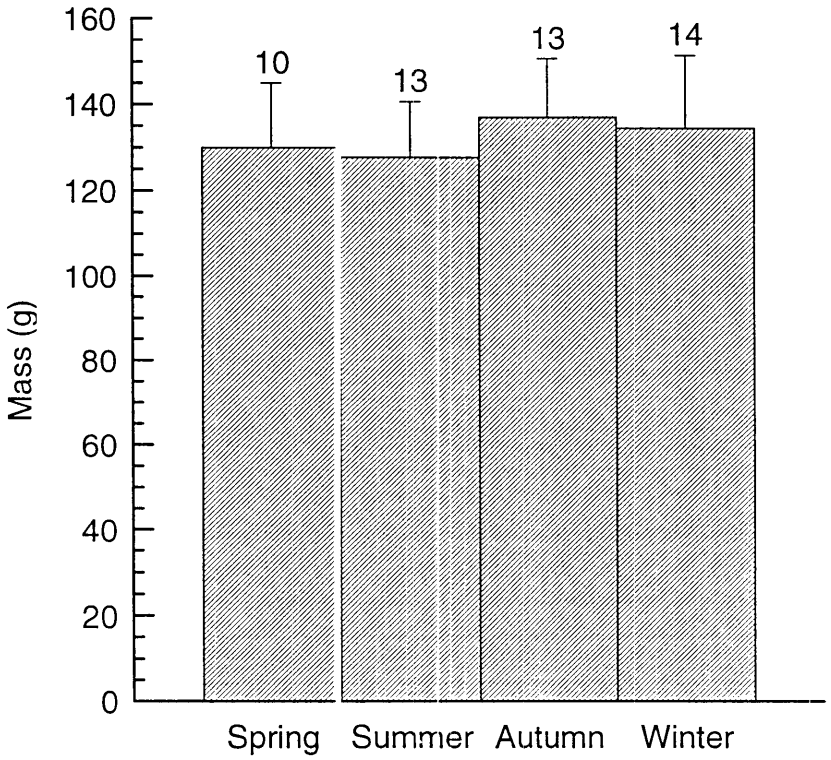


Fig. 3.6. Mean (±SD) body mass of *P. breviceps* for each season during basal metabolic rate (BMR) measurements. Numbers indicate number of individuals. No significant differences were observed in mean body mass (F=1.03 DF 3, 46 p=0.39, ANOVA).

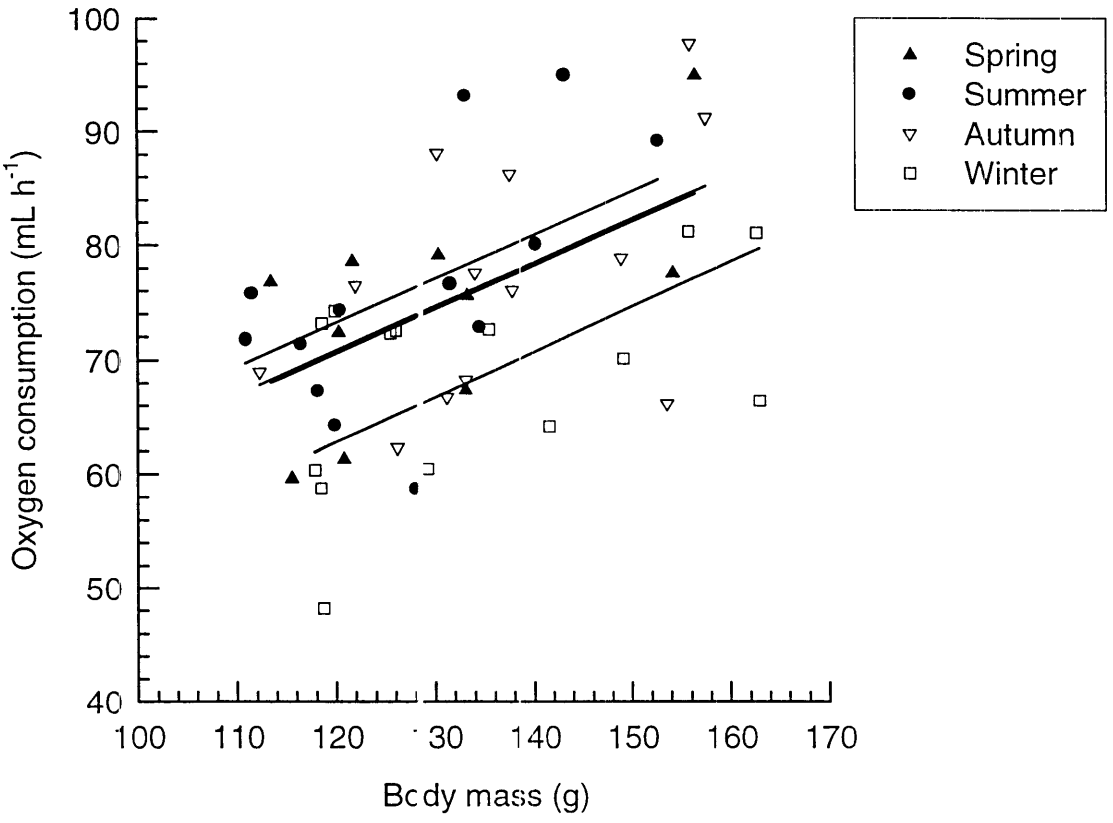


Fig. 3.7. Relationship between absolute basal metabolic rate (BMR) and body mass for *P. breviceps* during each season. Regression equations are listed below in Table 3.1. The regression equation for animals during winter was significantly lower than those during the other seasons ($F=3.72$ DF 3, 45 $p=0.018$, ANCOVA; $p<0.05$, Tukey).

Table 3.1 Regression equations for absolute BMR (mL h^{-1}) against body mass (g) of *P. breviceps* during each season (p and r^2 values are from original equations before computation of common slope equations and the pooled $r^2=0.30$; N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 24.53+0.384x	10	10	0.044	0.42
Summer	y = 27.22+0.384x	13	13	0.021	0.40
Autumn	y = 24.79+0.384x	13	13	0.075	0.26
Winter	y = 16.70+0.384x	14	14	0.074	0.24

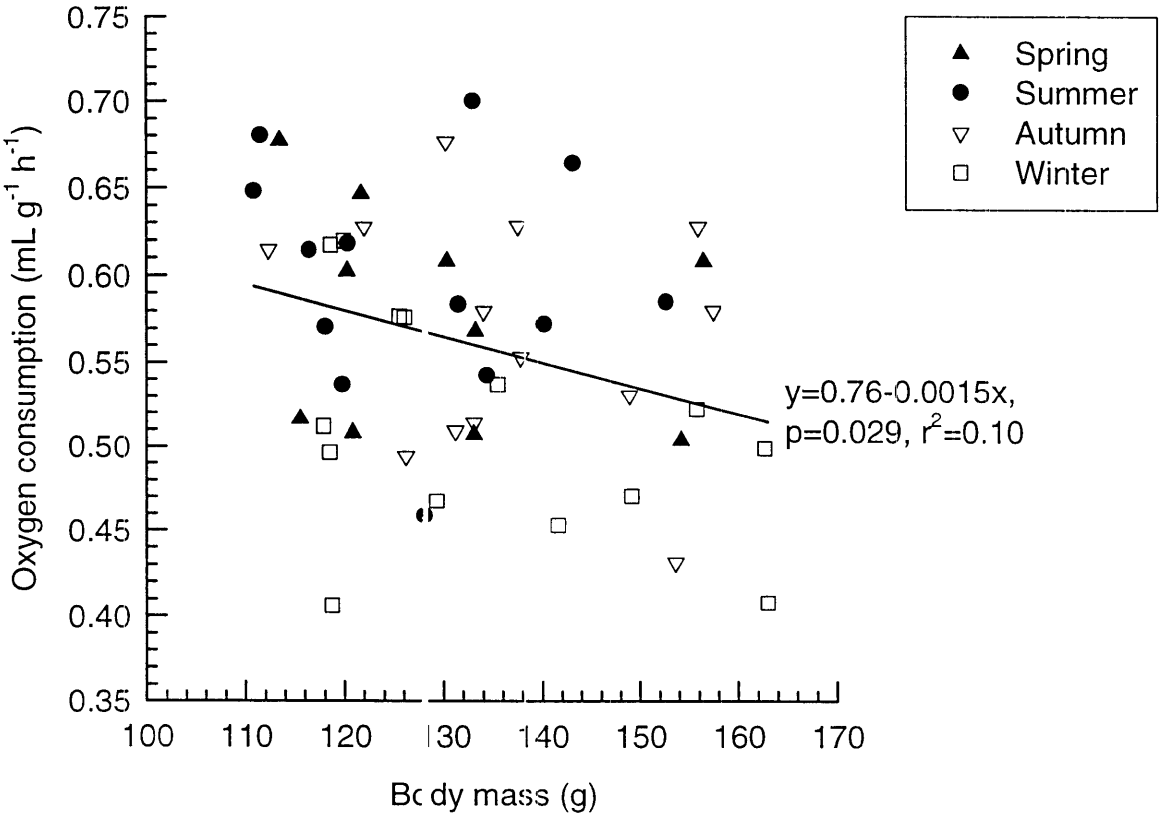


Fig. 3.8. Relationship between mass-specific basal metabolic rate (BMR) and body mass for *P. breviceps* during each season. A common regression line was calculated as no seasonal differences were detected Individual regression equations are listed below in Table 3.2.

Table 3.2 Regression equations for mass-specific BMR (mL g^{-1} h^{-1}) against body mass (g) for *P. breviceps* during each season (N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 0.713-0.0011x	10	10	0.481	0.06
Summer	y = 0.683-0.0007x	13	13	0.673	0.02
Autumn	y = 0.736-0.0012x	13	13	0.417	0.06
Winter	y = 0.762-0.0015x	14	14	0.136	0.18

evident that the majority of animals measured during spring and summer were less than 135 g, whereas during winter and autumn the masses were more evenly distributed.

3.3.2.1.2 Thermoneutral zone:

The mean T_{lc} did not differ among seasons (Table 3.3; F=1.12 DF 3, 42 p=0.353, ANOVA), and the lowest T_{lc} (winter) was only 1.0 °C below the highest T_{lc} (summer). In contrast, the T_{uc} showed significant seasonal differences (F=4.22 DF 3, 25 p=0.015, ANOVA). In winter the T_{uc} of 28.3±1.6 °C was the lowest value observed while the highest T_{uc} of 30.8±1.2 °C was measured in spring (Table 3.3), and the 2.5 °C difference between these two T_{uc} was significant (p<0.01, Tukey). The spring and winter T_{uc} were indistinguishable from those of autumn and summer (p>0.05, Tukey).

Although the T_{uc} differed among seasons, the TNZ ranges did not differ (Table 3.3; F=2.79 DF 3, 25 p=0.062, ANOVA), most probably due to the variance around each critical temperature. The overall mean TNZ range was 2.5±1.5 °C.

3.3.2.1.3 Resting metabolic rate:

The metabolic response of resting animals over a range of T_a during the diurnal phase followed the same pattern as seen in many other endothermic species. A distinct TNZ was bordered at both lower and higher T_a by increasing metabolic rates (Fig. 3.9).

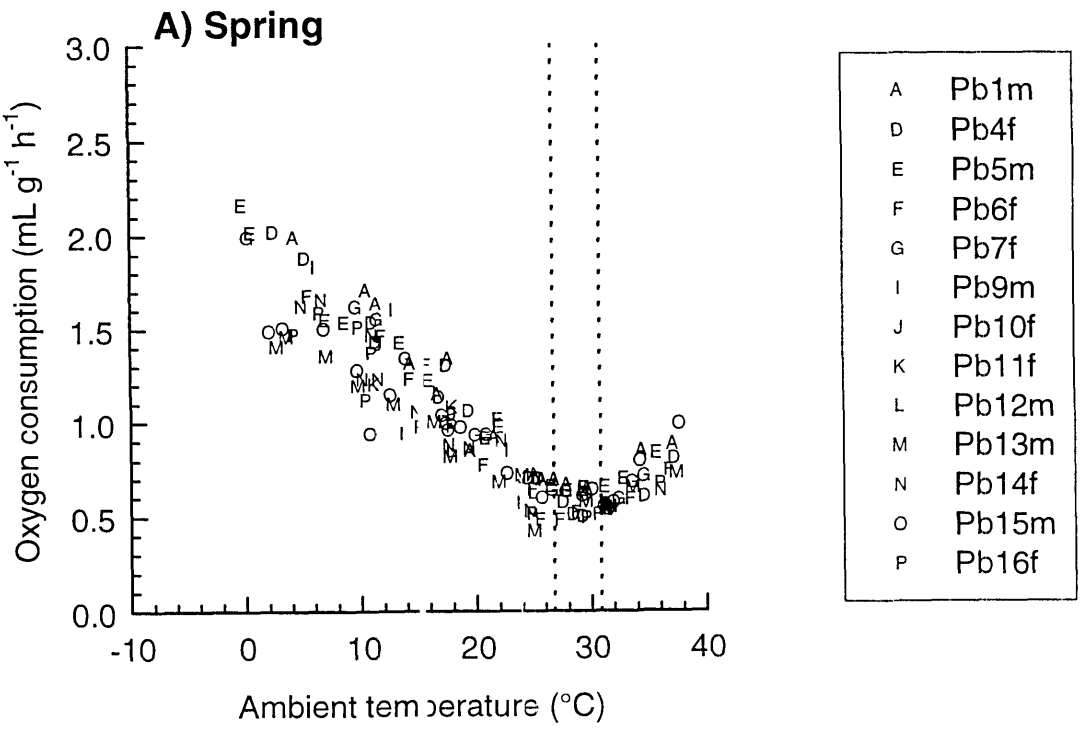
i) Below the TNZ:

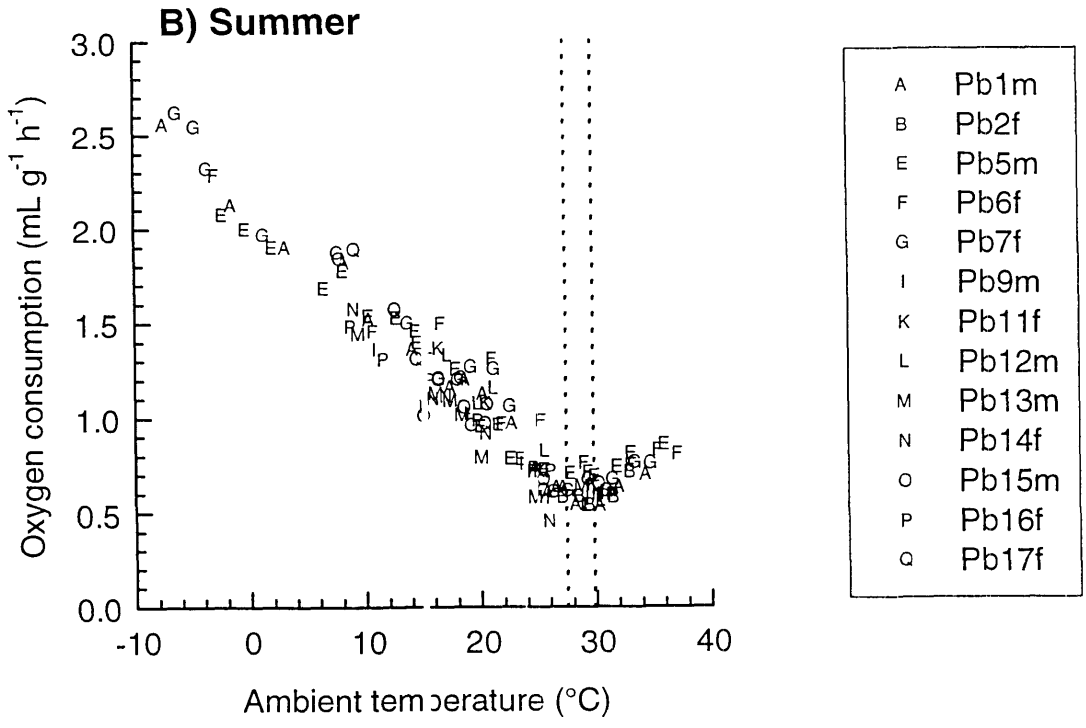
Below the T_{lc}, the RMR showed an inverse linear response to the decreasing T_a (Figs. 3.9; 3.10). There was no significant seasonal difference to the animals' response to the change in T_a (i.e. slope; Fig. 3.10; Table 3.4; F=1.76 DF 3, 397 p=0.154, ANCOVA), and a 10 °C drop in T_a elicited, on average, an increase of 0.512 mL g^{-1} h^{-1} in metabolic rate in all

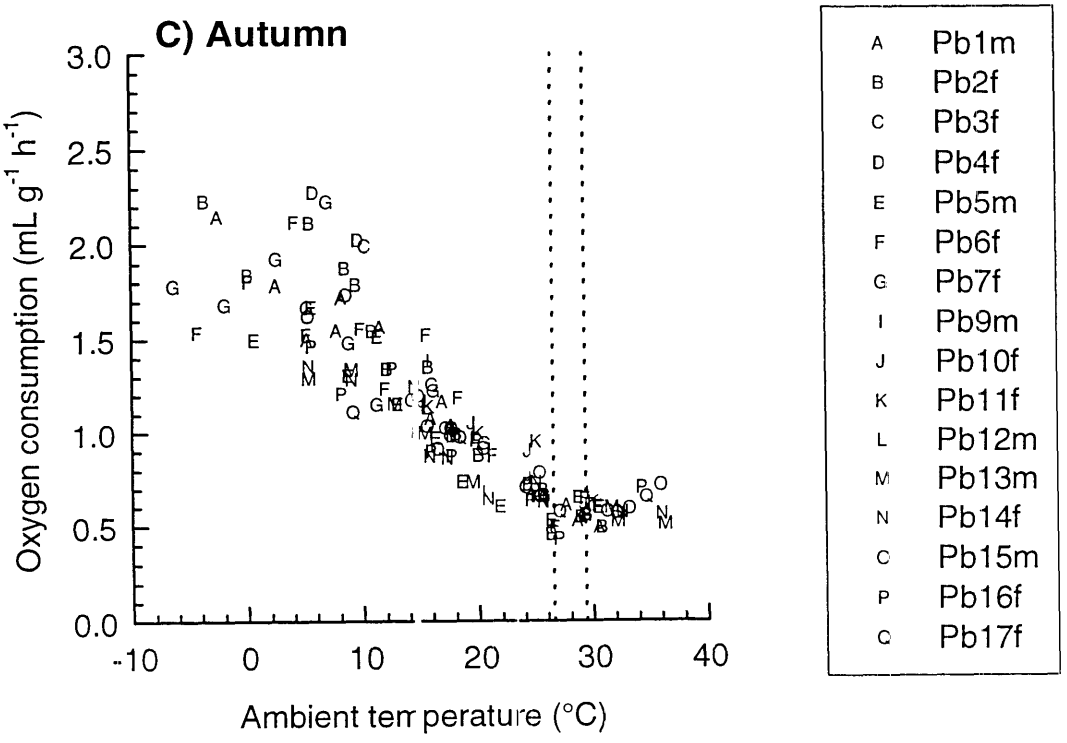
Table 3.3 Mean (±SD) lower critical (T_{lc}) and upper critical (T_{uc}) temperatures for *P. breviceps* during each season (N = number of individuals). Results from ANOVA tests for differences between seasons are shown below.

Season	T_{lc} (°C)	N	T_{uc} (°C)	N
Spring	26.94 ± 1.40	10	30.80 ± 1.20	6
Summer	27.40 ± 1.65	12	29.76 ± 0.93	8
Autumn	26.49 ± 1.22	10	29.33 ± 1.42	7
Winter	26.42 ± 1.62	14	28.31 ± 1.62	8
	F=1.12 DF 3, 42 p=0.353		F=4.22 DF 3, 25 p=0.015	

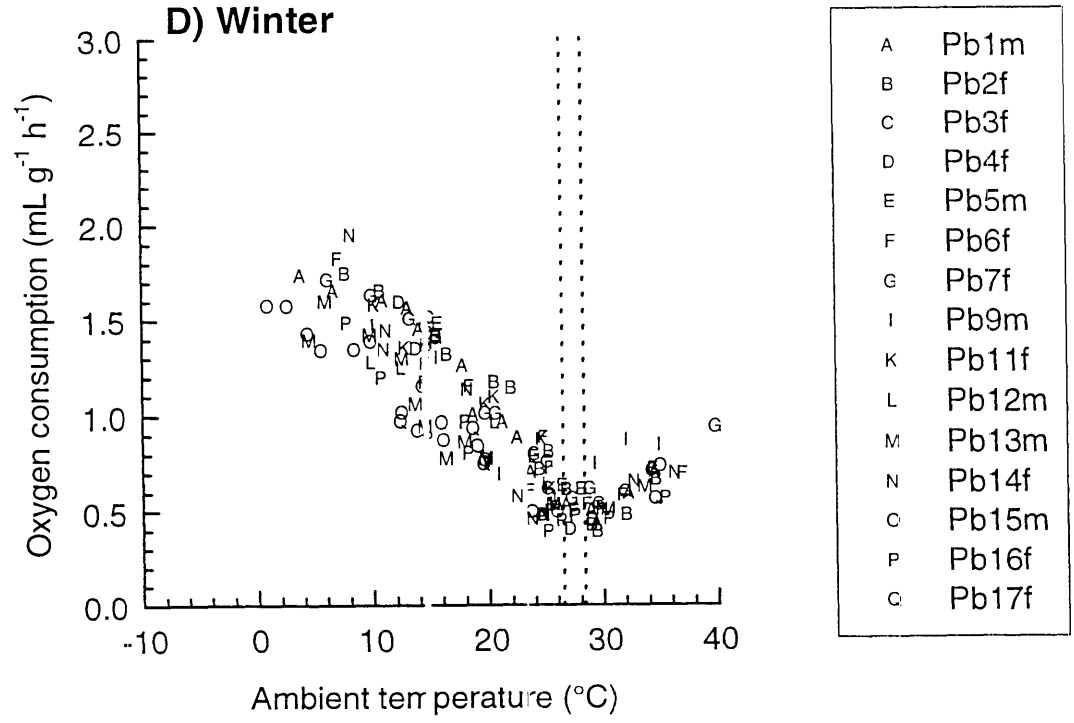
Fig. 3.9. (On following pages) Resting metabolic rates (RMR) over entire range of ambient temperatures (T_a) measured for individual *P. breviceps* during **A)** spring, **B)** summer, **C)** autumn and **D)** winter. Dashed lines represent region of thermoneutral zone (TNZ); 'm' and 'f' within legend indicate male or female gliders, respectively.


A) Spring
Oxygen consumption (mL g-1 h-1)
Ambient temperature (°C)
A Pb1m
D Pb4f
E Pb5m
F Pb6f
G Pb7f
I Pb9m
J Pb10f
K Pb11f
L Pb12m
M Pb13m
N Pb14f
O Pb15m
P Pb16f


B) Summer
Oxygen consumption (mL g-1 h-1)
Ambient temperature (°C)
A Pb1m
B Pb2f
E Pb5m
F Pb6f
G Pb7f
I Pb9m
K Pb11f
L Pb12m
M Pb13m
N Pb14f
O Pb15m
P Pb16f
Q Pb17f


C) Autumn
Oxygen consumption (mL g-1 h-1)
Ambient temperature (°C)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-10
0
10
20
30
40
A Pb1m
B Pb2f
C Pb3f
D Pb4f
E Pb5m
F Pb6f
G Pb7f
I Pb9m
J Pb10f
K Pb11f
L Pb12m
M Pb13m
N Pb14f
O Pb15m
P Pb16f
Q Pb17f

Winter


D) Winter
Oxygen consumption (mL g-1 h-1)
Ambient temperature (°C)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-10
0
10
20
30
40
A Pb1m
B Pb2f
C Pb3f
D Pb4f
E Pb5m
F Pb6f
G Pb7f
I Pb9m
K Pb11f
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M Pb13m
N Pb14f
O Pb15m
P Pb16f
Q Pb17f

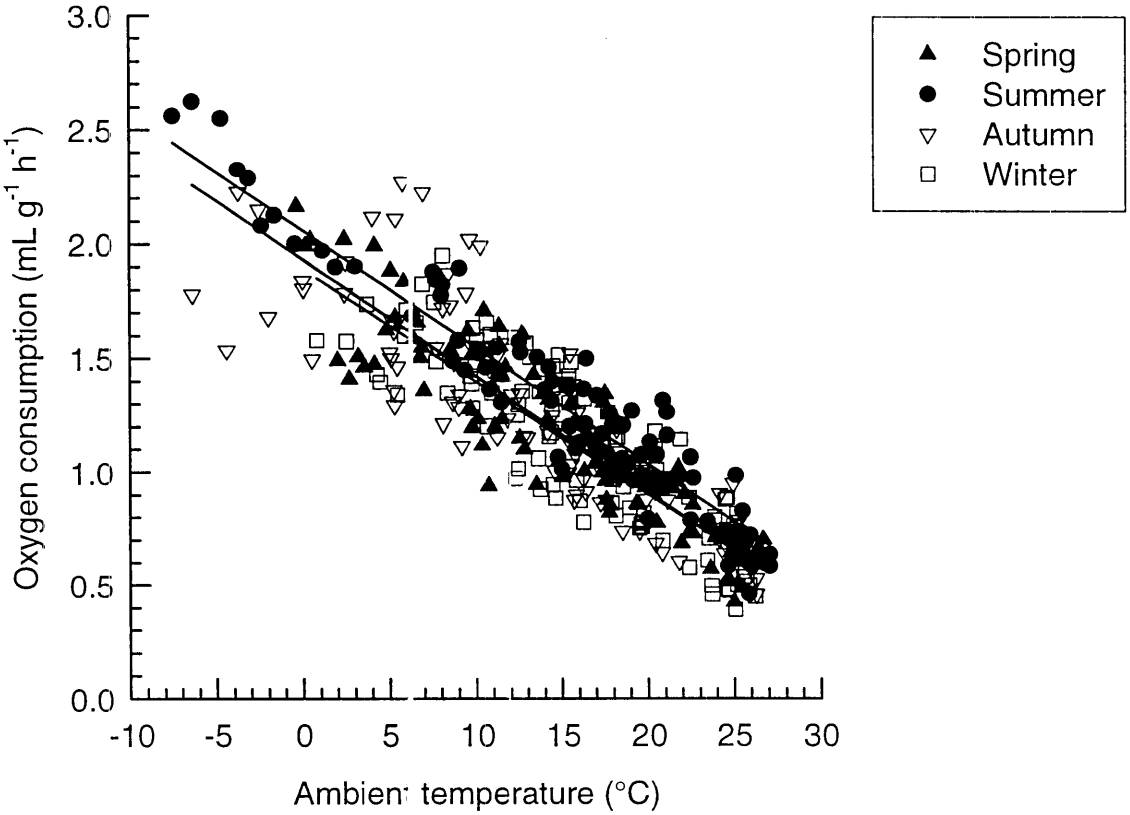


Fig. 3.10. Resting metabolic rates (RMR) for *P. breviceps* below the lower critical temperature (T_{lc}) during each season. Regression equations are listed below in Table 3.4. The regression equation for animals during summer was significantly higher than those during the other three seasons (F= 1.76 DF 3, 400 p<0.001, ANCOVA; p<0.01, Tukey).

Table 3.4 Regression equations for RMR (mL g^{-1} h^{-1}) versus T_a (°C) of *P. breviceps* below T_{lc} during each season (p and r^2 values are from original equations before computation of common slope equations; pooled r^2=0.82; N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 1.932-0.051x	13	101	< 0.001	0.83
Summer	y = 2.061-0.051x	13	92	< 0.001	0.93
Autumn	y = 1.934-0.051x	16	105	< 0.001	0.75
Winter	y = 1.936-0.051x	15	107	< 0.001	0.76

seasons. However, the elevation of RMR as a function of T_a differed ($F=11.76$ DF 3, 400 $p<0.001$, ANCOVA). Summer RMR below the T_{lc} were significantly higher than those in spring, autumn and winter (Fig. 3.10, Table 3.4; $p<0.01$, Tukey), but spring, autumn and winter RMR did not differ ($p>0.05$, Tukey). It should be noted that RMR during summer and, to a lesser extent, spring had a tighter fit around the regression lines ($r^2=0.93$ and 0.83, respectively) than those during autumn ($r^2=0.75$) and winter ($r^2=0.76$). At a T_a of 15 °C, a T_a that is likely to be encountered in all seasons, summer RMR derived from the regression line was over 10 % higher than those during spring, autumn and winter. Extrapolation of the regression equations resulted in intercepts of the abscissa at 37.88, 40.41, 37.92 and 37.96 °C for spring, summer, autumn and winter, respectively.

Animals at T_a below the T_{lc} usually remained curled up in a ball, with the head, limbs and patagium tucked under the body and the head covered by the tail. As the T_a decreased this "ball" posture appeared to get tighter, and was accompanied by occasional bouts of shivering. RMR were noticeably easier to obtain at T_a below 10 °C and above 25 °C, where the animals appeared to be more settled, than at T_a around 15 °C.

ii) Above the TNZ:

Above the T_{uc}, throughout the T_a range that was measured, RMR increased linearly (Figs. 3.9, 3.11). As for RMR below the T_{lc}, the slope of RMR above the T_{uc} showed no significant seasonal response to the change in T_a (Fig. 3.11, Table 3.5; $F=1.64$ DF 3,86 $p=0.186$, ANCOVA). However, the elevations of the regression equations for RMR above T_{uc} were significantly different ($F=3.68$ DF 3, 89 $p=0.015$, ANCOVA). Summer RMR were significantly higher than those in spring or winter (Fig. 3.11, Table 3.5; $p<0.05$, Tukey). The regression equation for autumn was not as strong ($p=0.042$) with a higher degree of scatter ($r^2=0.25$) than those for the other seasons and, therefore, the correlation between T_a and RMR may have disappeared when a new equation with a common slope was calculated. This was probably the reason why, despite being the furthest apart, the

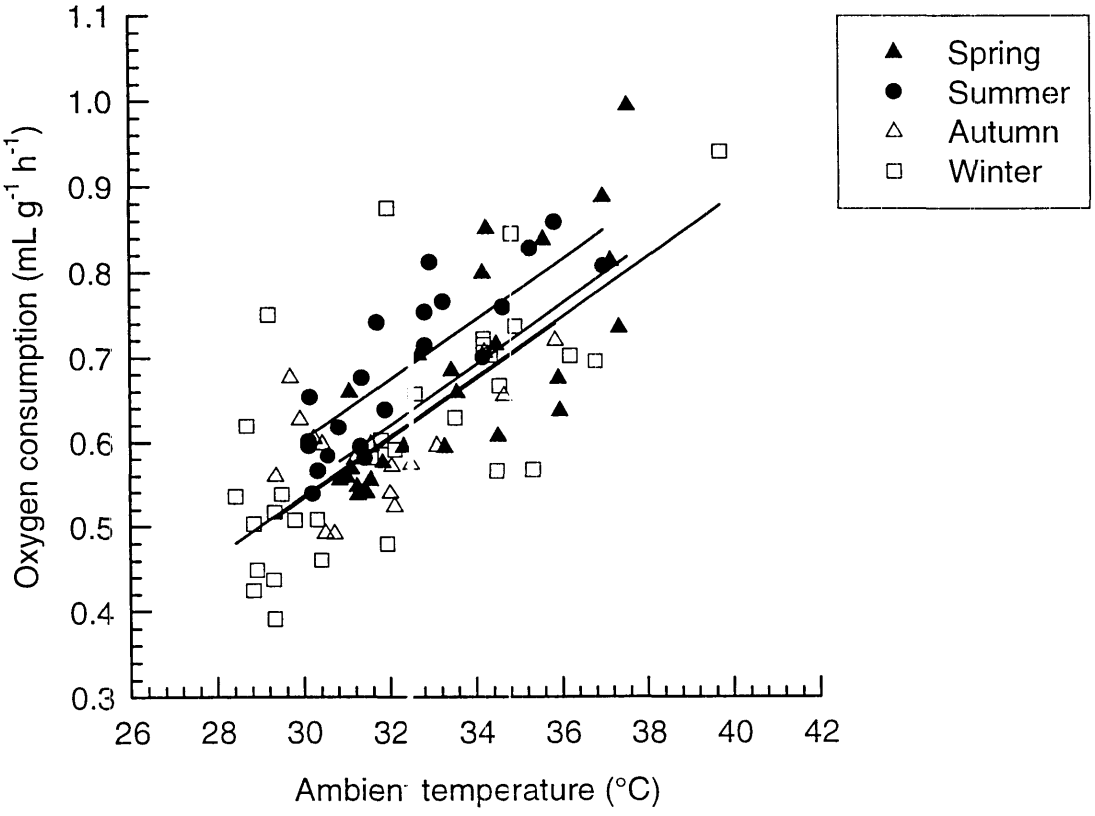


Fig. 3.11. Resting metabolic rates (RMR) for *P. breviceps* above the upper critical temperature (T_{uc}) during each season. Regression equations are listed below in Table 3.5. The elevation of the regression equation for animals during summer was significantly higher RMR than those during spring and winter ($F=3.68$ DF 3, 89 $p=0.015$, ANCOVA; $p<0.05$, Tukey).

Table 3.5 Regression equations for RMR (mL g^{-1} h^{-1}) versus T_a (°C) of *P. breviceps* above T_{uc} during each season (p and r^2 values are from original equations; pooled $r^2=0.54$; N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = -0.508 + 0.035x	10	25	< 0.001	0.63
Summer	y = -0.453 + 0.035x	10	21	< 0.001	0.74
Autumn	y = -0.523 + 0.035x	11	17	0.042	0.25
Winter	y = -0.520 + 0.035x	11	31	< 0.001	0.49

regression lines for autumn and summer were not significantly different from each other ($p>0.05$, Tukey).

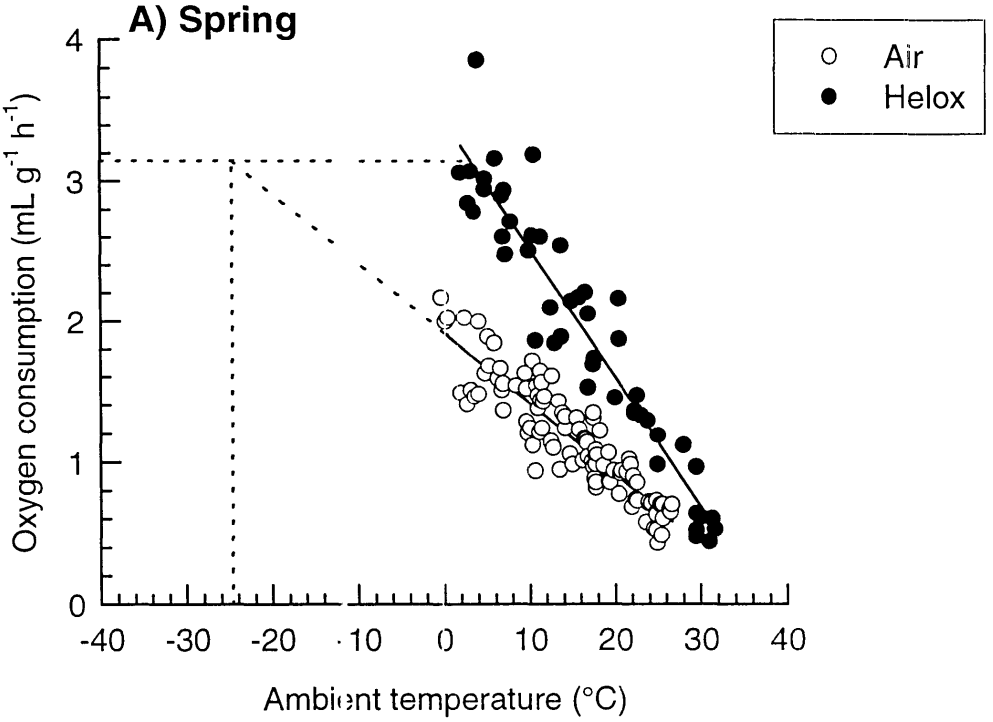
A comparison of the absolute slopes of RMR as a function of T_a above the T_{uc} and below the T_{lc} showed that they were similar during each season ($p>0.05$, Tukey). However, this is most likely because the maximum metabolic rates under heat stress were not measured to ensure the survival of the gliders. If higher T_a had been measured, RMR above the T_{uc} would have increased exponentially and a steeper slope should have been present. In these measurements, just the lower linear portion of that exponential curve is observed.

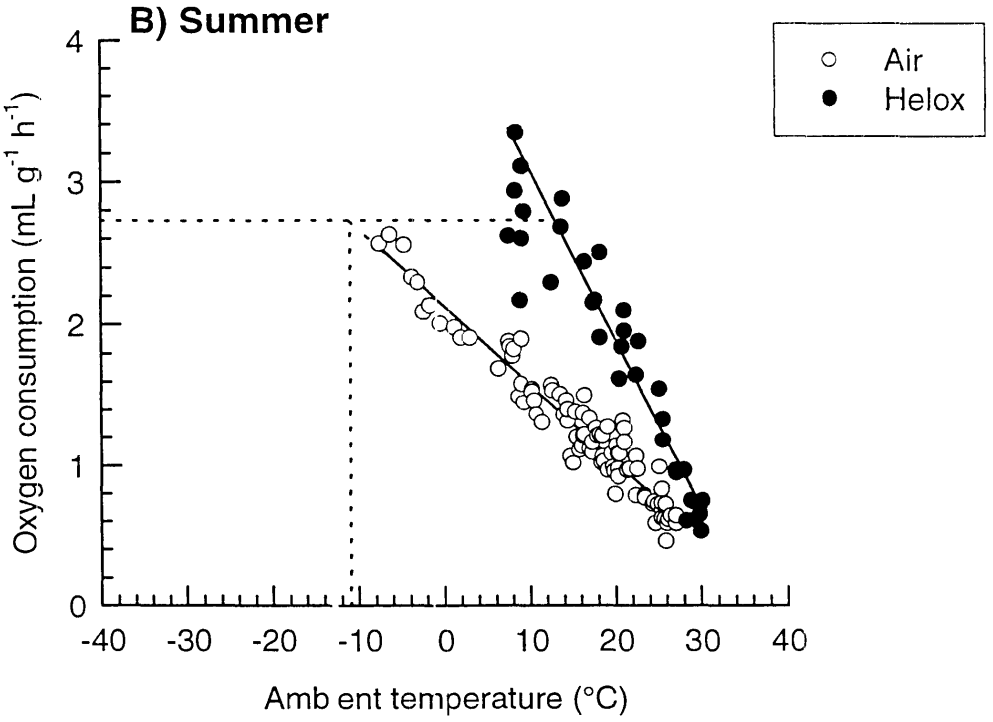
Animals at T_a above the T_{uc} lay sprawled on their back with their limbs extended above them. With this posture the patagium was also exposed. Animals were occasionally observed to lick their paws and wave them slowly in the air above them. The exposed parts of the animals (nose and pads) were noticeably darker pink in colouration than at lower T_a. Despite an animal surviving a T_a of approximately 39.5 °C for 1.5 h during winter, one animal died after 2 hours exposure to 37 °C (part of the time in helox, see Chapter 7) during autumn. When removed, this animal, and two others living individually in chambers at the same time, had wet faces indicating extensive salivation. It appeared that the animals most stressed by the excess heat were the heavier ones, and the heaviest animals were those in autumn.

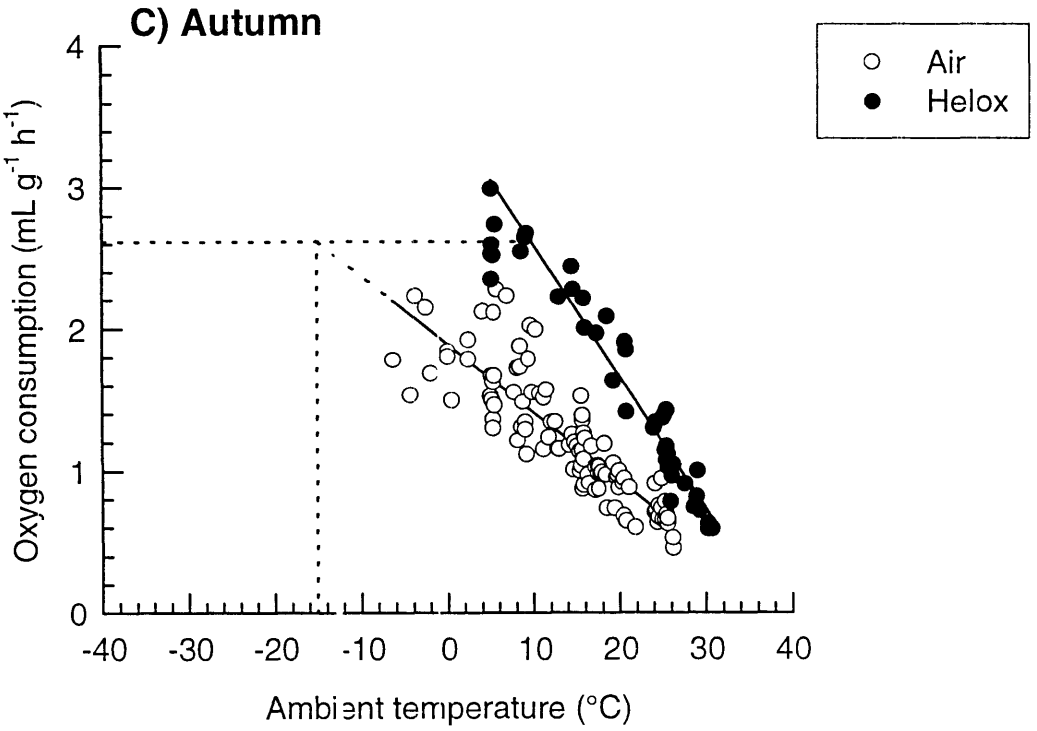
3.3.2.1.4 Maximum heat production:

The mean maximum metabolic rate attained by the animals under a helox atmosphere differed among seasons (Fig. 3.12; Table 3.6; $F=6.03$ DF 3, 21 $p=0.004$, ANOVA). Winter HP_{max} was significantly higher than that in summer and autumn ($p<0.05$, Tukey), but was similar to that in spring ($p>0.05$, Tukey). Spring HP_{max} was significantly higher than that in autumn ($p<0.05$, Tukey), but similar to HP_{max} in summer ($p>0.05$, Tukey). Summer and autumn values were also similar ($p>0.05$, Tukey). One animal in spring peaked with a

Fig. 3.12. (On following pages) Maximum metabolic rates (HP_{max}), measured in a helox atmosphere, for *P. breviceps* during **A)** spring, **B)** summer, **C)** autumn, and **D)** winter. Mean HP_{max} value (horizontal dashed line) was substituted into the regression line for resting metabolic rates (RMR) in air to determine the effective ambient temperature (T_a; vertical dashed line) the gliders can tolerate. Gliders had significantly higher metabolic rates in winter than animals in summer and autumn ($F=6.03$ DF 3, 21 $p=0.004$, ANOVA; $p<0.05$, Tukey). As a result gliders in winter could tolerate a lower effective T_a than those during summer and autumn ($F=9.41$ DF 3, 21 $p<0.001$, ANOVA; $p<0.05$, Tukey).


A) Spring
Air
Helox
Oxygen consumption (mL g-1 h-1)
0
1
2
3
4
-40
-30
-20
-10
0
10
20
30
40
Ambient temperature (°C)


B) Summer
Air
Helox
Oxygen consumption (mL g-1 h-1)
0
1
2
3
4
-40
-30
-20
-10
0
10
20
30
40
Amb ent temperature (°C)


C) Autumn
Air
Helox
Oxygen consumption (mL g-1 h-1)
0
1
2
3
4
-40
-30
-20
-10
0
10
20
30
40
Ambient temperature (°C)

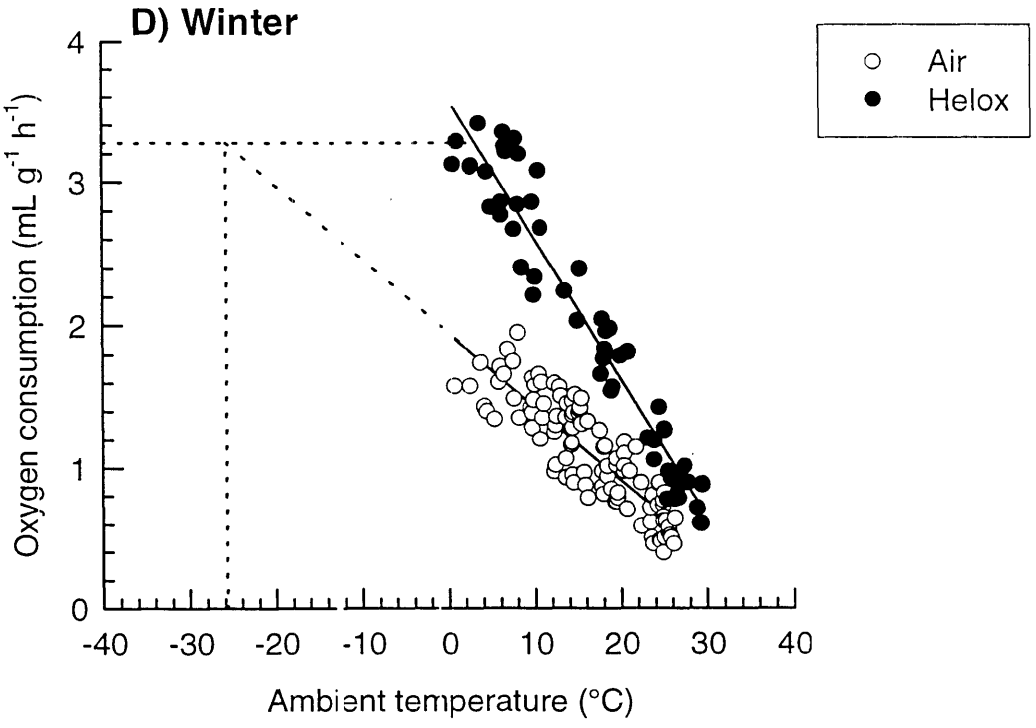

D) Winter
Air
Helox
Oxygen consumption (mL g-1 h-1)
0
1
2
3
4
-40
-30
-20
-10
0
10
20
30
40
Ambient temperature (°C)

Table 3.6 Mean (± SD) HP_{max} values, effective T_a cold limit and metabolic scope for *P. breviceps* during each season (N = number of individuals). Results from ANOVA tests for differences between seasons are shown below.

Season	HPmax ($mL\ g^{-1}\ h^{-1}$)	Ta (°C)	N	Metabolic Scope
Spring	3.144 ± 0.363	-24.69 ± 7.29	6	5.45 ± 0.32
Summer	2.272 ± 0.396	-11.02 ± 7.20	8	4.66 ± 0.96
Autumn	2.618 ± 0.219	-15.13 ± 4.57	6	4.81 ± 0.88
Winter	3.274 ± 0.115	-25.71 ± 2.23	5	6.38 ± 0.53
	F=6.03 DF 3, 21 p=0.004	F=9.41 DF 3, 21 p<0.001		F=6.14 DF 3, 21 p=0.004

maximum metabolic rate of 3.854 mL g^{-1} h^{-1}, but this animal was approximately 20 g lighter than the other animals (117 g *cf.* 139 g). When this animal was removed from the calculations, the mean HP_{max} for spring fell to 3.002 ± 0.118 mL g^{-1} h^{-1}, which was not significantly different from any of the other seasons.

The metabolic scope of a species is obtained by dividing the HP_{max} value by the BMR (Dawson & Dawson 1982). In *P. breviceps* the metabolic scope was substantially higher in winter compared to all other seasons (Table 3.6; F=6.14 DF 3, 21 p=0.004, ANOVA; p<0.01, Tukey), because BMR were low and HP_{max} were high. In fact, the metabolic scope of animals in winter (6.38±0.53) was approximately 37 % greater than those in summer (4.66±0.96).

The effective T_a at which HP_{max} occurred also differed among seasons (Fig. 3.12, Table 3.6; F=9.41 DF 3, 21 p<0.001, ANOVA). Animals in winter could tolerate significantly lower effective T_a (-25.7±2.2 °C) than those in autumn (-15.1±4.6 °C; p<0.05, Tukey) and summer (-11.0±7.2 °C; p<0.01, Tukey), but not those in spring (-24.7±7.3 °C; p>0.05, Tukey), while during spring animals could tolerate significantly lower effective T_a than those in summer (p<0.01, Tukey), but not those in autumn (p>0.05, Tukey). Autumn and summer animals were not significantly different from each other in their cold tolerance (p>0.05, Tukey). As above for HP_{max}, when the lighter animal was removed from spring values, the effective T_a at which HP_{max} occurred was raised to -21.8±2.4 °C for this season. However, this did not alter any of the significant differences found when the animal was included.

The effective range of T_a that gliders could tolerate, from the effective cold limit T_a to T_{uc}, was widest in spring (55.5 °C), followed closely by winter (54.0 °C). The ranges during autumn and summer were 10-15 °C narrower, with the range in autumn (44.5 °C) slightly wider than that during summer (40.8 °C). Obviously, the overall T_a range that sugar gliders

can tolerate is much wider than this, given that they can withstand T_a at least 7 °C above the T_{uc} in each season.

3.3.2.2 Active metabolism:

In all seasons a significant inverse linear relationship between T_a and metabolic rate during activity (AMR) below T_{lc} was observed (Fig. 3.13, Table 3.7). As was expected, AMR values were substantially (approximately two-fold) higher than RMR. During spring and summer the slopes of the AMR regression lines were not significantly different from those during RMR (spring: F=2.56 DF 1, 162 p=0.112; summer: F=0.28 DF 1, 148 p=0.596, ANCOVA), but there was a significant difference in the elevations (spring: F=951.8 DF 1, 163 p<0.001; summer: F=1456.3 DF 1, 149 p<0.001, ANCOVA) and AMR values were, on average, 1.26 mL g^{-1} h^{-1} higher than that for RMR in both seasons. The slopes for both autumn and winter regression equations were significantly steeper for AMR than for RMR (autumn: F=14.16 DF 1, 172 p<0.001; winter: F=5.54 DF 1, 182 p=0.02, ANCOVA).

Significant differences were found between AMR, as a function of T_a, during the different seasons (Fig. 3.13, Table 3.7). The slopes of the regression equations differed with season (F=4.29 DF 3, 267 p=0.006, ANCOVA), because in autumn AMR showed a significantly steeper increase with a reduction of T_a than in spring (Fig. 3.13, Table 3.7; p<0.01, Tukey). All other comparisons of slopes were not significantly different from each other. From examination of the residuals, it was noticeable that some individuals were fairly consistent in their level of activity, generally being either continuously above or below the regression equation during all seasons.

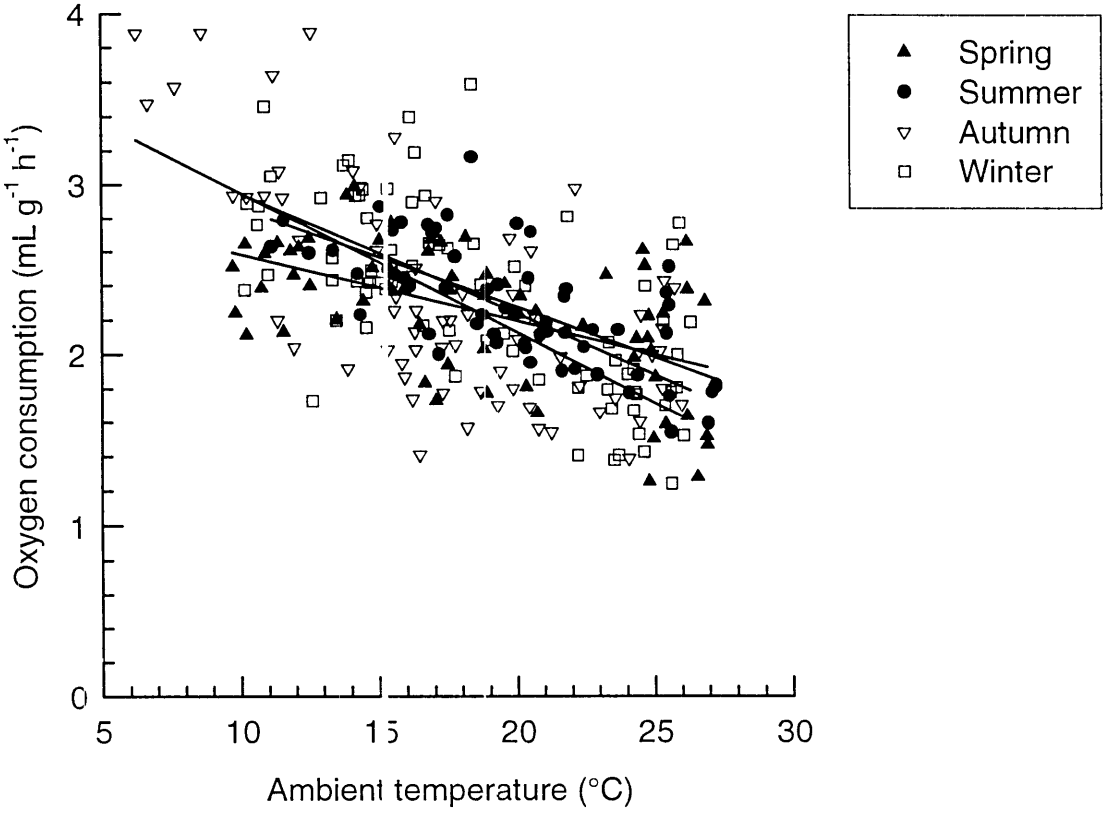


Fig. 3.13. Active metabolic rates (AMR) for *P. breviceps* at ambient temperatures (T_a) below the lower critical temperature (T_{lc}) during each season. Regression equations are listed below in Table 3.7. The slope of the regression line for gliders during autumn was steeper than that for animals during spring (F=4.29 DF 3, 267 p=0.006, ANCOVA; p<0.01, Tukey).

Table 3.7 Regression equations for AMR (mL g^{-1} h^{-1}) versus T_a (°C) of *P. breviceps* during each season (N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 2.98 - 0.039x	13	65	< 0.001	0.29
Summer	y = 3.45 - 0.059x	13	60	< 0.001	0.47
Autumn	y = 3.78 - 0.083x	16	71	< 0.001	0.44
Winter	y = 3.66 - 0.071x	15	79	< 0.001	0.43

3.3.2.3 Average daily metabolic rate:

As with RMR and AMR, ADMR, measured over approximately 23 hours, increased with decreasing T_a (Fig. 3.14, Table 3.8). The gliders' response to a decrease in T_a (i.e. slope) was the same in all seasons ($F=2.27$ DF 3, 138 $p=0.083$, ANCOVA), but there was a significant difference in the elevation of the ADMR at each T_a ($F=2.78$ DF 3, 141 $p=0.043$, ANCOVA). However, when a common slope was calculated, no such difference was detected using the Tukey test, presumably due to the high level of scatter about the regression lines, and it can only be assumed that the two extremes of ADMR regression lines, spring (the lowest) and autumn (the highest), were different from one another.

3.3.2.3.1 Total metabolic rate:

When metabolic rates were totalled and adjusted to a 24 hour period for comparison, total metabolic rate also increased linearly with a decreasing T_a (Fig. 3.15). However, there were no seasonal differences in the slopes ($F=2.58$ DF 3, 133 $p=0.056$, ANCOVA) or the elevations ($F=2.55$ DF 3, 136 $p=0.058$, ANCOVA) of these regression lines, and the common equation for all seasons combined was: $y=62.8-1.42x$, $p<0.001$, $r^2=0.56$.

i) Photophase:

Metabolic rates totalled over the entire photophase (when measured at a constant T_a) were negatively correlated with T_a and the slopes of these equations differed among seasons ($F=3.85$ DF 3, 118 $p=0.011$, ANCOVA). The slope of the regression line for total photophase metabolic rates during autumn were steeper than those during spring ($p<0.05$, Tukey). All other seasonal comparisons between slopes were indistinguishable. However, this difference in the slope of total photophase metabolic rates may have been due to the fact that animals during autumn were measured at lower T_a than during the other seasons (6 °C *cf.* 10 °C). When a comparison was made over the same T_a range (10-26 °C), no

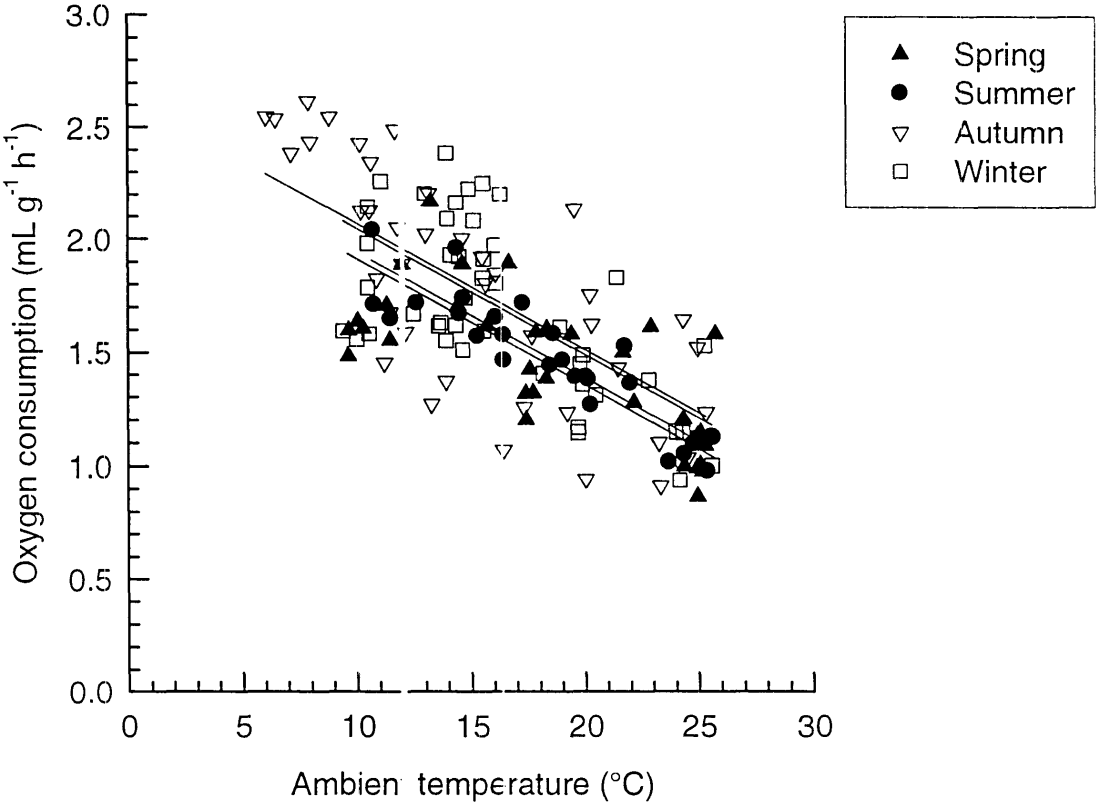


Fig. 3.14. Average daily metaboli : rates (ADMR), measured over a 23 h period, for *P. breviceps* at ambient temperatu es (T_a) below the lower critical temperature (T_{lc}) during each season. Regression equations are listed below in Table 3.8. The elevations of the lines differed significantly (F=2.78 DF , 141 p=0.043, ANCOVA).

Table 3.8 Regression equations fc r ADMR (mL g^{-1} h^{-1}) against T_a (°C) of *P. breviceps* during each season (p and r^2 value s are for original equations before computation of common slope; pooled r^2=0.54; N = number of individuals; n = number of observations).

Season	Regression equa tion	N	n	p	r^2
Spring	y = 2.47 - 0.05 6x	10	33	< 0.001	0.50
Summer	y = 2.51 - 0.05 6x	10	27	< 0.001	0.82
Autumn	y = 2.63 - 0.05 6x	7	41	< 0.001	0.60
Winter	y = 2.61 - 0.05 6x	13	45	< 0.001	0.44

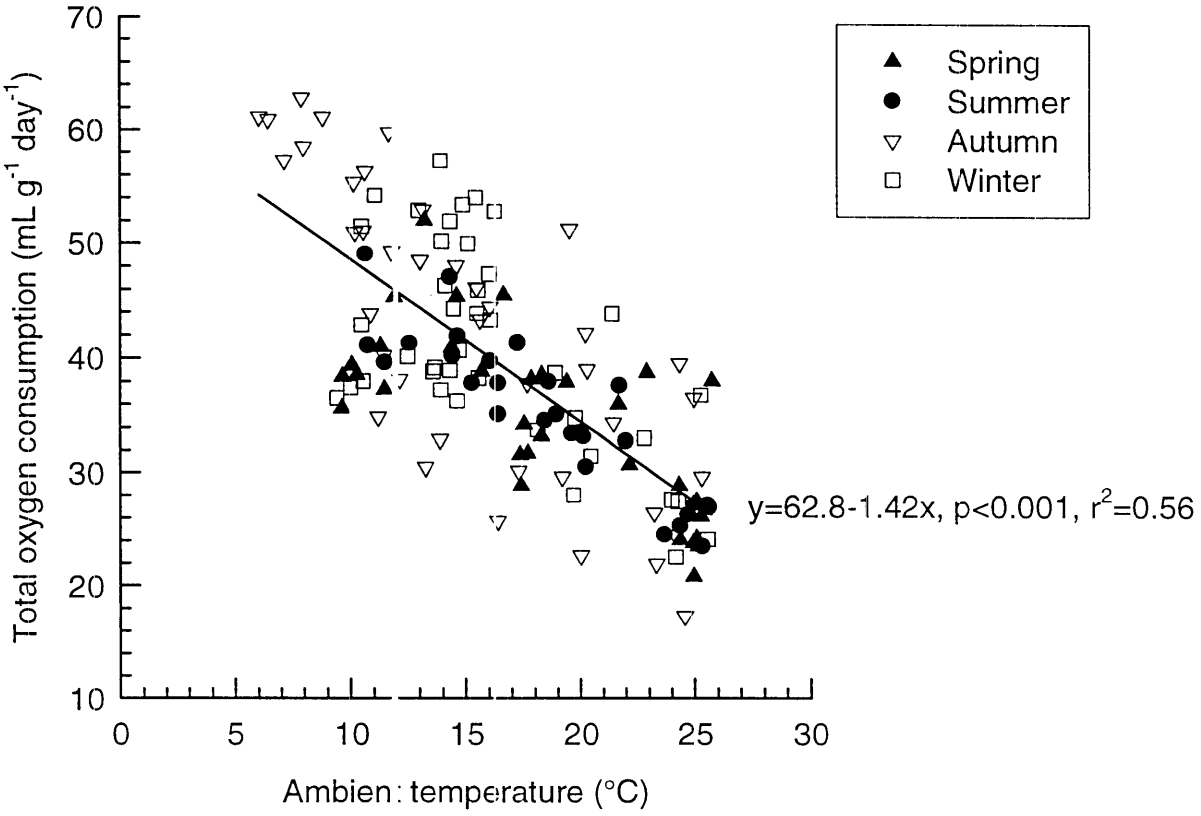


Fig. 3.15. Total daily metabolic rates, corrected for 24 h, for *P. breviceps* at ambient temperature (T_a) below the lower critical temperature (T_{lc}) during each season. As no differences were observed between the regression lines for each season, a common equation was calculated.

difference in the slope of the regression lines was found (Fig. 3.16, Table 3.9; F=0.61 DF 3, 108 p=0.607, ANCOVA), although the elevations did differ (F=22.83 DF 3, 111 p<0.001, ANCOVA). Total metabolic rates during the photophase in autumn were significantly lower than during all other seasons (p<0.01, Tukey), while winter metabolic rates were lower than those in summer (p<0.01, Tukey).

ii) Scotophase:

To determine if there was any metabolic compensation for the difference in the length of the activity period in different seasons, metabolic rates were totalled over the entire scotophase and included both AMR and RMR values. Total scotophase metabolic rates changed with season, with a significant difference in the slopes of the regression equations (Fig. 3.17, Table 3.10; F=8.80 DF 3, 268 p<0.001, ANCOVA). In autumn, with its longer scotophase, the equation for the total night metabolic rates of the gliders was steeper than those in both spring and summer (p<0.01, Tukey). However, the slope of the regression line in winter was only steeper than that during spring (p<0.01, Tukey), and was similar to that during summer. This is despite the fact that the length of the scotophase, averaged over the nights measured, in winter (13.13±0.50 h, n=55), like that in autumn (13.33± 0.36 h, n=47), was approximately 2 hours longer than the scotophases in both spring and summer (11.45±0.45 h, n=32, and 1.04±0.59 h, n=30, respectively). Neither autumn and winter scotophase metabolic rates, nor spring and summer scotophase metabolic rates were significantly different from each other (p>0.05, Tukey). Further, this result was not due, like that of the total photophase metabolic rates, to the lower T_a measurements made during autumn, as a comparison of the regression equations over a similar T_a range (10-26 °C) yielded the same results. Therefore, it would appear that there may be at least some partial compensation occurring to counteract the longer activity period during autumn and winter, at least at mid-higher T_a.

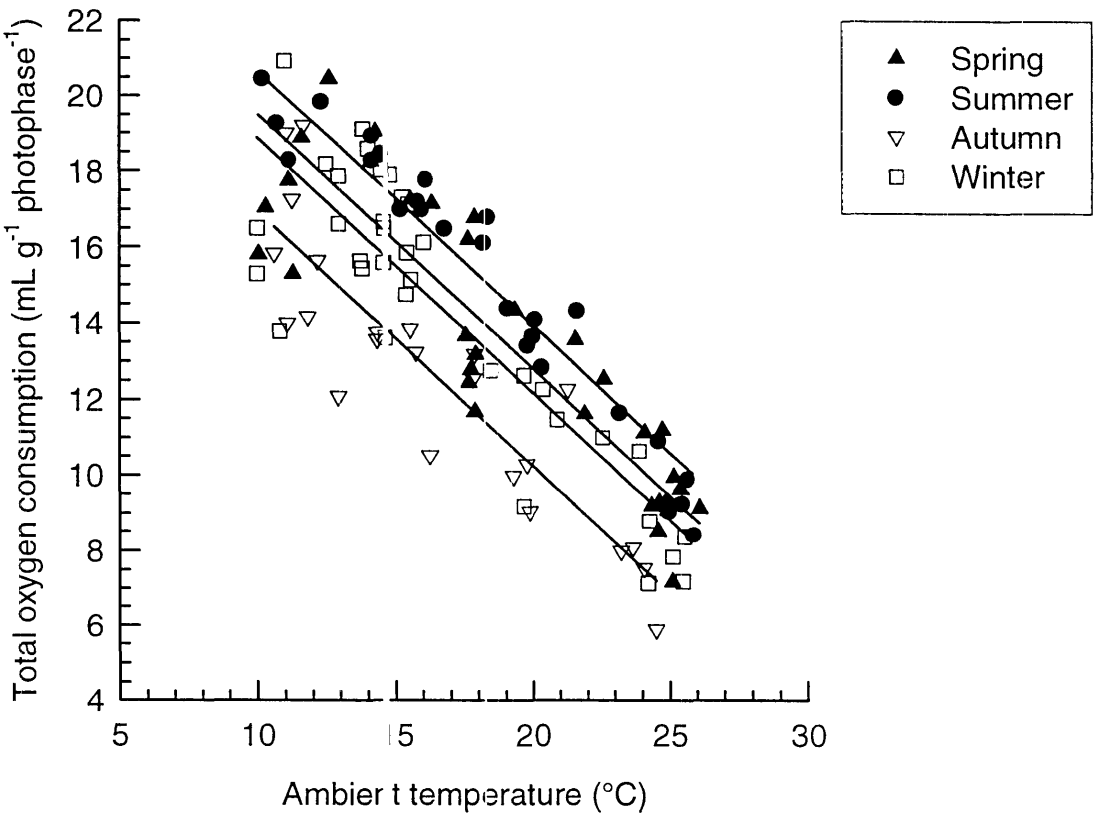


Fig. 3.16. Total metabolic rates for *P. breviceps* during the photophase, adjusted to a 24 h period within the chamber, at ambient temperatures (T_a) below the lower critical temperature (T_{lc}) during each season. Regression equations are listed below in Table 3.9. The elevation of the regression equation for animals during autumn was significantly lower than that during all other seasons ($F=22.83$ DF 3, 111 $p<0.001$, ANCOVA; $p<0.01$, Tukey), while the elevation of the line for animals during winter was significantly lower than that during summer ($p<0.01$, Tukey).

Table 3.9 Regression equations for total metabolic rates of *P. breviceps* summed over entire photophase period (adjusted to 24 hours total time within chamber; mL g^{-1} h^{-1}) against T_a (°C) (p and r^2 values are from original equations before computation of common slope equations and the pooled $r^2=0.81$; N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	$y = 26.2 - 0.67x$	10	31	< 0.001	0.77
Summer	$y = 27.3 - 0.67x$	10	26	< 0.001	0.94
Autumn	$y = 23.6 - 0.67x$	7	23	< 0.001	0.79
Winter	$y = 25.6 - 0.67x$	13	36	< 0.001	0.78

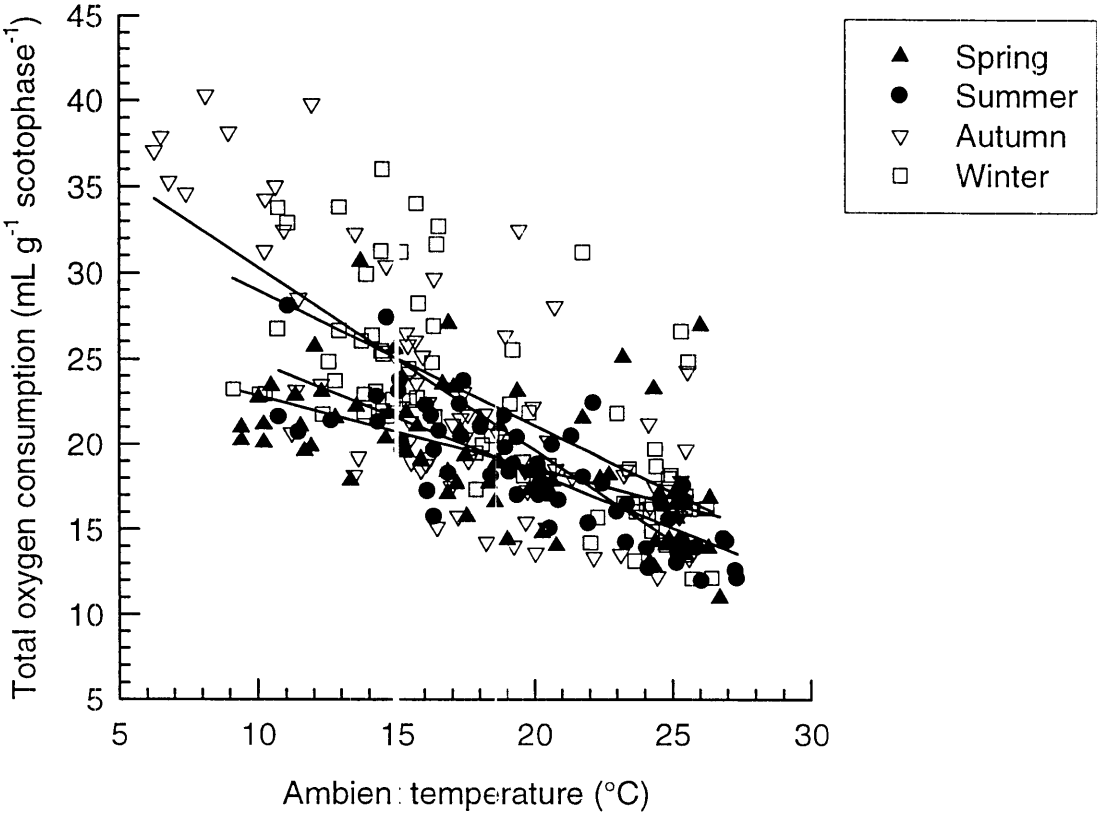


Fig. 3.17. Total metabolic rates for *P. breviceps* during the scotophase, at ambient temperatures (T_a) below the lower critical temperature (T_{lc}) during each season. Regression equations are listed below in Table 3.10. The slope of the equation for animals during autumn was significantly steeper than those for spring and summer (F=8.80 DF 3, 268 p<0.001, ANCOVA; p<0.01, Tukey), whereas the slope of the equation for animals during winter was only steeper than that of spring (p<0.01, Tukey).

Table 3.10 Regression equations for total metabolic rates of *P. breviceps* summed over entire scotophase period (mL g-1 h-1) versus T_a (°C) (N = number of individuals; n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 23.8-0.374x	13	66	< 0.001	0.31
Summer	y = 27.5-0.570x	13	61	< 0.001	0.64
Autumn	y = 35.9-0.936x	16	77	< 0.001	0.57
Winter	y = 32.4-0.693x	15	72	< 0.001	0.47

Given the higher AMR compared to RMR, it was not unexpected to find that the elevations of the regression lines during the scotophase were significantly higher than those during the photophase for each season (spring: F=79.60 DF 1, 96 p<0.001; summer: F=95.93 DF 1, 84 p<0.001; autumn: F=128.76 DF 1, 103 p<0.001; winter F=154.77 DF 1, 107 p<0.001, ANCOVA).

iii) % of total daily metabolic rate comprised of scotophase and photophase:

The percentage of total daily metabolic rate comprising of metabolism during the scotophase was correlated with T_a during all seasons except autumn (Fig. 3.18a, Table 3.11a). As would be expected given the difference in length of scotophase, the elevations of the regression equations differed among seasons (Fig. 3.18a, Table 3.11a; F=37.69 DF 3, 159 p<0.001, ANCOVA). Spring and summer both had significantly lower elevations (p<0.001, Tukey) than autumn and winter, while no significant differences in the elevations of the regression lines were observed during either spring and summer or autumn and winter.

Total metabolism during the photophase, expressed as a percentage of the total daily metabolic rate, also displayed significant differences in elevation between seasons (Fig. 3.18b, Table 3.11b; F=31.59 DF 3, 159 p<0.001, ANCOVA). In contrast to percent scotophase, the percentages during winter and autumn were lower than those during spring and summer (p<0.001, Tukey). Further, rather than a positive linear relationship as was found with the percentage of scotophase metabolic rates, the percentage of total daily metabolic rate comprised of photophase metabolism showed an inverse correlation with T_a. These factors, combined with the lower RMR during winter, autumn and spring, and the reduction in the proportion of AMR, may account for the lack of seasonal differences observed in total daily metabolic rate.

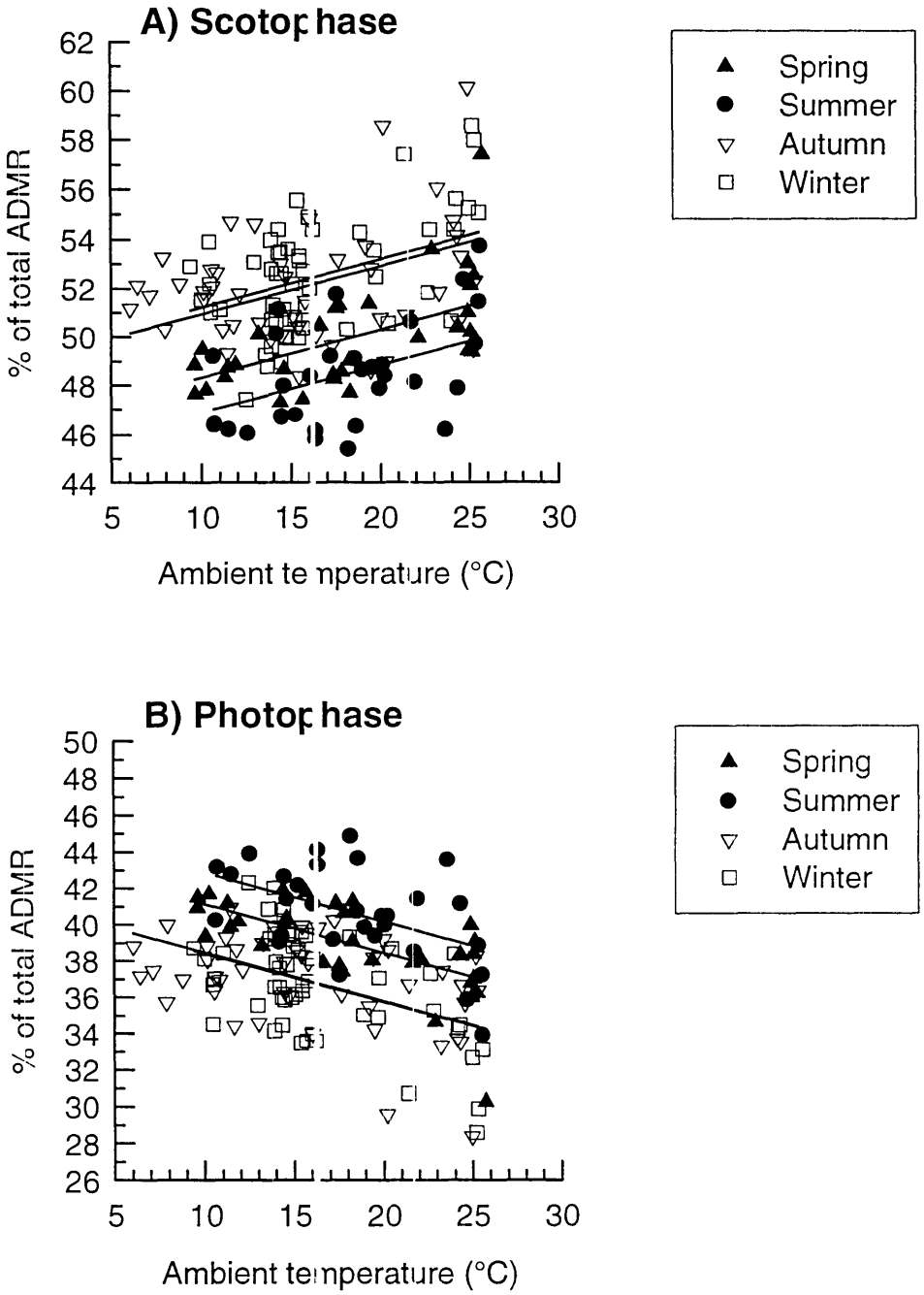


Fig. 3.18. Percentage of total daily metabolic rate comprising of metabolic rate during the **A)** scotophase and **B)** photophase. Regression equations are listed on the following page in Tables 3.11a and 3.11b. During the scotophase the regression lines for animals during spring and summer were significantly lower than those for animals during autumn and winter ($F=37.69$ DF 3, 159 $p<0.00$, ANCOVA; $p<0.001$, Tukey), whereas during the photophase the elevations of the regression lines for autumn and winter were significantly lower than those for animals during spring and summer ($F=31.59$ DF 3, 159 $p<0.001$, ANCOVA; $p<0.001$, Tukey).

Table 3.11a Regression equations for the percentage of total daily metabolic rate comprised of total scotophase metabolic rate versus T_a (°C) for *P. breviceps* during each season (p and r^2 values are for original equations before computation of common slope; pooled r^2=0.19; N = number of individuals, n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 46.4 + 0.2(x	10	33	< 0.001	0.39
Summer	y = 44.9 + 0.2(x	10	30	0.012	0.21
Autumn	y = 49.0 + 0.2(x	7	46	0.107	0.06
Winter	y = 49.3 + 0.2(x	13	55	< 0.001	0.28

Table 3.11b Regression equations for the percentage of total daily metabolic rate comprised of total photophase metabolic rate versus T_a (°C) for *P. breviceps* during each season (p and r^2 values are for original equations before computation of common slope; pooled r^2=0.26; N = number of individuals: n = number of observations).

Season	Regression equation	N	n	p	r^2
Spring	y = 43.8 - 0.27x	10	33	< 0.001	0.43
Summer	y = 45.5 - 0.27x	10	30	0.005	0.25
Autumn	y = 41.1 - 0.27x	7	46	0.004	0.17
Winter	y = 41.1 - 0.27x	13	55	< 0.001	0.28

3.3.2.3.2 ADMR versus mass loss:

No significant relationship was detected between the overall amount of mass lost during a measuring period and the total ADMR, except during autumn, although there was a high degree of scatter associated with this regression line ($y=9.74+0.054x$, $p=0.034$, $r^2=0.11$). When analysed using ANCOVA, no seasonal differences were found in the slopes or elevations of the regression lines and a common equation was formed. However, as this line was not significant ($y=11.3+0.032x$, $p=0.141$, $r^2=0.01$), and the mean amount of mass lost during an ADMR measurement during each season also displayed no difference (Table 3.12; $F=1.72$ DF 3, 149 $p=0.17$, ANOVA), the overall mean amount of mass lost during a 23±1.0 h measuring period over a T_a range between 6-25 °C was calculated as 12.43± 2.51 g. Therefore, a high ADMR appears to have no consequences in terms of mass reduction. T_a also had no effect on the degree of mass loss, except during winter when mass loss showed a positive relationship with T_a ($y=9.12+0.22x$, $p=0.023$, $r^2=0.10$). However, the high level of scatter makes this relationship rather questionable.

3.3.3 Body temperature:

The T_b of all sugar gliders within the respirometer displayed a similar pattern which closely tracked that of metabolic rate (Fig. 3.19). In the afternoon, when they were placed within the chambers, the animals were still agitated from their transfer from the aviaries, as indicated by their elevated T_b. Once the animal settled down, T_b decreased by 1-2 °C, and remained at this lower value until the lights went off, whereupon it once again increased. T_b remained elevated during the periods of activity throughout the night, only dropping when the animal rested for prolonged periods. When the lights came on, simultaneous with the drop in metabolic rate, T_b decreased 4-6 °C over a period of 1-2 hours. T_b then slightly increased throughout the remainder of the photophase, with larger increases and subsequent decreases during short bursts of activity. These data from within the chambers, when the animals were without food or water, displayed a similar pattern and closely

Table 3.12 Mean amount of mass lost by *P. breviceps* during a metabolic measurement (approximately 23 hours) for each season when measured at a constant T_a (range 6-25 °C; N = number of individuals; n = number of observations). Results from ANOVA tests for differences between seasons are shown below.

Season	Mass loss (g)	SD	N	n
Spring	13.05	2.26	10	32
Summer	12.09	2.41	10	28
Autumn	11.88	1.94	7	42
Winter	12.70	3.01	13	51

p=0.17; F=1.72; DF 3, 149

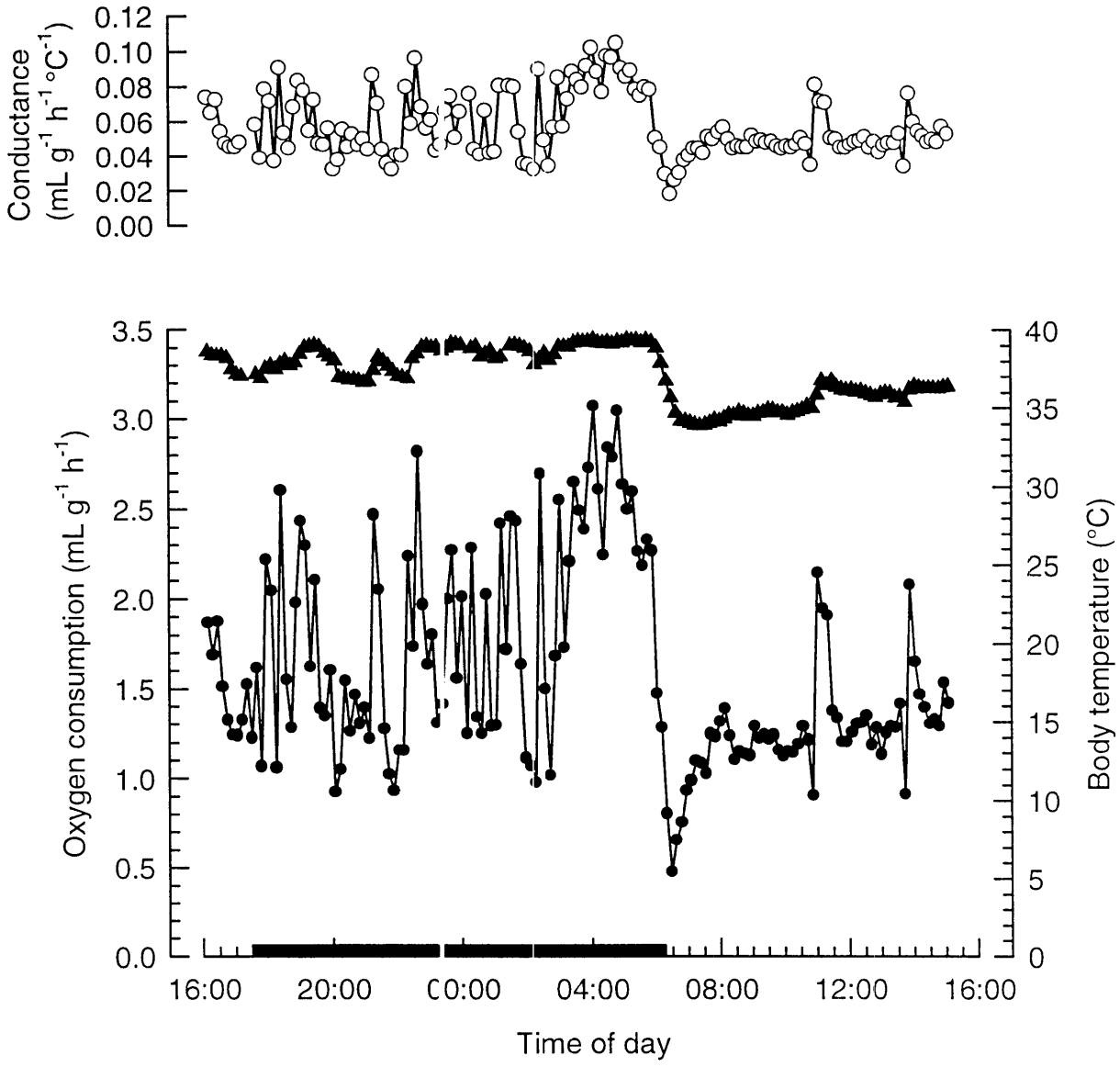


Fig. 3.19. Example of simultaneous measurements of metabolic rate, body temperature (T_b), and calculated conductance for an individual *P. breviceps* (Pb15) at an ambient temperature (T_a) of 10 °C during winter. Food and water were not available; dark bar indicates scotophase.

resembled those recorded within the nest boxes when the animals were within their family groups with access to both food and water.

3.3.3.1 Resting body temperature:

Over the T_a range -6.4-37.6 °C, no homothermic, resting T_b of *P. breviceps* ranged from 33.5-39.9 °C. The mean T_b below the turnpoint (the point where T_b started to increase due to heat load) did not differ among seasons (Fig. 3.20, Table 3.13; F=0.42 DF 3, 166 p=0.74, ANOVA), and the overall mean T_b was 35.3±0.7 °C. The turnpoints themselves, however, did differ among seasons (Fig. 3.20, Table 3.13; F=7.85 DF 3, 16 p=0.002, ANOVA) and the increase in T_b occurred at a higher T_a in summer (28.4±0.4 °C) than in autumn and winter (26.1±0.8 °C and 26.3±0.8 °C, respectively; $p<0.05$, Tukey). The turnpoints of spring (27.1±1.0 °C), autumn and winter, and spring and summer, were indistinguishable ($p>0.05$, Tukey). During both spring and summer the turnpoints occurred within the TNZ, whereas during autumn and winter they were just below the T_{lc}, though still within 0.5 °C. Above the turnpoint T_b and T_a were correlated. However, no seasonal difference was found between the slopes or elevations of the regression equations and the common line formed the equation: $y=23.4+0.43x$, $p<0.001$, $r^2=0.83$.

3.3.3.2 Active body temperature:

As would be expected, mean T_b of gliders during peak activity were higher than those during rest (between 2.5-3.5 °C; all seasons $p<0.0001$, t-tests). However, unlike resting T_b, seasonal differences were observed (Fig. 3.21; F=11.83 DF 3, 123 $p<0.001$, ANOVA). T_b during summer (38.0±0.6 °C) and autumn (38.0±0.5°C) activity was lower than those during winter (38.4±0.8 °C) or spring (38.6±0.4 °C) activity ($p<0.05$, Tukey). Although significant, this difference was quite small (0.6 °C). Mean T_b during the peak of activity were indistinguishable between both summer and autumn, and winter and spring ($p>0.05$, Tukey).

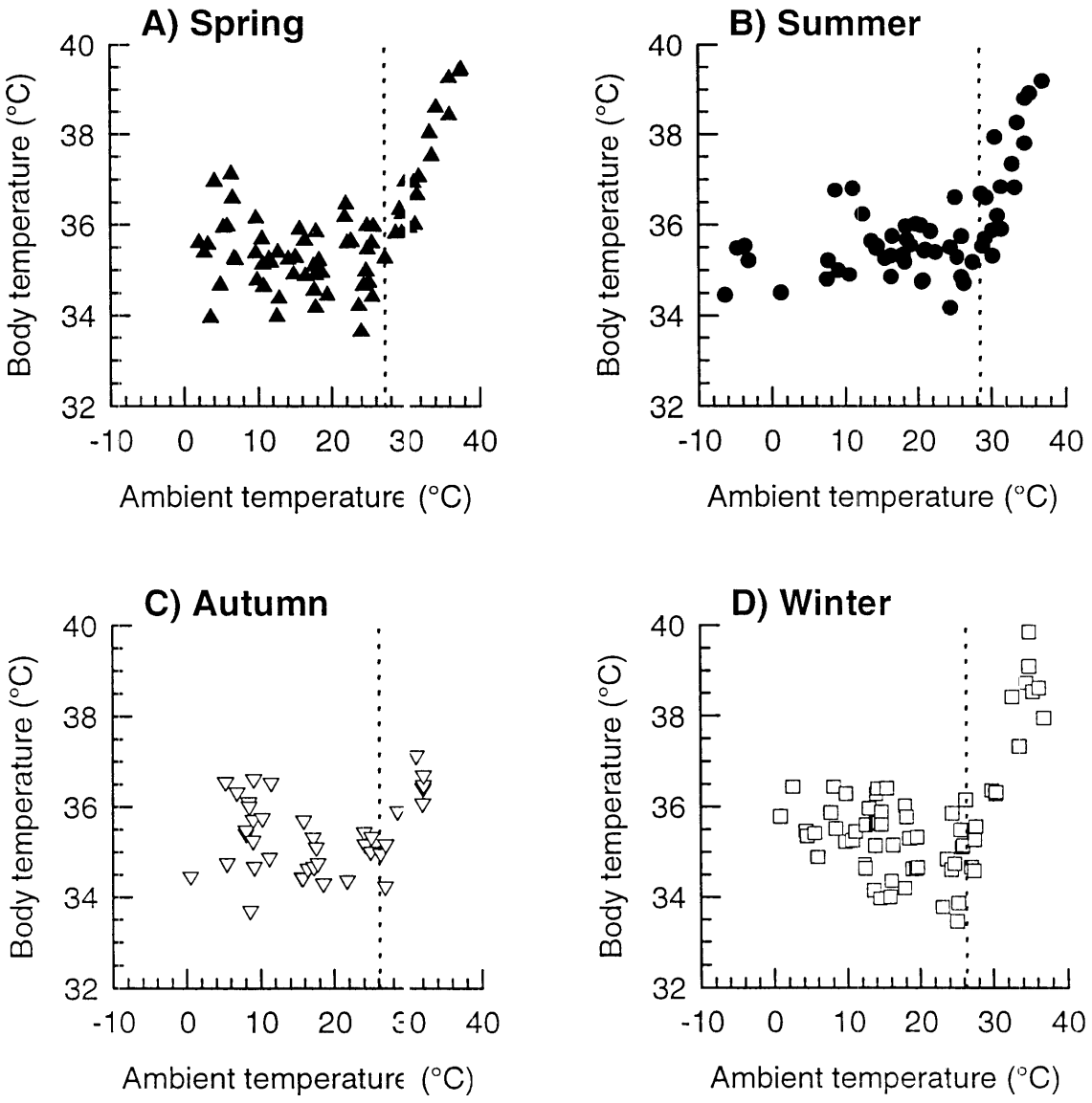


Fig. 3.20. Resting body temperatures (T_b) of *P. breviceps* during **A)** spring, **B)** summer, **C)** autumn and **D)** winter. Dashed line indicates the turnpoint, the ambient temperature (T_a) at which T_b started to rise in response to increasing T_a.

Table 3.13 Mean body temperatures (T_b) and turnpoints of *P. breviceps* for each season (N = number of individuals; n = number of observations). Results from ANOVA tests for differences between seasons are shown below.

Season	T_b (°C)	SD	N	n	Turnpoint (°C)	SD	N	n
Spring	35.27	0.74	7	52	27.13	0.95	5	70
Summer	35.40	0.60	7	39	28.44	0.43	4	57
Autumn	35.29	0.71	9	29	26.11	0.81	6	40
Winter	35.24	0.77	9	50	26.33	0.84	5	65

F=0.42 DF 3, 166 p=0.74 F=7.85 DF 3, 16 p=0.002

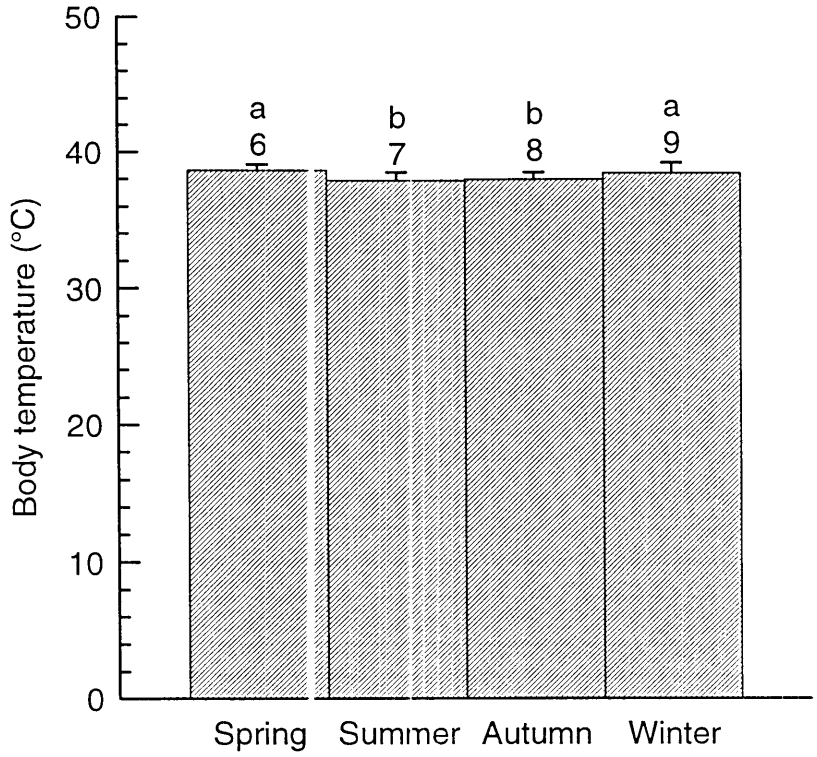


Fig. 3.21. Mean (±SD) body temperatures (T_b) of *P. breviceps* during activity within each season. Numbers indicate the number of individuals; different letters indicate significant differences ($p<0.05$) between seasons.

3.3.4 Conductance:

Since calculated conductance values are derived by dividing metabolic rate by the difference between T_b and T_a, the daily pattern of conductance was similar to both metabolic rate and T_b (Fig. 3.19). Upon entry into the chamber conductance was high, but settled down once the animal became rested. During the night conductance generally fluctuated markedly, coinciding with activity, until lights came on and the animal once again settled, whereupon conductance remained stable throughout the rest of the day, apart from small rises when the animal was briefly active.

3.3.4.1 Resting conductance:

Over the T_a range -6.4-37.6 °C, resting conductance displayed a curvilinear relationship, with conductance increasing markedly beyond the TNZ of each season (Fig. 3.22). Data had to first be transformed before seasonal comparisons could be made over the entire T_a range. An inverse transformation of conductance values reduced the curve to an extent that it was possible for linear regression analysis to be performed. The slopes of the transformed regression equations during all seasons were similar ($F=1.84$ DF 3, 220 $p=0.14$, ANCOVA), however, the elevation for conductance in summer was significantly higher than those in all other seasons ($F=11.35$ DF 3, 223 $p<0.001$, ANCOVA; $p<0.05$, Tukey). Conductance during spring, autumn and winter were indistinguishable ($p>0.05$, Tukey).

3.3.4.1.1 Below the TNZ:

Below the T_{lc} there was a weak linear relationship between T_a and conductance during both summer and spring (r^2 of 0.16 and 0.21 for spring and summer, respectively), but this was not evident during either autumn or winter. Regression analysis between the four seasons showed that, while the slopes for conductance below T_{lc} were all similar, the elevation for conductance in summer was significantly higher than those in all other seasons

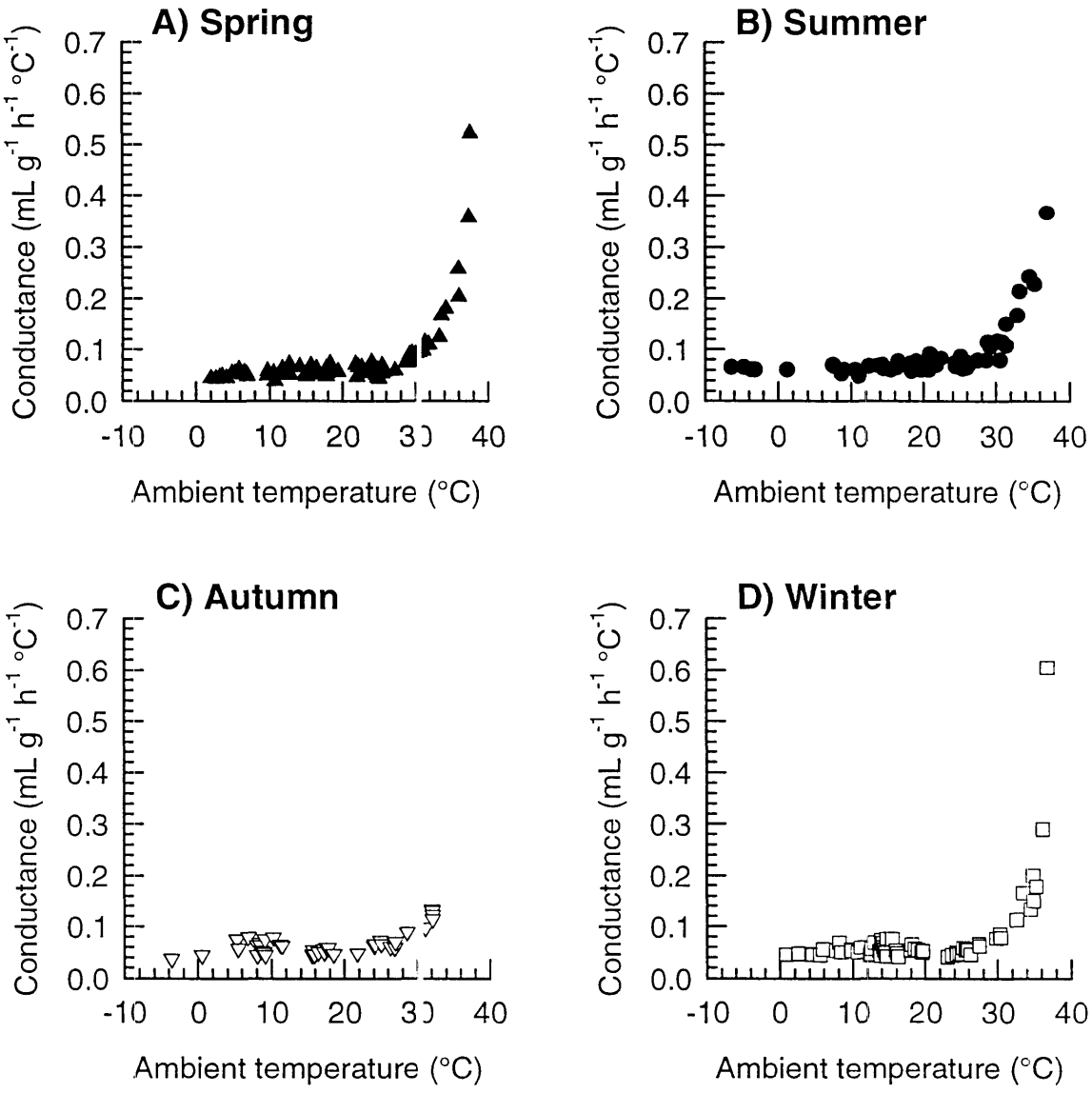


Fig. 3.22. Resting conductance for *P. breviceps* during **A)** spring, **B)** summer, **C)** autumn and **D)** winter over the entire range of ambient temperature (T_a) measured.

(Fig. 3.22; F=6.96 DF 3, 123 p<0.001, ANCOVA; p<0.01, Tukey). In addition, the mean minimum values for conductance (taken below T_a 10 °C where no correlation between conductance and T_a existed during any season) also differed among seasons (Fig. 3.23; F=4.97 DF 3, 51 p<0.004, ANOVA). The mean minimum conductance for summer (0.062±0.005 mL g^{-1} h^{-1} $°C^{-1}$) was 22 % higher than that for both spring (0.051±0.006 mL g^{-1} h^{-1} $°C^{-1}$), and winter (0.051±0.007 mL g^{-1} h^{-1} $°C^{-1}$; p<0.05, Tukey). Mean minimum conductance in autumn (0.059±0.014 mL g^{-1} h^{-1} $°C^{-1}$) was indistinguishable from those in all other seasons (p>0.05, Tukey).

3.3.4.1.2 Above the TNZ:

Above the TNZ, the slopes of the regression equations were similar for all seasons (Fig. 3.22; F=1.91 DF 2, 28 p=0.167, ANCOVA). In contrast, the elevation for conductance in summer was higher than that during winter (F=6.52 DF 2, 30 p=0.004, ANCOVA; p<0.05, Tukey). The elevation for conductance during spring was indistinguishable from both winter and summer (p>0.05, Tukey). Unfortunately, the low number of data above the TNZ during autumn precluded this season from being included in the analysis.

3.3.4.2 Active conductance:

When animals were at their peak of activity, conductance showed a positive linear response to increasing T_a during spring, summer and winter (Fig. 3.24, Table 3.14). However, an extremely high degree of scatter was evident for the conductance during winter (r^2=0.12). No linear relationship between T_a and conductance was observed during autumn. The slopes of the regression equations differed among the four seasons (F=14.89 DF 3, 117 p<0.001, ANCOVA). The slopes of the lines during spring and summer were steeper than those of autumn and winter (p<0.05, Tukey). The slopes of the regressions during both autumn and winter, and spring and summer were indistinguishable (p>0.05, Tukey).

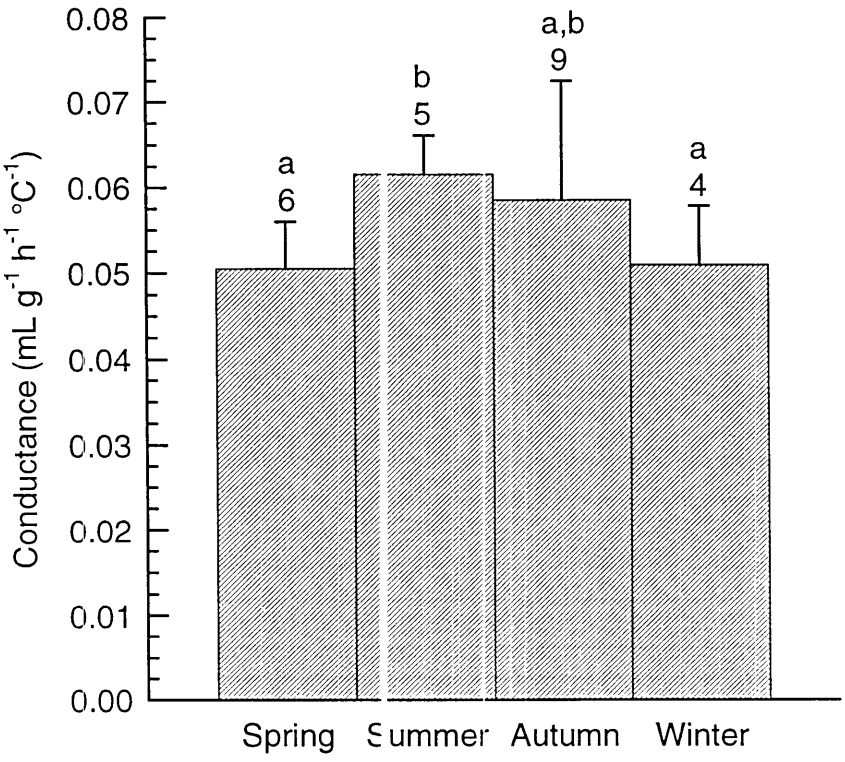


Fig. 3.23. Mean (±SD) minimum conductance of *P. breviceps* during each season. Means were calculated for values below ambient temperature (T_a) 10 °C, as no correlation existed between conductance and T_a during any season in this region. Numbers indicate the number of individuals; different letters indicate significant differences ($p<0.05$) between seasons.

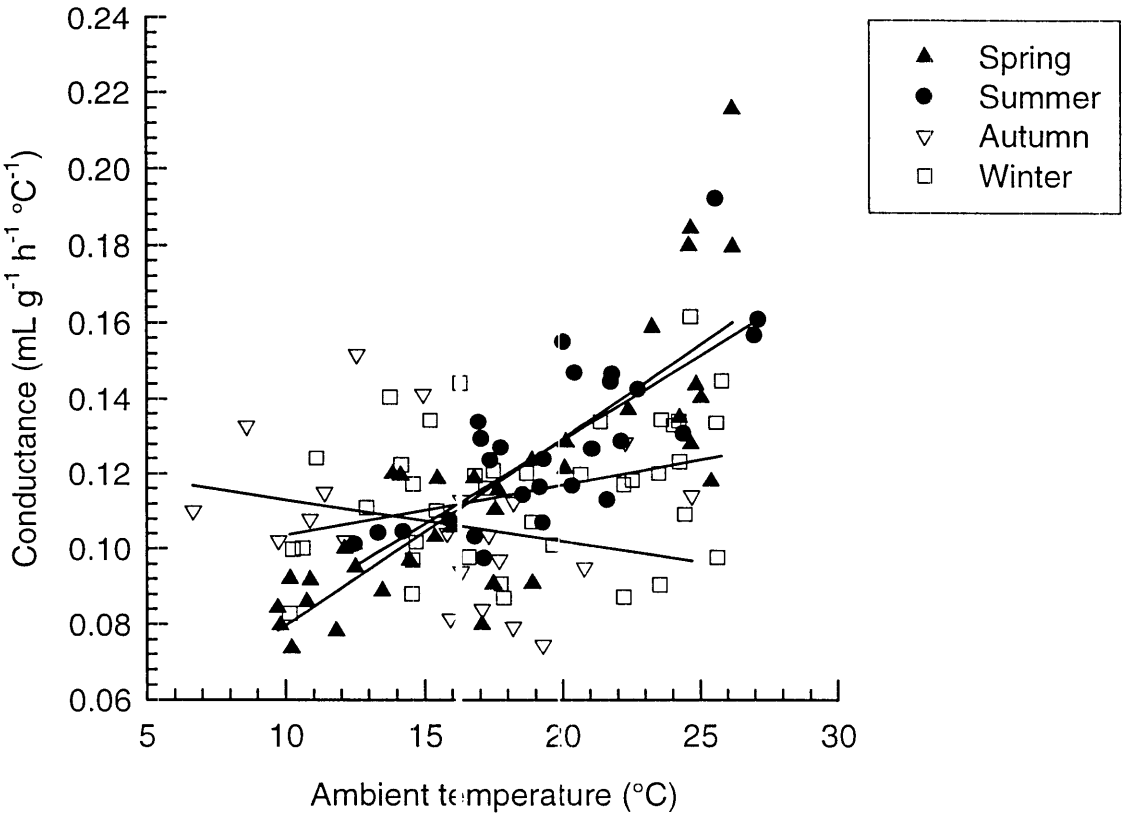


Fig. 3.24. Conductance of *P. breviceps* during peak activity within each season. Regression equations are listed below in Table 3.14. The slopes of the regression lines were significantly steeper for the active conductance of animals during spring and summer than for those during autumn and winter (F=14.89 DF 3, 117 $p<0.001$, ANCOVA; $p<0.05$, Tukey).

Table 3.14 Regression equations for conductance (mL g^{-1} h^{-1} $°C^{-1}$) of *P. breviceps* during peak activity versus T_a (°C) for each season (N = number of individuals; n = number of observations)

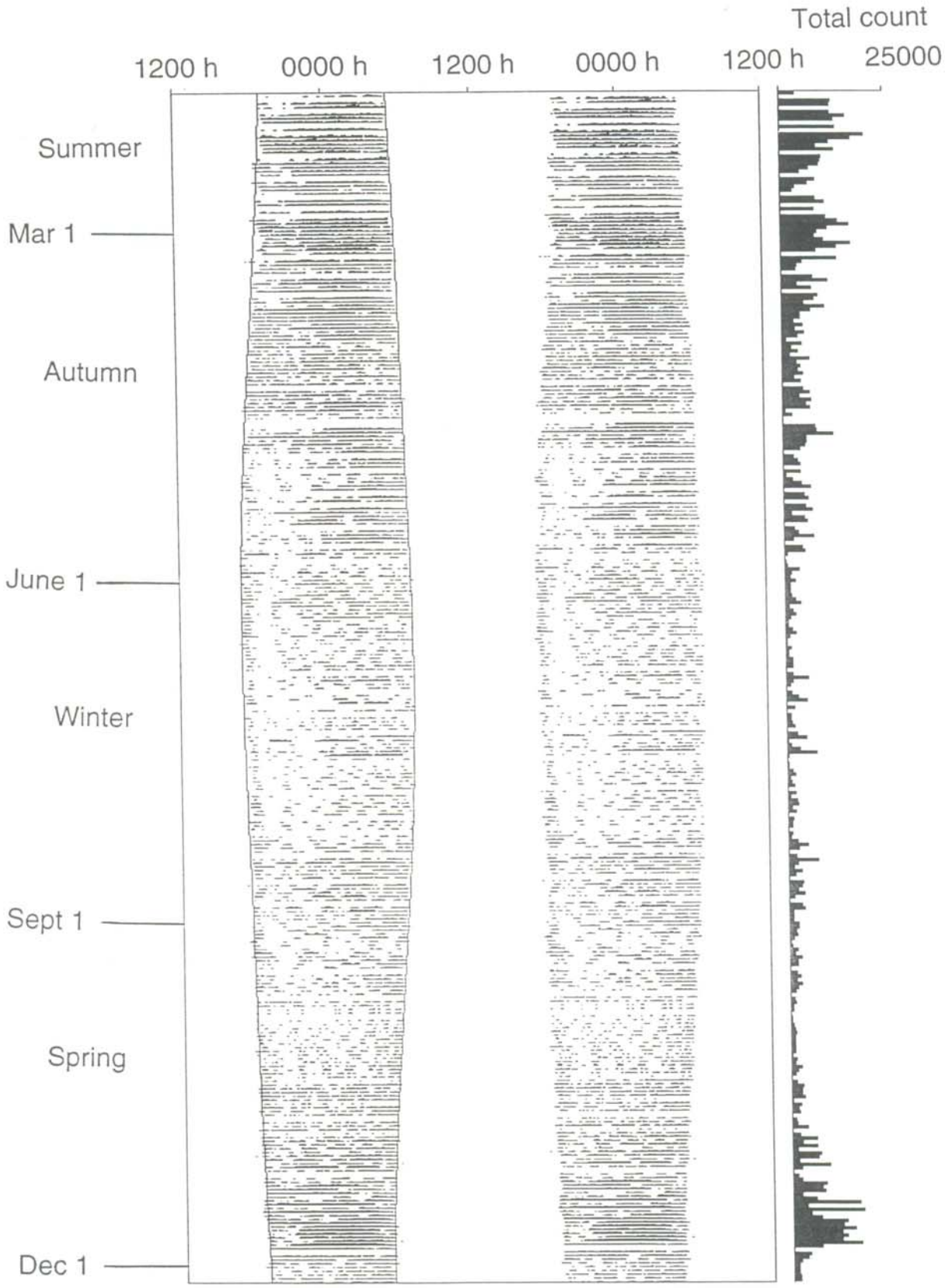
Season	Regression equation	N	n	p	r^2
Spring	y=0.030+0.0050x	6	37	< 0.001	0.68
Summer	y=0.040+0.0045x	7	28	< 0.001	0.58
Autumn	y=0.124-0.0011x	8	21	0.26	0.07
Winter	y=0.090+0.0013x	9	39	0.03	0.12

3.3.5 Locomotor activity:

Locomotor activity of *P. breviceps*, detected using PIRs within each aviary, was primarily nocturnal (Fig. 3.25). On the whole, gliders rarely ventured outside the nest box between sunrise and sunset. However, some gliders were observed to poke their heads through the slit in the nest box during the day but, due to the protection of the overhanging lid, these movements were not detected by the PIRs. Movement could also be heard within the nest boxes sometimes during the day, along with some vocalisations, and these, obviously, were also not detected by the PIRs. In addition, at certain times of the year certain animals (in particular lactating females or, later in the year, the young offspring) would come out when food was placed within the cages and have a quick feed before returning back to the nest box. However, as these feeding bouts were only short (generally only for 10 minutes after the food was placed within the cages through observation and PIR activity recordings) and occurred during the time when cages were being checked, the data within 15 minutes of feeding time were deleted as there was a high probability that they contained human activity. Gliders also often had short daytime feed and watering bouts when returned to the aviary after a night in the metabolic chamber. Again, these data were deleted to exclude influences on activity due to the presence of humans.

During late autumn to early spring 1996, some diurnal activity in two of the three cages was observed. However, during this time there was also a small mouse plague, and a number of mice, plus a rat, were captured within the outer cage, which contained the aviaries, over this period. While the mice were not actually within the aviaries, the positioning of the PIRs meant that the sensors would be triggered by movement of any animal just outside or on the wire of the aviaries. Considering that there was no corresponding diurnal activity during any other year and the gliders were rarely seen out during the daytime, it was assumed that the recorded diurnal activity was due to mice and not gliders. Unfortunately, the presence of these mice precluded the data from May 1996

Fig. 3.25. Daily double plots of locomotor activity for Cage 1 (2 animals, except during November and early December when an offspring became independent) from 22/1/95 to 6/12/95. Sunset and sunrise are indicated by the two solid lines for the left half of the plot. The sum of activity counts per day is given as a horizontal bargraph next to each plot. Days without any activity measurements are due to the removal of the gliders to the laboratory.


Total count
1200 h
0000 h
1200 h
0000 h
1200 h
25000
Summer
Mar 1
Autumn
June 1
Winter
Sept 1
Spring
Dec 1

onward being included in any analyses, although the general seasonal changes appeared to be, for the most part, similar to those observed during other times.

Analyses of locomotor activity data were also complicated by the fact that each cage contained a number of animals and this number varied, both between cages and over time (Cage 1: 2-3 animals; Cage 2: 3-6 animals; Cage 3: 4-5 animals). In addition, the cages could not be compared with each other because there was no direct correlation between the number of animals within a cage and the degree of activity. However, despite this, seasonal changes in activity were still evident (Fig. 3.25).

3.3.5.1 Total activity:

Total activity, summed over 24 hours, differed throughout the year. The mean total amount of activity during late autumn, winter and early spring months were lower than in the summer months (Figs. 3.25, 3.26). This pattern was also evident in Cage 1 during 1994. These data are not shown due to the use of a different system which recorded over a different time interval and only to a maximum of 255 movements, thus making a comparison impossible. The large increase in activity observed in Cage 1 during November (Figs. 3.25, 3.26) was probably due to 3 animals being present at that time (2 adults and an offspring that became independent within that month) instead of 2 animals that were present for the rest of the months (unfortunately, the mother died in early December). However, this pattern was not seen in Cage 2 when 2 young became independent during December (Fig. 3.26).

A possible reason for the seasonal difference in total activity is T_a (Fig. 3.27). In both Cages 1 and 2, with 2 and 3 animals, respectively, the amount of activity increased with warmer T_a. It is also evident that the degree of scatter is much less below T_a 10 °C.

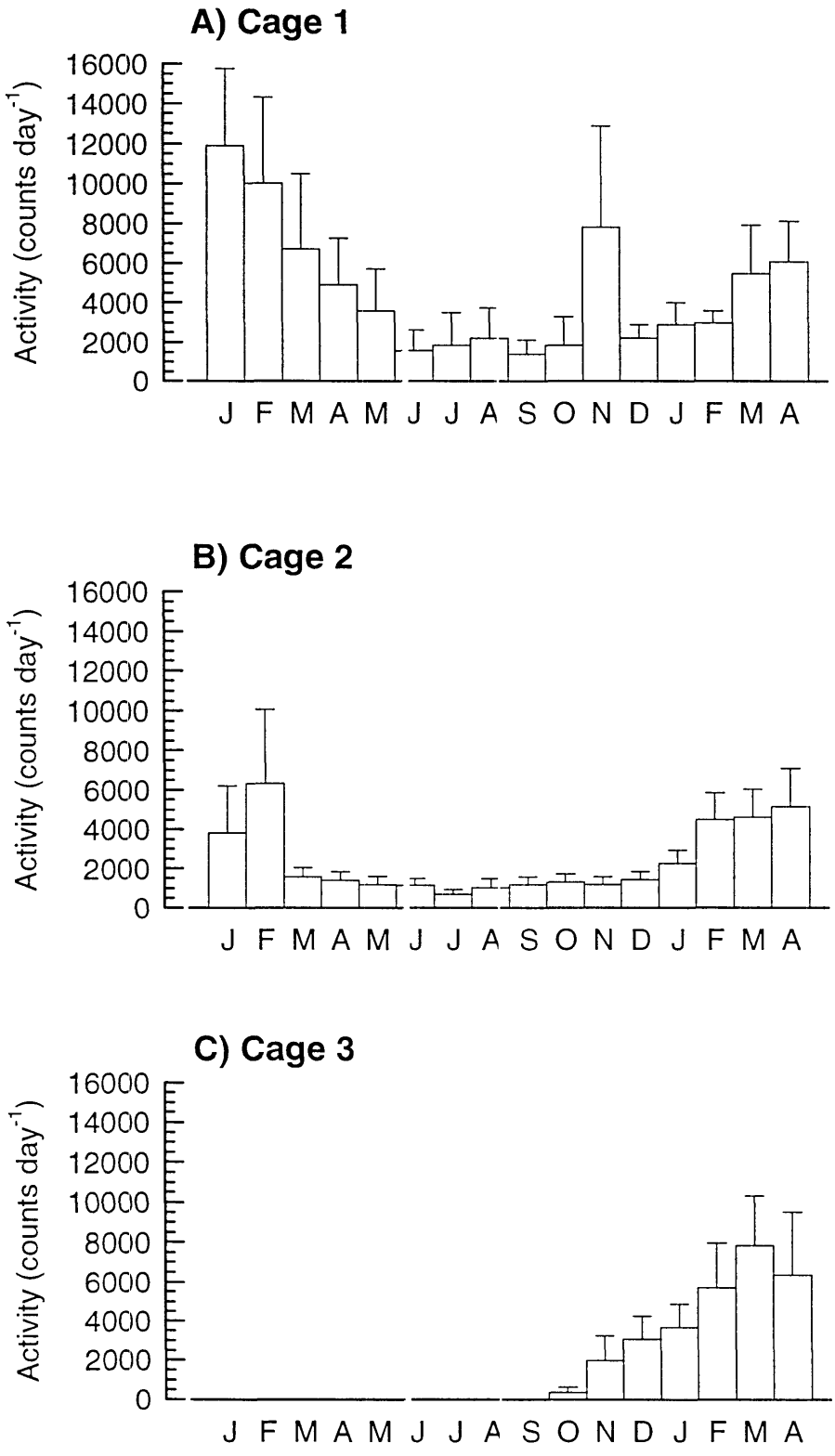


Fig. 3.26. Mean (±SD) monthly activity, totalled over 24 h, for **A**) Cage 1: 2 animals except from 2nd half of Nov. to 6 Dec. when three 3 animals were present; **B**) Cage 2: 3 animals Jan.-Nov., 5 animals Dec.-April; **C**) Cage 3: 5 animals Oct.-April.

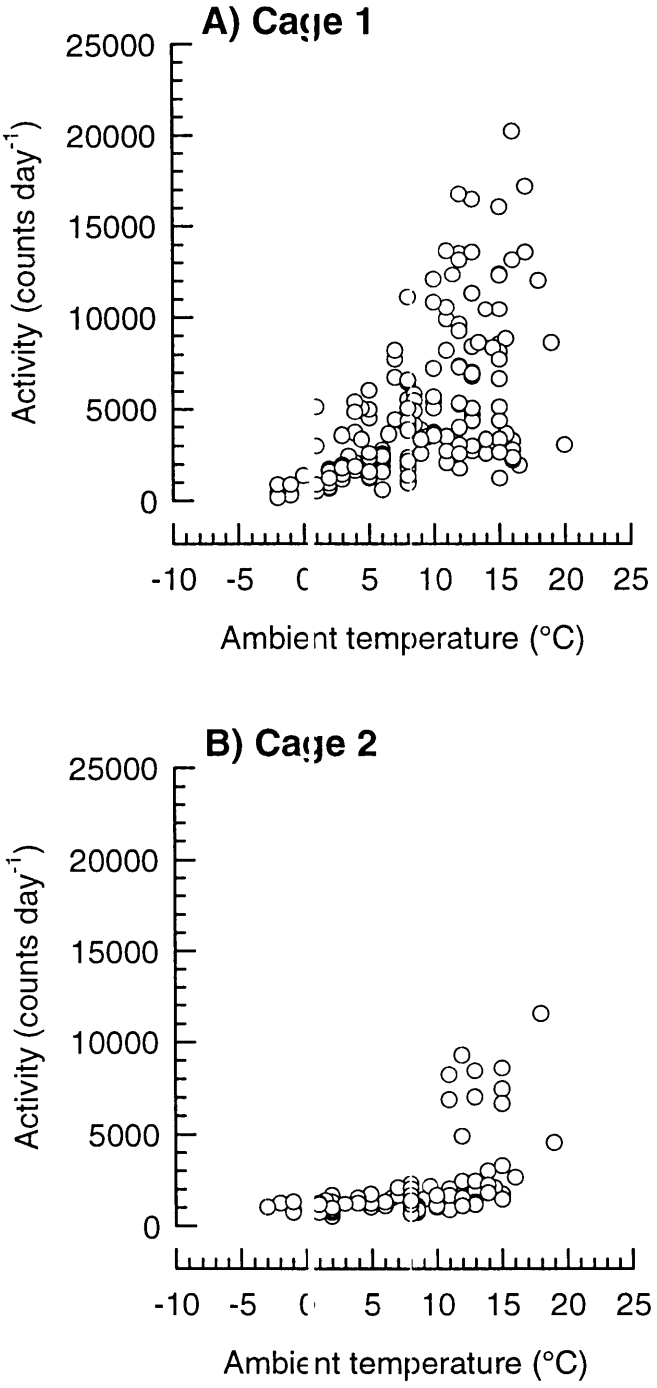


Fig. 3.27. Locomotor activity of *P. breviceps*, totalled over 24 h, in response to ambient temperature (T_a) in **A)** Cage 1 when 2 animals were present, and **B)** Cage 2 when 3 animals were present.

3.3.5.2 Activity patterns:

The pattern of activity within each cage also changed with season (Figs. 3.25, 3.28). Animals were almost continuously active throughout the night during summer and early autumn, but numerous short bouts of a few hours duration with long periods of no activity predominated during winter and early spring, concomitant with the reduction in total activity. During this time, animals tended to have an early short bout of activity, close to sunset, which was followed by a long period of rest. The main portion of activity appeared to occur between midnight and sunrise.

3.3.5.3 Daily commencement and cessation of activity:

The times at which gliders began and ended their activity were analysed after removal of all days when food was not available to the animals, plus the following day in case of any after-effect. This included nights in the metabolic chambers. Times within 6 minutes of sunset or sunrise could be counted as being on sunset or sunrise as the system was set up only to record in 6 minute intervals. Gliders generally began their activity within 30 minutes after sunset in all seasons, but there was a high degree of variability within each month (Fig. 3.29). The animals were more prone to start their activity later during the winter months, when the scotophase was longer, compared to the other seasons ($F=7.57$ DF 11, 491 $p<0.001$, ANOVA; $p<0.05$, Tukey). In keeping with their nocturnal nature, activity generally stopped prior to sunrise, and this distance increased during the winter months (Fig. 3.29; $F=16.31$ DF 11, 489 $p<0.001$, ANOVA; $p<0.05$, Tukey). The amount of variation within the months regarding the cessation of activity also appeared to increase during winter. In addition, during winter, there appeared to be a greater differential between the cessation of activity and sunrise than was present between sunset and the commencement of activity.

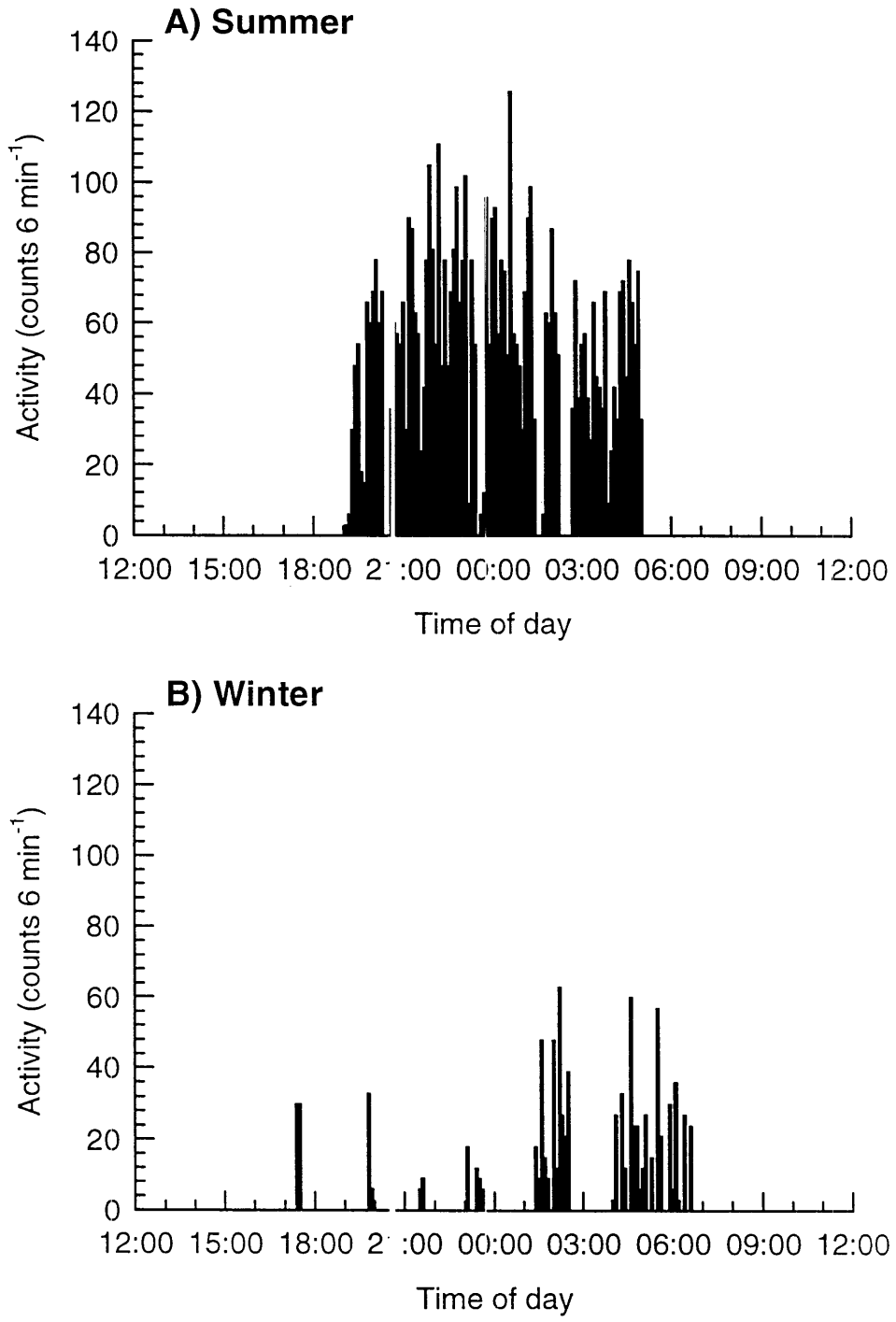


Fig. 3.28. Locomotor activity of Cage 1 *P. breviceps* (2 animals) during a day in **A)** summer (24-25/1/96) and **B)** winter (16-17/6/95).

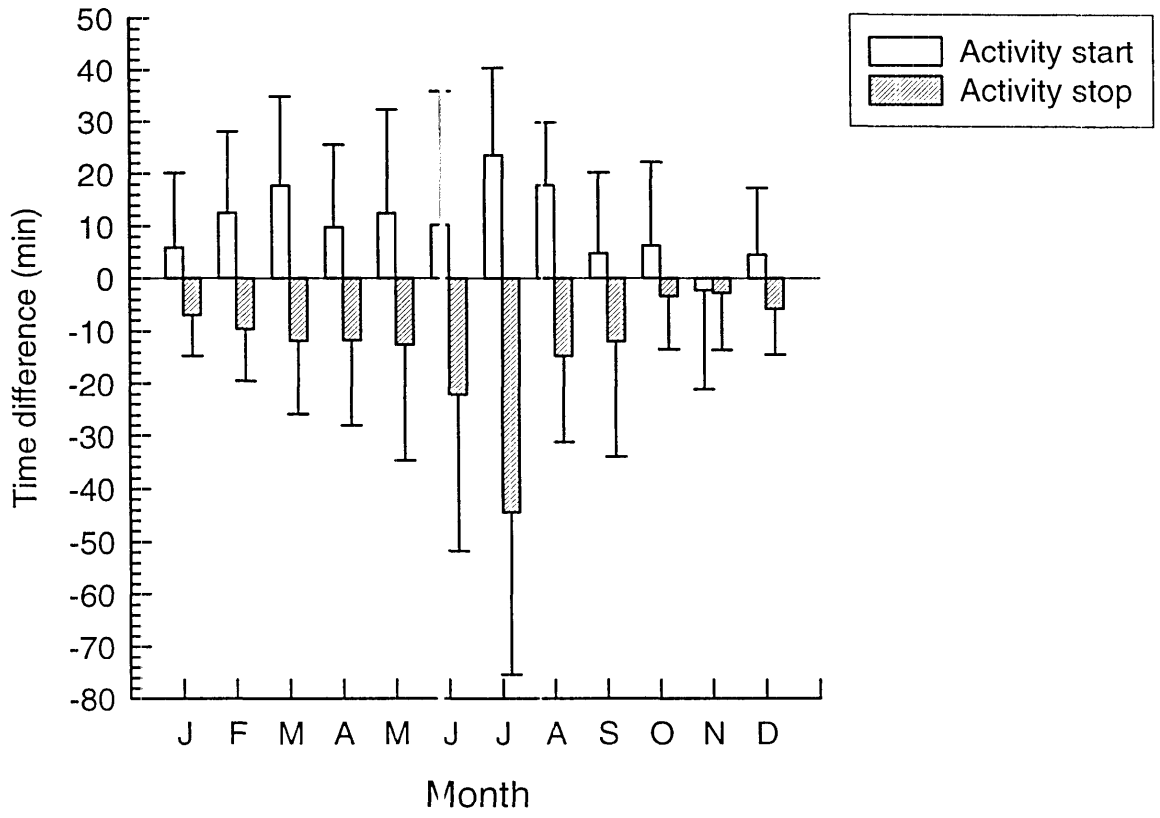


Fig. 3.29. Mean (±SD) monthly commencement and cessation times of activity by *P. breviceps* in comparison to sunset and sunrise. The zero line indicates time of sunset or sunrise. Activity of the gliders generally commenced within 30 min after sunset and ceased within an hour prior to sunrise.

3.3.6 Food consumption:

As for locomotor activity, it was impossible to determine the amount of food eaten by individual gliders. However, unlike for locomotor activity, there appeared to be a correlation between the number of gliders within a cage and the amount of food eaten. Unfortunately, when the amount of food consumed was divided by the number of animals within the cage, food intake per animal differed among the cages during each of the four measurement periods (Fig. 3.30; March: F=9.71 DF 2, 81 p<0.001; May: F=4.57 DF 2, 107 p=0.012; August: F=8.33 DF 2, 125 p<0.001; December: F=11.50 DF 2, 54 p<0.001, ANOVA). The animals in Cage 2 (5-8 individuals) consistently ate less per animal than the other two cages while animals in Cage 3 (3-5 individuals) consistently ate more. This difference among the cages was not due to different degrees of activity within the cages, as there was no correlation between the amount of food consumed per animal and total activity per day, but was most probably due to the difference in the size of the animals (Fig. 3.31). Animals within Cage 2 were, on average, lighter than those in Cage 3 throughout the year, though it was only significant during May and December (May: F=7.01 DF 2, 11 p=0.011, ANOVA; p<0.05, Tukey; December: F=5.91 DF 2, 9 p=0.023, ANOVA; p<0.05, Tukey). The mean mass of animals within Cage 1 did not differ from either of those in Cage 2 or Cage 3, however, there were only 2 animals within this cage making statistical analysis difficult. In addition to the mass differences among the cages, animals within Cage 3 were the only animals to significantly change their mass between the months (F=4.66 DF 3, 13 p=0.026, ANOVA), with a mean increase of approximately 32 g between August 96 and May 97 (p<0.05, Tukey). However, whether animals in Cage 3 ate more because they were larger or they were larger because they ate more, is a matter of conjecture.

Despite the differences among the cages, animals in each of the cages responded in a similar way regarding the amount of food consumed at different times of the year (Fig. 3.30). Animals in all cages reduced their food consumption during March

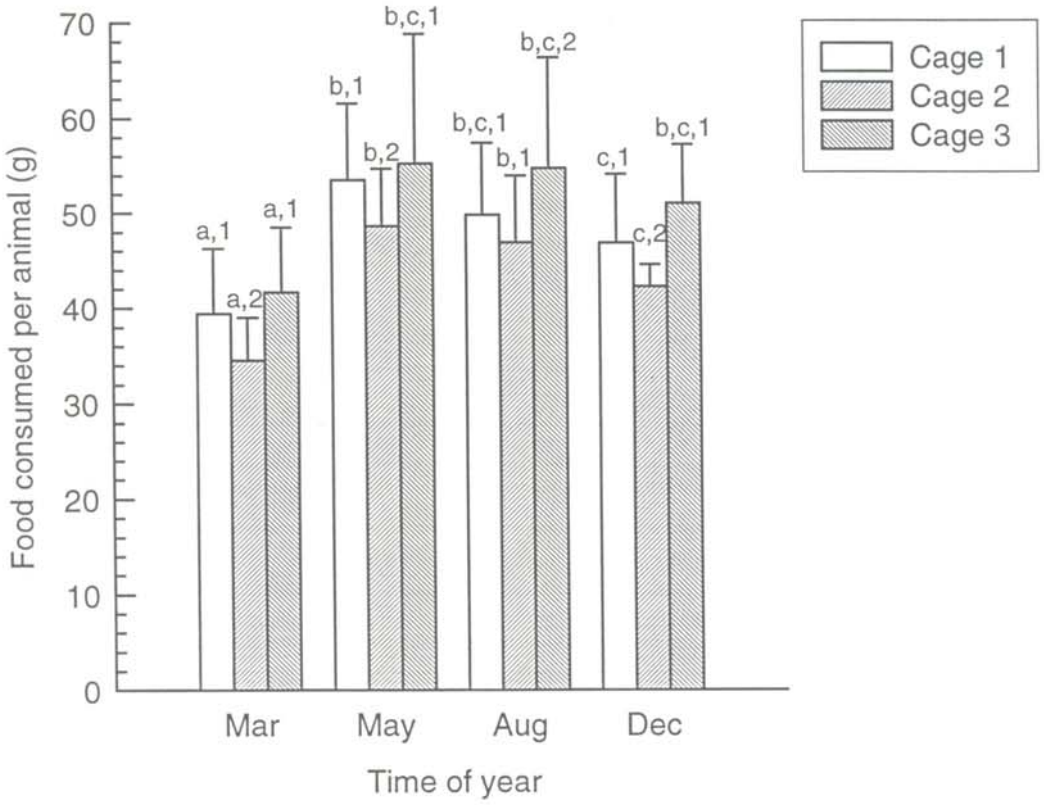


Fig. 3.30. Mean (±SD) amount of food consumed per individual *P. breviceps* at various times of the year. Different letters indicate significant differences ($p<0.05$) between months; different numbers indicate significant differences ($p<0.05$) between cages.

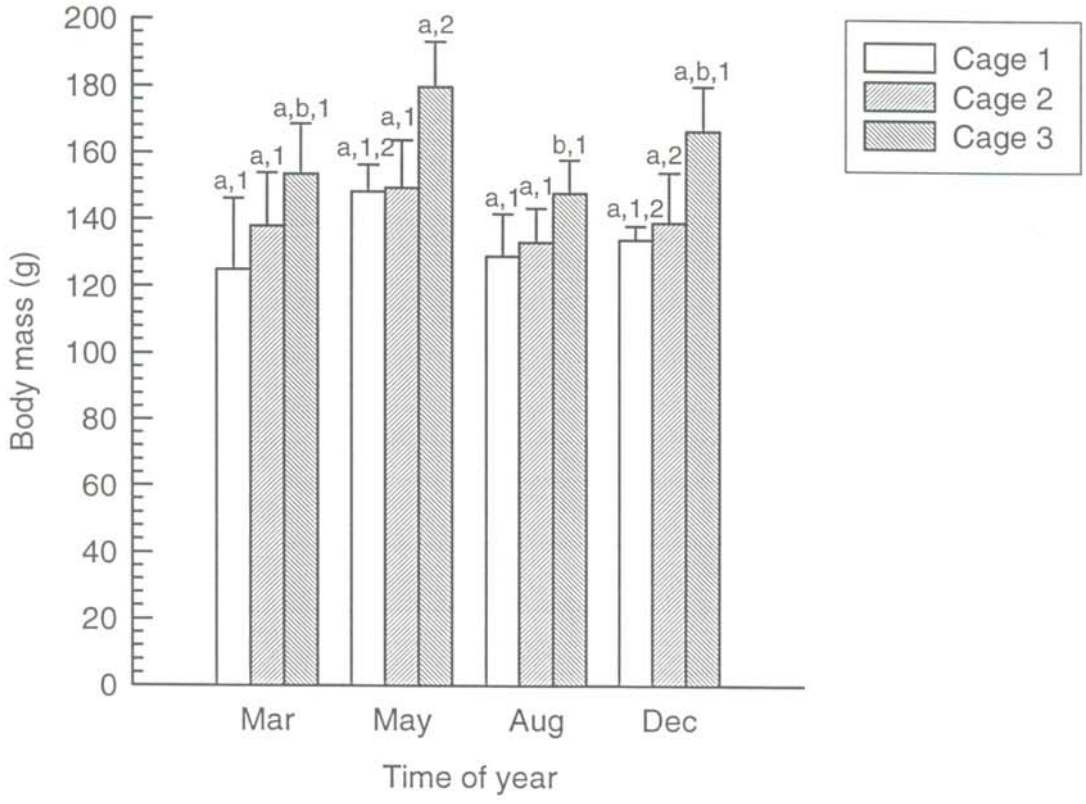


Fig. 3.31. Mean (±SD) body mass of *P. breviceps* during the periods when the amount of food consumed was measured. Different letters indicate significant differences ($p<0.05$) between seasons; different numbers indicate significant differences ($p<0.05$) between cages.

(Cage 1: 39.4±6.9 g; F=19.75 DF 3, 122 p<0.001;,ANOVA; p<0.01, Tukey; Cage 2: 34.55±4.5 g; F=38.10 DF 3, 123 p<0.001, ANOVA; p<0.01, Tukey; Cage 3: 41.7±6.9 g; F=10.70 DF 3, 122 p<0.001, ANOVA; p<0.01, Tukey). Food consumption was greatest in May, with a 36, 41 and 33 % increase in Cages 1 (53.5±8.0 g), 2 (48.7±6.1 g) and 3 (55.3± 13.5 g), respectively, over the amount eaten during March. August measurements showed a slight decrease in intake from that in May, though this difference was indistinguishable in all cages (Cage 1: 49.8±7.6 g, p>0.05; Cage 2: 47.0±7.0 g, p>0.05; Cage 3: 54.8±11.6 g, p>0.05, Tukey). Apart from Cage 3 (51.0±6.1 g), food consumption during December was significantly less than that during May (Cage 1: 46.9±7.2 g, p<0.05; Cage 2: 42.3±2.2 g, p<0.05, Tukey), and in Cage 2 it was also significantly less than that during August (p<0.05, Tukey). It should be noted that the food intake during May might be a slight underestimate, as there were a higher proportion of days during this measuring interval when the cereal mixture, despite efforts to try and prevent it happening by providing larger quantities of food, was completely eaten. Carrots and apples were also available to the gliders throughout the year, and while the amount eaten was not measured directly, a note was made of the relative proportion consumed. This was also noticeably higher in May, as gliders tended to eat the cereal mixture and revert to the apple and carrot when the cereal was gone.

Since colder T_a elicits higher metabolic rates, it would be expected that the amount of food consumed would match the energy expenditure and that during times of colder T_a, food consumption would increase. However, as there was no overall relationship between the two variables (F=2.23 DF 1,124 p= 0.138, r^2=0.02), the observed differences in food consumption were not due to differences in T_a. In addition, mean minimum T_a during August (3.91±3.1 °C) was significantly lower than during all other measuring intervals (F=80.82 DF 3, 122 p<0.001, ANOVA; p<0.01, Tukey), including May (7.34±2.4 °C) during which time food intake was at its peak. Despite the significant difference in food intake, mean minimum T_a during March (12.21±1.8 °C) and December (13.11±3.1 °C) were indistinguishable (p>0.05, Tukey).

3.3.7 Body composition:

Although data are presented for all animals CAT scanned at different times of the year (Table 3.15), analysis (repeated measures ANOVA) was restricted to only those 5 animals (Pb1, Pb6, Pb10, Pb11 and Pb12) that underwent all 4 scans.

3.3.7.1 Fat:

In agreement with the changes in locomotor activity and food consumption, the mean fat content of all gliders, calculated from CAT scans of live animals, also changed throughout the year (Table 3.15a; F=7.71 DF 3, 12 p=0.004, Repeated Measures ANOVA). The reduction in activity and increase in food intake observed during late autumn resulted in an overall increase in fat content during May compared to those same animals during September, December and March. All individuals underwent this increase, however, the amount of fat deposited was quite variable, with one animal (Pb10) doubling its fat content between the March and May measurements while others only had a marginal increase of 5 g. In all gliders apart from one (Pb1), the lowest amount of fat was found during September, and it appears that the animals may deposit excess fat and then rely on these stores to see them through the winter when they are most likely to have a negative energy balance. From examination of the CAT scans, it would appear that the excess fat is primarily deposited subcutaneously, with the layer of fat surrounding the body becoming thicker and more noticeable during May compared to all other scanning periods (Plate 3.1).

The relative percentage of body mass consisting of fat also differed with season (Table 3.15a; F=6.61 DF 3, 12 p=0.007, Repeated Measures ANOVA). An increase in May in the relative amount of fat was observed, with all individuals apart from one (Pb12) increasing the relative proportion of mass composed of fat. Again, all individuals apart from one (Pb9) subsequently decreased the proportion of fat between May and September.

Table 3.15 Body composition, as mass (g) and as a percentage of body mass, of *P. breviceps*, as derived from CAT scans at different times of the year for **A)** fat, **B)** muscle/organs, **C)** bone, and **D)** mass at the time of measurement.

A) Fat

Animal #	March		May		September		December	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
1	35	25.00	39	27.27	34	24.64	32	23.36
6	22	17.46	37	25.87	14	11.76	17	13.71
7	23	16.67	38	24.35	-	-	-	-
9	-	-	35	21.74	28	22.22	30	19.11
10	30	27.27	64	41.59	25	20.83	45	12.98
11	29	23.39	39	26.17	20	14.29	25	19.38
12	21	15.22	25	15.06	14	9.79	21	12.98
18	-	-	37	22.56	-	-	32	24.81
Mean	26.67	20.84	39.25	25.58	22.50	17.26	28.86	18.03
sd	5.54	5.01	0.99	7.52	7.99	6.11	9.12	4.93

B) Muscle/Organs

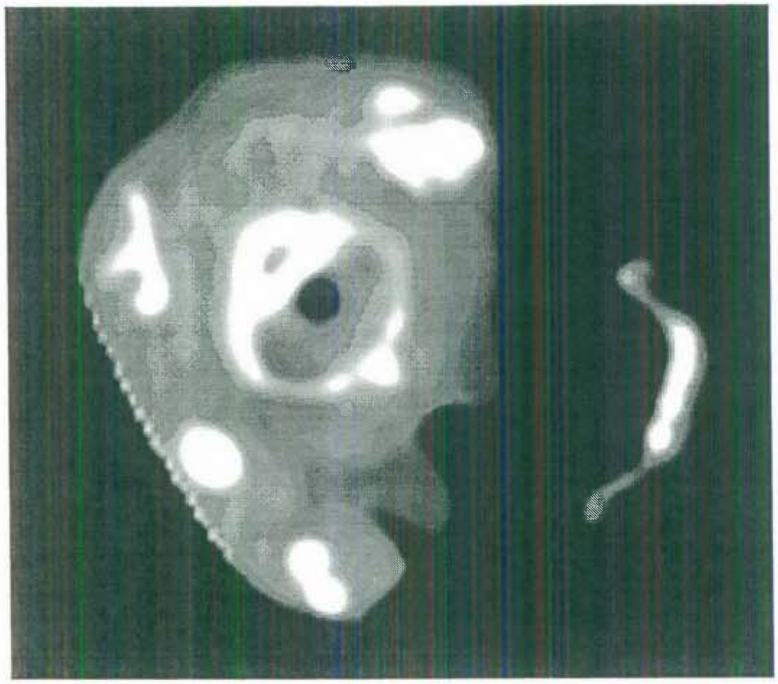
Animal #	March		May		September		December	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
1	54	38.57	61	42.66	36	26.09	32	34.31
6	55	43.65	53	37.06	60	50.42	58	46.77
7	59	42.75	54	34.74	-	-	-	-
9	-	-	76	47.20	53	42.06	65	41.40
10	44	40.00	47	30.52	55	45.83	38	29.01
11	54	39.13	62	41.61	69	49.29	64	49.61
12	50	36.23	87	52.41	61	42.66	64	40.19
18	-	-	74	45.12	-	-	46	35.66
Mean	52.67	40.06	64.25	41.42	55.67	42.73	52.43	39.56
sd	5.13	2.75	3.60	7.09	11.13	8.82	13.69	7.20

C) Bone

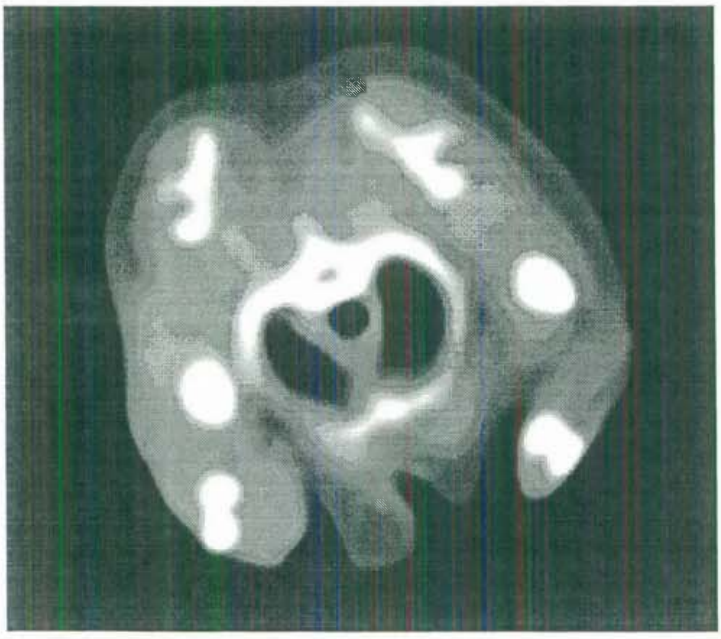
Animal #	March		May		September		December	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
1	20	14.29	22	15.38	11	7.97	19	13.87
6	20	15.87	19	13.29	25	21.01	22	17.74
7	22	15.94	21	13.64	-	-	-	-
9	-	-	22	13.66	23	18.25	28	17.83
10	17	15.45	19	12.34	23	19.17	11	8.40
11	17	13.71	22	14.77	23	16.43	19	14.73
12	12	8.70	34	20.48	23	16.08	26	16.14
18	-	-	26	15.85	-	-	14	10.85
Mean	18.00	13.99	23.13	14.93	21.33	16.49	19.86	14.22
sd	3.52	2.74	4.91	2.52	5.13	4.55	6.09	3.53

D) Mass at time of measurement

Animal #	March (g)	May (g)	September (g)	December (g)
1	140	143	138	137
6	126	143	119	124
7	138	154	-	-
9	-	161	126	157
10	110	154	120	131
11	124	149	140	129
12	138	166	143	158
18	-	164	-	129
Mean	129.33	154.25	131.00	137.86
sd	11.64	8.94	10.62	13.96



A) Pb1m: March



B) Pb1m: May

Plate 3.1. Example of CAT scan images of Pb1m taken during **A)** March and **B)** May. On the images, white = bone, light grey = muscle/organs, and dark grey = fat. Note the marked increase in subcutaneous fat of the animal during May compared to the animal in March.

3.3.7.2 Muscle/organs:

The mean amount of muscle, which also included organ tissue as they could not be distinguished by the grey scales, did not change with season, either in the absolute amount (Table 3.15b; F=1.28 DF 3, 12 p=0.327, Repeated Measures ANOVA), or the relative amount (Table 3.15b; F=0.19 DF 3, 12 p=0.904, Repeated Measures ANOVA). Furthermore, no consistent trend was observed within the individual gliders, with the amount of muscle/organs relatively consistent throughout the year. However, although not significant, a mean increase of approximately 11.5 g of muscle and organ tissue was present between the March and May measurements. The overall mean proportion of mass made up of muscle and organs was 40.92±6 59 %.

3.3.7.3 Bone:

As with the muscle and organ tissue, no seasonal changes in the absolute amount of bone (Table 3.15c; F=1.13 DF 3, 12 p=0.376, Repeated Measures ANOVA) or the relative amount of bone (Table 3.15c; F=0.34 DF 3, 12 p=0.799, Repeated Measures ANOVA) were observed. There was a marginal mean increase in bone of just over 5 g between March and May, but all measurements were, for the most part, relatively consistent throughout the seasons and bone made up 14.88±3.30 % of total body mass.

3.3.7.4 Body mass and body composition:

The increases seen in absolute amounts of fat (12.58 g) and muscle/organs (11.58 g) between March and May measurements accounted for 97 % of the observed increase in total body mass (Table 3.15d) between these measurements. When the increase in bone (5.13 g) is added, the increase in the components overshoots the increase in body mass by 4.37 g. Conversely, the decrease in fat, muscle and bone between May and September measurements is also greater than the decrease in total body mass during the same time

period. Therefore, there may be other changes occurring (eg. changes within the gastrointestinal tract or body water content) that could not be examined in this study.

3.4 Discussion:

Petaurus breviceps, maintained under natural photoperiod and temperature conditions, has adapted both its physiology and behaviour to cope with the seasonal changes in climate found in the New England Tablelands region of NSW. Body mass, BMR, metabolic scope, TNZ, RMR, AMR, ADMR, conductance, activity patterns, food consumption, and body composition all changed with season. These changes meant that during winter, presumably the time of highest stress due to colder T_a and lower food availability, animals had a much greater thermal capacity and tolerance of the cold.

A seasonal change in body mass of *P. breviceps* was also observed in wild animals at Willung, Victoria (Suckling 1984). However, animals at Willung were heaviest during summer and autumn, whereas in this study, while there was a small peak in mass during summer, the main increase occurred in late autumn/early winter. Quin (1993) also observed a seasonal change in body mass within a wild glider population located within the New England Tablelands region of NSW. However, the animals in Quin's (1993) study were heaviest in summer and lightest during autumn. Given that only three animals were weighed during autumn while no measurements were obtained during winter, plus the possibility that juveniles may have been included as the ages were not stated (Quin 1993), any conclusions made from this study would have to be viewed with caution.

Presumably, the mass increase occurs at a time when food is most abundant and is then used as a mechanism to improve survival during the winter - a time when food is more likely to be restricted and energy requirements high. Increased survival occurs because a larger body size reduces thermal conductance (Haim *et al.* 1991), thereby reducing the

amount of heat lost to the environment and the amount of energy required to maintain a stable T_b. Conversely, a decrease in mass would also aid animals in summer as it would facilitate heat dissipation. The increase in mass can be due to an increase in fat reserves, which an animal can rely on throughout periods of food stress, or an increase in the insulation layer, be it subcutaneous fat or thicker/denser fur, which would also add to the reduction in thermal conductance during times of cold stress. A number of other species also follow this strategy, including the pouched mouse, *Saccostomus campestris* (Haim *et al.* 1991); the collared lemming, *Dicrostonyx groenlandicus* (Reynolds & Lavigne 1988); streaked tenrecs, *Hemecentetes nigriceps* and *H. semispinosus* (Stephenson & Racey 1994); the mountain pygmy possum *Burramys parvus* (Körtner & Geiser 1995b); the fat-tailed dunnart *Sminthopsis crassicaudata* (Morton 1978c) and possibly male rufous rat-kangaroos, *Aepyprymnus rufescens* (Wallis & Green 1992), though this last observation was only based on a few animals.

However, there is another advantage to the sugar glider in increasing its mass during autumn, and that is reproductive success. Sugar gliders in temperate regions give birth between June and November, depending on their location (Fleay 1947; Suckling 1984; Stoddart *et al.* 1994). They live in large groups, up to 12 animals, of mixed sexes and have a social hierarchy (Fleay 1947; Suckling 1984). They are thought to be a polygynous species, and it is believed that the dominant male of the group, the one which is heaviest and also exhibits the highest concentration of testosterone (Stoddart *et al.* 1994; Bradley & Stoddart 1997), is responsible for most of the matings (Mallick *et al.* 1994). In addition, Klettenheimer *et al.* (1997) found that females which showed subordinate behaviour did not breed or were unable to successfully rear their young to independence. However, this may not be quite accurate or may be an artefact of captivity as Suckling (1984) observed that 99 % of all females aged 2 years and older, some of which must have been subordinates, on the Willung study site bred. Further, in two instances in the present study, young of two females in the same cage have been successfully reared to independence. Nevertheless, the advantages of increasing mass prior to the breeding season would still be

both ecologically and evolutionarily significant. It should be noted, however, that since all animals in the present study increased their mass during winter, including the small and presumably subordinate individuals, it has to be assumed that the main reason for the increase in body mass is to increase fat stores and decrease thermal conductance for survival over the winter months, rather than for the purposes of reproductive success.

While some species have adopted the strategy of increasing mass just prior to winter, many others do the reverse and decrease their mass and, in some instances, even shorten their body length through resorption of cartilage and flattening of the invertebral discs (Hyvärinen 1984). Species which employ this strategy include several of the vole and shrew families (Wunder *et al.* 1977; Dark *et al.* 1983; Hyvärinen 1984; Merritt 1984, 1986; McDevitt & Andrews 1995; McDevitt & Speakman 1996); the Djungarian hamster, *Phodopus sungorus* (Hoffmann 1973; Heldmaier & Steinlechner 1981); and the Australian bush rat, *Rattus fuscipes* (Stewart & Barnett 1983). In addition, Corp *et al.* (1997) observed that winter-acclimatised male wood mice, *Apodemus sylvaticus*, also decreased their mass in winter, which is the opposite result to what Haim *et al.* (1995) found with acclimated male and female wood mice of the same species. This difference may be due a number of factors including acclimation/acclimatisation effect, the effect of gender, latitude, habitat or individual variation within populations of the same species.

The reasoning behind the reduced mass strategy in winter is that a smaller body requires less energy to maintain (Wunder *et al.* 1977; Feist & White 1989). While a smaller size, due to its larger surface area to volume ratio, means a higher mass-specific metabolic rate (i.e. each gram of body tissue requires more energy to maintain), if mass is reduced sufficiently total caloric requirements for the whole animal would be less. In addition, the foraging time required would also be reduced, thereby resulting in a reduction in the time exposed to the colder T_a and more time enclosed within an insulated nest at T_a closer to thermoneutrality. In fact, a prairie vole, *Microtus ochrogaster*, requires less energy at

7.5 °C in winter than it does at the same T_a in summer (Wunder *et al.* 1977). However, given that summer T_a are actually a lot warmer and closer to thermoneutrality than they are in winter, the total energy expenditure involved in maintaining a stable T_b would most probably still be higher in winter than that in summer. Further, Reynolds & Lavigne (1988) have found that, even with a larger size in winter, collared lemmings (*Dicrostonyx groenlandicus*) do not require absolutely more food than their smaller summer counterparts.

It is interesting to note that, with the exception of the Australian bush rat, species which reduce their body mass in winter compared to summer are generally a lot smaller than those species which increase their mass in winter, and this may have some bearing on the strategy utilised. Due to their body size, very small animals are unable to carry much excess fat or longer fur and, therefore, are unable to greatly increase their insulation (Scholander *et al.* 1950c). While the bush rat (approximately 100 g) does have a lower mass in winter compared to summer, it does actually increase its mass to some extent during May/June (late autumn/early winter) before it slowly declines (Stewart & Barnett 1983). Consequently, it is thought that food availability is limited during this time and this species is unable to obtain enough food to maintain its mass. This brings up the interesting point as to when in the year body mass is measured. If sugar gliders are compared midwinter (July) to midsummer (January), the gliders are either heavier in summer than they are in winter or there is no change, depending on the year analysed. This is due to the increase occurring in late autumn and a subsequent slow decline of mass throughout winter. A mass increase similar to that observed here also occurs in the mountain pygmy possum, *Burramys parvus*, which fattens in autumn in preparation for winter hibernation (Körtner & Geiser 1995b). Therefore, determinations of body mass at only two time periods are not sufficient to quantify a seasonal pattern. This is especially important with regard to studies utilising photoperiodic acclimation.

The increase in body mass observed in *P. breviceps* during autumn appears to be correlated with a reduction in activity and a concomitant increase in food consumption. Activity is the most energetically expensive component of normothermic daily metabolic rates (Ruf & Heldmaier 1992; Holloway & Geiser 1996a). This is due to the additional energy required for muscular activity, the increase in conductance due to postural changes which results in a greater amount of surface area exposed, and the fact that an animal is exposed to the adverse environmental conditions. Active metabolic rates may also increase with decreasing T_a (McCarron & Dawson 1984; Holloway & Geiser 1995; present study), although this may only occur when activity is at low or moderate levels (Wunder 1970). Therefore, any behavioural modification involving a reduction in activity should result in energy savings.

Many species show an overall reduction in the intensity and/or duration of activity during autumn and winter (Kenagy 1973; Stebbins 1984; Frey 1991; present study) or under short photoperiod (Moffatt *et al.* 1993; Lindgård *et al.* 1995; Holloway & Geiser 1996a). Modifications to daily activity patterns may also involve the use of more thermally favourable foraging places or times; eg. decreasing surface activity to become more fossorial, and increasing diurnal activity in comparison to nocturnal foraging (Hoogenboom *et al.* 1984; Stebbins 1984; Reynolds & Gorman 1994). These changes in activity often appear to be particularly prevalent during periods of intense cold or inclement conditions (Kenagy 1973; Hoogenboom *et al.* 1984; Merritt 1986; Frey 1991). However, some observed seasonal changes in activity are not concerned with energy savings, but are primarily due to the effects of the reproductive season (Hall 1980; Körtner & Geiser 1995a), and not all result in an increase in body mass, but may also be utilised by those species that decrease their mass in winter. Stewart & Barnett (1983) postulated that the decrease in body mass may be due to the decrease in skeletal muscle due to the reduction in activity. However, in the sugar glider there did not appear to be any decrease in muscle mass associated with the decrease in activity.

The decrease in activity usually results in an increase in the time spent within a nest or burrow. This further facilitates the decrease in energy requirements due to the insulative properties of the nest, which may be further enhanced if a number of individuals occupy the same nest (Fedyk 1971; McDevitt & Andrews 1994). These savings, as discussed in Chapter 5, can be quite substantial.

With the increase in energetic demands due to the colder T_a, an increase in food intake should be required to at least maintain stable body mass. However, sugar gliders augment their food intake due to reasons other than just temperature, and this, combined with the reduction in activity, probably facilitates the observed increase in body mass. In some species of ground squirrel and marmot there exists a sliding set-point for body mass (Mrosovsky & Fisher 1969; Körtner & Heldmaier 1995), and it is possible that this is what regulates the seasonal change in body mass observed in sugar gliders. While some other species also show an increase in food intake concurrent with an increase in body mass (Haim *et al.* 1990; Lindgård *et al.* 1995), others show a decrease (Dark *et al.* 1983; Dark & Zucker 1984; Moffatt *et al.* 1993; Masuda & Oishi 1995). However, these decreases were all observed in those species which also decrease their mass during winter as an energy-saving mechanism.

Despite a reduction in total activity during winter, and maintaining a high intake of food, there was a steady decline in the body mass of *P. breviceps* throughout this season. Consequently, it appears that the sugar glider's overwintering strategy may be to increase body mass prior to the onset of winter, through a decrease in activity and an increase in food intake, and then remain in their nests as much as possible throughout the most stressful period of the year, although there is some foraging and activity during this period, and rely on their stores of fat. To further enhance their survival and reduce their energy requirements, some physiological processes, involving maintenance and resting metabolism, also undergo seasonal changes.

The BMR of an animal reflects the energetic requirements necessary for the maintenance of that animal. Marsupials are known to have BMR that are generally lower than those of placentals (Dawson & Hulbert 1970), and, as such, *P. breviceps* fits this pattern. However, whereas Dawson & Hulbert (1970) calculated that the BMR of marsupials are generally 30 % lower than those of placentals, the BMR of sugar gliders fell, on average, 45 % below the allometric equation for placentals calculated by Kleiber (1961). Consequently, the BMR of sugar gliders were also substantially less (79.6, 82.6, 80.7, and 70.5 % of prediction for spring, summer, autumn and winter, respectively) than that predicted by Dawson & Hulbert (1970). Hayssen & Lacy (1985) also calculated an allometric equation for marsupials and, once again, the values obtained from the present study fell well below those predicted for an animal of a similar mass.

When Fleming (1980) measured BMR of sugar gliders, the value he obtained was slightly above (106 %) that predicted for a marsupial of a similar size. Furthermore, Dawson & Hulbert (1970) measured the BMR of 6 gliders and obtained a similar, though slightly lower, value which was subsequently used in the calculation of an allometric equation for marsupial BMR. As the mean masses were similar in all studies, the reason for the discrepancy between these values and the ones obtained in the present study was not due to differences in body mass. Rather the difference may be due to the extent of time the animals were allowed to acclimate to the chambers, as this may be a source of great variation if animals are exhibiting elevated metabolism in response to handling (Hayes *et al.* 1992). In both of the previous studies, measurements began after only a short period (1 hour in the case of Fleming 1980) within the chamber and the effects of stress may have been reflected in the higher T_b obtained in these studies compared to the present one. Attempts were made in the present study to measure animals placed within the chamber early in the morning of the day of measurements. However, T_b, and presumably metabolic rate, remained elevated throughout the entire day and it was not until after a period of activity, i.e. the night or at least part of it, that T_b dropped to levels obtained when the gliders were

left undisturbed in their nest box. In addition, the period overnight within the chambers assured that these animals were truly postabsorptive.

The BMR of a species may not only be associated with the phylogeny of that species but also with diet, habitat, use of torpor, geography and evolutionary history (McNab 1986, 1988; Lovegrove 1996). Of the known BMR of other Australian arboreal possums and gliders, only that of the small feathertail glider (*Acrobates pygmaeus*) and eastern pygmy possum (*Cercartetus nanus*) were substantially lower than the predicted level (Fleming 1985; Song *et. al* 1997). Other recorded values (*Trichosurus vulpecula*, Dawson & Hulbert 1970; *Pseudocheirus occidentalis*, Kinnear & Shield 1975; *Petauroides volans*, Foley 1987) were either indistinguishable or slightly above the predicted values. Even the BMR of *Gymnobelideus leadbeateri* (Smith *et al.* 1982), a species of similar habits and size, with the exception of the gliding membrane, to that of *P. breviceps*, was similar to the predicted level. Therefore, it appears unlikely that the low BMR measured in the present study was due to the above factors, but it may be due to a difference in methodology. All the species mentioned, like *P. breviceps*, are nocturnal. As such, they may also require a period of nighttime activity prior to any measurements being taken in order to ensure that the animals are absolutely settled.

Despite the debate over which grouping best determines BMR (eg. phylogeny, habitat, zoogeography), the most powerful predictor is still size (Kleiber 1961), in particular total body mass (Scott *et al.* 1996). Even over the relatively small mass range in the present study, size accounted for 24 % of the variation found in the absolute BMR of sugar gliders, though it was less (10 %) when interpreting the mass-specific values. Furthermore, when divided into seasons, the size relationship improved in all instances. The form of the allometric relationship is generally $BMR=aM^{0.75}$, where "a" is a constant and "M" is body mass (Kleiber 1961). However, there is some debate over what the precise value for the mass exponent should be (Feist & White 1989). In a number of studies involving marsupials the exponent has been calculated to be approximately 0.75 (Kleiber 1961;

MacMillen & Nelson 1969; Dawson & Hulbert 1970; Hayssen & Lacy 1985). However, Heusner (1991) determined the exponent for 391 species of mammal, including 48 marsupial species, to be 0.678. In the present study, when all seasons were combined, the exponent was calculated to be 0.624, which is close to the Heusner (1991) two-thirds value. Nevertheless, it must be remembered that there was only a 52 g range in mass in the present study, far from the greater than 9:1 size ratio required for establishment of a slope different to 0.67 (Schmidt-Nielsen 1972).

Scholander *et al.* (1950a) concluded from studies involving mammals from the arctic and the tropics that the BMR of terrestrial mammals is "fundamentally determined by size, and is phylogenetically nonadaptive to external temperature conditions". However, BMR in a number of species has been known to change in response to season. These include certain species of shrew (Merritt 1986), voles (Wunder 1984; McDevitt & Speakman 1996) and mice (Lynch 1973; Ellison & Skinner 1991; Haim *et al.* 1991), and the Djungarian hamster, *Phodopus sungorus* (Heldmaier & Steinlechner 1981), all of which were seasonally acclimatised; the Cape porcupine, *Hystrix africaeaustralis* (Haim *et al.* 1990), and the marsupials *Dasyuroides byrnei* (Smith & Dawson 1984) and *Monodelphis domestica* (Dawson & Olson 1988), which were all seasonally acclimated to photoperiod and T_a. All of these species exhibited elevated BMR under winter conditions compared to summer. On the other hand, the seasonally acclimatised pygmy shrew, *Sorex minutus* (McDevitt & Andrews 1995), red-backed vole, *Clethrionomys gapperi* (Merritt 1984), and *P. breviceps* (present study), all decreased their BMR in winter. This dichotomy of strategies is not confined to just mammals. In seasonally acclimatised birds, the sage grouse *Centrocercus urophasianus* elevates its basal metabolism in winter (Sherfy & Pekins 1994), whereas the reverse occurs in the knot, *Calidris canutus* (Piersma *et al.* 1995).

The seasonal difference in BMR can be partially explained by seasonal differences in body mass - a smaller body mass results in a larger mass-specific metabolic rate, and vice versa. As mentioned above, size accounts for up to 25 % of the variability witnessed in the sugar

glider. However, it is not the whole answer as, apart from the unaccounted variability, some animals, such as *Apodemus sylvaticus* (Haim *et al.* 1995) and *Dicrostonyx groenlandicus* (Reynolds & Lavigne 1988) may increase their mass without changing their BMR, while others (eg. *Sorex minutus*; McDevitt & Andrews 1995) may decrease both their body mass and basal metabolism. In addition, while the relationship between mass and BMR remained the same in the present study, the elevation of the regression equations differed when the data were divided into individual seasons and the amount of variability substantially decreased. Therefore, there must be some seasonal acclimatisation apart from just a difference in size or mass.

One explanation for the unaccounted difference is that BMR is related to maximum metabolic capacity; an increase in BMR may be a consequence of an increase in metabolic capacity (Wunder 1984). However, in the case of sugar gliders this does not provide an answer as metabolic capacity increased with a decrease in BMR.

As mentioned previously, BMR is basically the energetics of maintaining the body and its components. Therefore, since body organs are metabolically active and expensive to maintain (Piersma & Lindström 1997), a reduction in the size of some or all of the body's organs, should result in a reduction in BMR. Indeed, studies investigating seasonal changes in body composition have shown that a number of systems, including the digestive, integumentary, cardiovascular, adipose, muscular, reproductive, urinary, hemal and hemopoietic systems, may alter with season (Lynch 1973; Stewart & Barnett 1983; Quay 1984; Dawson 1989; McDevitt & Speakman 1994). Unfortunately, with the sugar gliders, the set-up during the measurements of the CAT scans made it impossible to calculate the size of each organ or to differentiate them from skeletal muscle. It is therefore possible that, while the absolute and relative amounts of total muscle and organ tissue varied only slightly throughout the year, there may have been substantial decreases in some structures and increases in others. Since the contribution of different organs to the level of BMR and the physiological mechanisms controlling it are currently unknown (Heldmaier *et al.* 1986),

this may be a reason for the seasonal change in BMR. However, a detailed budget on the energy gains and losses connected with seasonal changes in organs has not yet been calculated (Piersma & Lindström 1997). It has been estimated that it costs the burmese python, *Python molurus*, 30 % of the assimilated energy from a large meal to double the mass of the small intestine and increase the masses of the liver and kidneys by 45 % (Secor & Diamond 1995). Consequently, it is possible that, if there are any changes in the size and composition of organs in the sugar glider, the energy savings to be achieved are only small. Therefore, other, as yet unknown, factors may also be contributing to the seasonal change in BMR witnessed in *P. breviceps*.

Along with seasonal changes in BMR, alterations may also occur in the length or the placement of the TNZ. The TNZ is the region where normothermic T_b can be maintained via changes in conductance, without the need to increase metabolism from basal levels (Scholander *et al.* 1950b). In a number of species there is a seasonal shift in the T_{lc}, with a decrease usually occurring in winter (Heldmaier & Steinlechner 1981; Reynolds & Lavigne 1988; Haim *et al.* 1990, 1991, 1995; Corp *et al.* 1997). This shift may just be the result of having an elevated BMR during winter. However, for this to be the case, thermal conductance must remain constant throughout the year (Heldmaier & Steinlechner 1981), which it often is not. Another reason for the shift in the T_{lc} may be as a direct result of changes in conductance making the animal less susceptible to lower temperatures. Conversely, the shift downwards in the T_{lc} during winter means that there may be a similar shift upwards in the T_{uc} in summer, resulting in a more heat tolerant animal (Reynolds & Lavigne 1988; Haim *et al.* 1991, 1995). However, this may not always be the case as the shift downwards in T_{lc} may be the result of a widening of the TNZ and the T_{uc} may remain unchanged throughout summer and winter (McDevitt & Andrews 1995). Unfortunately, much less work appears to be have been done, probably due to the high risk of heat stress to the animals, on seasonal changes in the T_{uc}.

Fleming (1980) calculated the TNZ of sugar gliders held under natural photoperiod, but at constant-temperature and season unknown, to be 27-31°C. This closely resembles that calculated for spring from the present study. While the T_{lc} of *P. breviceps* was not significantly different among the seasons, there was a tendency toward lower T_{lc} during the colder seasons, which may have been a result of a decrease in conductance during these seasons. Deviation from a mass-predicted T_{lc} is thought to be a measure of adaptation of an animal's thermal physiology, and an equation to predict the T_{lc} of marsupials was derived by Fleming (1980) from the equations of Dawson & Hulbert (1970) and Kinnear & Shield (1975): $T_{lc} = T_b - 3.2W^{0.171}$, where "W"=body mass in grams. From this equation, it can be determined that the measured T_{lc} from the present study were between 0.7 and 1.4 °C lower than those predicted. This deviation below the mass-predicted T_{lc} implies that this species on the New England Tablelands is thermally adapted to a cold environment (Scholander *et al.* 1950a; Bartholomew 1982), whereas a deviation above that predicted is more often found in those species that primarily use torpor in cold conditions (Morrison 1960).

The upward shift in T_{uc} of *P. breviceps* during spring, summer and autumn results in an increased tolerance of T_a up to 2.5 °C higher than those in winter before the necessity for physiological cooling to commence. Due to the arbitary delineation of the seasons, both spring and autumn may experience both hot and cold extremes of T_a. Despite being mid-autumn in the New England region, T_a may occasionally approach 31 °C in April with the highest T_a recorded being 31.6 °C, while maximum T_a in October (mid-spring) has been recorded as high as 32.4 °C (Bureau of Meteorology 1997). The shift in T_{uc}, however, appears to be the only physiological adaptation to heat in this species. Above the TNZ summer RMR, probably due to the elevated BMR, are still substantially higher in comparison to the other seasons, despite the significant increase in conductance and the lighter body mass. However, in the New England Tablelands region of NSW, lack of adaptation to heat is not a major problem as maximum T_a are, on average, generally lower than the T_{uc}. The highest maximum T_a that has been recorded in Armidale since 1857 is

39.6 °C, which was recorded during January (P. Burr, pers. comm.). While this T_a might be close to the thermal limit of some of the heavier animals in autumn, it would appear that animals in all other seasons, especially summer during which the highest T_a occur, should be able to tolerate the heat, especially given that this was a rare extreme. Further, it should be noted that the animals reside in tree hollows during the day where T_a should be cooler than those experienced in the open

On the other hand, adaptation to cold appears to be a much more important and necessary adjustment for this nocturnal species in the New England Tablelands region, as sugar gliders are active when daily T_a are low. T_a have dropped as low as -11.0 °C in July (midwinter; average 0.4 °C) and even in January may fall as low as 4.4 °C, although the average minimum T_a for this month is 13.4 °C (Bureau of Meteorology 1997).

For homeothermic animals restricted in their habitat, there are basically two options for coping with the cold: i) reduce heat loss which will also reduce the amount of energy required to maintain T_b; and ii) increase the maximum heat output which would result in a greater tolerance to the cold (Scholander 1955; Wunder 1979). *Petaurus breviceps* does both.

The seasonal reduction in RMR observed in *P. breviceps* during winter is comparable to that observed in a number of other species (Heldmaier & Steinlechner 1981; Reynolds & Lavigne 1988; Andrews & Belknap 1993; Stephenson & Racey 1994; McDevitt & Andrews 1995), including some dasyurid marsupials (Geiser & Baudinette 1987). Alternatively, several other species increase their RMR during winter (Wunder *et al.* 1977; Smith & Dawson 1984; Merritt 1986; Corp *et al.* 1997). This increase in RMR appears to be correlated with a reduction in body mass, which results in a larger surface area to volume ratio, thus necessitating an increased metabolic output in order to maintain a stable T_b. However, in those species observed to decrease RMR in winter there appears to be no such correlation, with body mass either increasing, decreasing or remaining the same.

Rather, the reduction in RMR in *P. breviceps,* and those species in which both parameters were measured, appears to be due to a decrease in thermal conductance, i.e. a reduction in the amount of heat lost from the body.

Despite their relatively small size, which should preclude them from substantially altering their insulation (Scholander *et al.* 1950c), sugar gliders are able to reduce their conductance by approximately 20 % in winter compared to summer. This change is achieved primarily by the deposition of subcutaneous fat which, apart from increasing the mass of the animal and thereby reducing the surface area to volume ratio, also acts as insulation around the tissues and the body itself, thus retarding heat flow. Another possible avenue for changes in conductance is via alterations to fur length and/or density. However, in the present study fur characteristics were not measured and, if any changes did occur, they were not visually apparent.

Seasonal changes in conductance have been observed in many species and, for the most part, involve a reduction during winter (Reynolds & Lavigne 1988; Haim *et al.* 1990, 1991, 1995; Andrews & Belknap 1993; Corp *et al.* 1997). These reductions in conductance can range from 20 % to as high as 70 % (see Feist & White 1989). However, in some species such as the Djungarian hamster, *Phodopus sungorus*, conductance remains stable throughout the year, despite an increase in fur insulation (Heldmaier & Steinlechner 1981). The reason for this disparity is due to a concomitant reduction in body mass which would otherwise result in an increase in the rate of heat loss if insulation was not also increased. With *P. breviceps*, the combination of an increase in body mass with an increase in insulation results in a decrease in conductance in winter, which ultimately causes a reduction in RMR.

As with BMR, the RMR values obtained by Fleming (1980) were substantially, between 1.2 to 1.5 times depending on the season, higher than those measured here. In addition, the slope of the linear regression of RMR as a function of T_a below the T_{lc} was steeper. Again,

as was the case with the BMR measurements, this is most probably due to the difference in methodology. However, it is possible that the difference may also be in part due to latitudinal differences, as Fleming's (1980) animals were located in Victoria (35 km north-east of Melbourne) and those measured here in the New England Tablelands, New South Wales. While maximum T_a are similar between the two areas throughout the year, monthly minimum T_a between April and October are up to 4 °C lower in the Tablelands region (Bureau of Meteorology 1997).

Another possible reason for the higher RMR values may be a higher conductance. Fleming (1980) calculated that his animals had a mean conductance value of 0.084 mL g^{-1} h^{-1} °C, which was 65, 35, 42 and 65 % higher than the values obtained in the present study for spring, summer, autumn and winter, respectively. It would appear that Fleming (1980) derived the conductance value from the slope of the regression line of RMR versus T_a below the T_{lc}. However, this method can only be applied if conductance is constant and minimal below the TNZ, T_b is constant, and the regression line extrapolates to T_b at the intersection of the abscissa (Bradley & Deavers 1980). In the case of sugar gliders only one of these assumptions, the constant T_b, is correct. Further, given that the slopes of the regression lines were the same in all seasons, by using the slope of the correlation between RMR and T_a no seasonal difference in conductance would have been discerned. Consequently, use of the equation Conductance=RMR/(T_b-T_a) is considered to be the more accurate method (Herreid & Kessel 1967; Bradley & Deavers 1980; McNab 1980).

Conductance and body size are inversely related (Scholander *et al.* 1950a, b, c). Using the allometric equation calculated by Bradley & Deavers (1980), the resting conductance values obtained in the present study are substantially lower, between 36-47 % depending on season, than predicted. This allometric equation is considered to be a good estimate of the line representing all mammalian species as it has narrow confidence intervals and a high correlation coefficient. Further, it also included a number of marsupials among the 192 species used for its derivation. However, when certain groups and orders were analysed

separately (eg. heteromyid and cricetid rodents, Chiropterans), different relationships were found (Bradley & Deavers 1980). These deviations are thought to be due to body form, the naked wings of Chiroptera facilitate heat loss thereby resulting in a higher than expected conductance, or, for those species with lower than predicted values, an adaptation to nocturnal activity in regions with low T_a during the night (Bradley & Deavers 1980). This last factor also applies to sugar gliders and may be the reason for their lower than predicted values, although no similar difference was observed in dasyurid marsupials, many of which also experience low T_a during their nocturnal activity (MacMillen & Nelson 1969). It should be noted that despite the fact the lightly furred patagium contributes about 51 % to the surface area of sugar gliders (Dawson & Hulbert 1970), during rest it is not exposed and, therefore, probably only influences thermal transfer during activity or in warm environments.

In addition to decreasing heat loss through a reduction in conductance, *P. breviceps* also increases its maximum heat output during winter compared to summer. This is the first time that a change such as this has been observed in a seasonally acclimatised marsupial. In cold acclimated *Dasyuroides byrnei* (Smith & Dawson 1985; Dawson *et al.* 1986) and *Monodelphis domestica* (Dawson & Olson 1988) maximum metabolic rates were indistinguishable from warm acclimated animals. However, the length of time that the summit metabolism (HP_{max} sustained over a longer period, 1-2 h, in contrast to peak metabolism which can only be sustained for 3-20 min: Hart 1971; Smith & Dawson 1985) could be maintained was longer for both species in the cold acclimated animals. Therefore, it is possible that metabolism may have peaked higher if T_a had been lowered further in the cold acclimated group, although the slight decline observed in T_b may be an indication that the animals were close to their maximum rate.

Seasonal changes in peak metabolism have been observed in a number of placental species (Rosenmann *et al.* 1975; Feist 1984; Andrews & Belknap 1985; Heldmaier *et al.* 1986;

Haim *et al.* 1991; McDevitt & Speakman 1996). Basically, there are three forms of heat production: i) basal metabolic heat from the maintenance of tissues and organs; ii) shivering thermogenesis, from the action of skeletal muscles; and iii) non-shivering thermogenesis (NST), from which the primary source is believed to be brown adipose tissue (BAT). NST is thought to be primarily responsible for the increased capacity for heat production in the aforementioned species during winter (Heldmaier *et al.* 1986). However, this may not be true for all species as some animals rely on a reduction in heat loss and/or shivering thermogenesis, with little or no change in NST (Blank & Ruf 1992). Further, if marsupials do use NST, and at present there is only limited evidence for certain macropods (Nicol *et al.* 1997), it must be via a different source than BAT as unequivocal evidence has not yet been found for the presence of BAT in any marsupial. Currently, skeletal muscle is being investigated as a possible source of NST in marsupials (Eldershaw *et al.* 1996).

Unfortunately, it is impossible to determine from this study whether NST was present and was the cause of the observed increase in HP_{max} in sugar gliders. However, there may have been a seasonal increase in shivering thermogenesis. Although no seasonal change in the combined mass of muscle and organ tissue was observed, it is possible that muscle mass increased while some organs decreased in size. Given the apparent lower cost of maintenance of muscle compared to that of many organs (Schmidt-Nielsen 1984), this would also correspond to the winter reduction in BMR. It should be noted, however, that the degree of seasonal change in shivering is limited by the size of the animal, with small animals unable to achieve significant increases in muscle mass (Wunder 1984). Further, while shivering increases heat production, it also increases convective heat losses from the body surface (Webster 1974). Consequently, heat production via shivering may not be as efficient a source of heat as NST.

The combination of a lower BMR and a higher peak metabolism results in a metabolic scope for *P. breviceps* that is 37 % higher in winter compared to summer. The metabolic scopes measured in this study are lower than others recorded for some marsupials (4.7-6.4,

present study *cf.* 8-13: Dawson & Dawson 1982; Smith & Dawson 1985; Dawson *et al.* 1986; Dawson & Olson 1988), but are quite adequate to deal with the lowest T_a experienced in the Northern Tablelands region. Further, the values obtained here were for fasted animals. Therefore, as food digestion may add as much as 30 % to resting metabolism (Hill 1976), it is possible that the HP_{max} values obtained in the present study are underestimated.

From the values obtained in this study, *P. breviceps* are able to effectively withstand T_a as cold as -26 °C, 15 °C colder than during summer. Consequently, as the lowest recorded minimum T_a in Armidale (New England Tablelands) is only -8.2 °C (Bureau of Meteorology 1997), sugar gliders are well adapted to cope thermogenically with the colder T_a experienced in this region. This cold limit also allows them a certain amount of latitude to withstand the effects of windchill and rain which can substantially reduce T_a. When HP_{max} is divided by minimum conductance, the maximum temperature differential tolerable by an animal can be calculated (Rosenmann & Morrison 1974). Using this method, sugar gliders can tolerate a T_a range of 61.2, 44.3, 44.8 and 64.3 °C during spring, summer, autumn and winter, respectively. These values are in good agreement with the range of T_a the animals actually coped with during this study, although animals in autumn and, to a lesser extent summer, had a slightly wider effective T_a range.

As most energy is expended on maintaining T_b, it would be reasonable to assume that a reduction in T_b would result in a reduction in energy expenditure. However, the savings to be gained from this method are only slight (Scholander *et al.* 1950a), unless there is a substantial drop in T_b like that found in torpor (Holloway & Geiser 1995). Therefore, observed seasonal changes in T_b (Wollnik & Schmidt 1995) may not be due to the need to save energy, but rather due to some other factor such as reproductive status (Körtner & Geiser 1995a).

At the same T_a, the reduction in RMR in *P. breviceps*, combined with the shorter daylength, results in a lower total photophase metabolic rate in winter compared to summer. In addition, at lower T_a the proportion of daily metabolic rate comprised of the photophase metabolism increases. This is especially important since photophase metabolic rates are much lower than those during the scotophase. Consequently, the changes in activity combined with the lower RMR and the differing proportions of photo-/scotophase metabolism results in total daily expenditure which displays no seasonal differences, despite the different length of activity periods in each season. Therefore, it would appear that sugar gliders have the same total daily energy expenditure in winter as they do in summer. However, since T_a in summer are considerably higher than those in winter, animals will, in reality, still expend more energy on a winter's day. In fact, by using average minimum and maximum T_a to calculate daily expenditure, sugar gliders require approximately 70 % more energy to maintain their normothermic T_b in midwinter (54.0 mL g^{-1} day^{-1}) compared to midsummer (31.7 mL g^{-1} day^{-1}).

Nagy & Suckling (1985) calculated a field metabolic rate for *P. breviceps* at Willung, Victoria during spring to be 169 kJ day^{-1}, which is comparable to Quin's (1993) calculation of 157 kJ day^{-1} throughout the year at Newholme, Northern Tablelands, NSW. While these figures are reasonably close to the above estimate from the average maximum and minimum for winter, they are substantially higher than that for summer (winter 145.8 kJ day^{-1}; summer 81.3 kJ day^{-1}; conversion factor 20.083 J (mL O_2)$^{-1}$; Schmidt-Nielsen 1990). What must be remembered, however, is that in the wild activities such as foraging, territorial defence of the 0.5 to 5 ha home ranges (Suckling 1984; Quin *et al.* 1992) and competition for reproductive dominance and success would probably be more energetically expensive than the activity measured in the present study.

What is interesting is the fact that Quin (1993) observed no differences in field metabolic rates associated with season, despite the obvious changes that would be experienced in T_a throughout the year, and the above estimates from this study. If it can be assumed that the

differential between the field and estimated metabolism from the present study is due to higher expenditure for activity, then sugar gliders probably conserve more energy in winter via the reduction in their nocturnal activity. In addition, this species probably utilises modifications such as huddling and increased use of nests, combined with daily torpor (discussed in Chapter 5), to assist in maintaining their daily metabolic rates in the field stable throughout the seasons. In fact, although it was not quantified, it was noticeable during the present study that nests were more prevalent and thicker during the colder days.

In conclusion, *P. breviceps* modifies many aspects of its thermal physiology, morphology and behaviour to cope with the seasonal changes in climate and the associated environmental stresses these bring. What controls these modifications is not yet known. Photoperiod, T_a, and food availability have all been linked to such seasonal changes. In this study at least, food availability does not appear to be a factor as food was available at all times *ad libitum*. The most likely cause would be photoperiod, either critical length or rate of change, as it is a more predictable seasonal cue than T_a, the depth and timing of which can change from year to year.