Chapter 6

Nutritional Status Studies

6.1 Introduction

Urodacus manicatus do not actively seek out their prey. The scorpions remain at the entrances of their burrows ("door-keeping") instead and ambush prey that, by chance, move into close proximity to the scorpions. Therefore the feeding events of *U. manicatus* are dependent on the prey abundance. *U. manicatus* are long lived (Smith 1966) and they must be able to survive many seasons of low prey abundance. Being ectothermic, the lower microhabitat temperatures of the cooler months reduce metabolic expenditure at a time when prey numbers have decreased. However, heating of the home site by solar radiation can increase burrow temperatures (Chapter 3) such that metabolic expenditure increases during the day in winter. In addition, prey abundance may also decrease during summer when seasonal microhabitat temperatures are greatest.

In this chapter, the means by which *Urodacus manicatus* adjust to different nutritional states are determined by:

1. examining the effect of feeding and starvation on mass and metabolic rate.

2. examining the effect of feeding and starvation on temperature selection and activity.

6.2 Materials and Methods

Adult male and non-gravid female scorpions were collected from Black Mountain in early October (mid spring) and were maintained at 25°C in the laboratory and fed and watered *ad libitum* for a week. Animals were divided into two groups to separately examine the effect of

food on $\dot{V}O_2$ (Section 2.3) and temperature selection (Section 2.4) so that each could be measured soon after prey consumption. Food was withheld for three weeks in an attempt to ensure feeding over one night occurred after pre-feeding measurements were taken. On the day after initial measurements were conducted three *Tenebrio molitor* larvae where introduced into each animal's container just prior to darkness. The following morning, $\dot{V}O_2$ was measured or animals were introduced to the temperature gradient apparatus depending on which group they belonged to. Containers were checked the next morning for the number of larvae consumed 14 hours after their introduction. Measurements and the feeding of animals from each group were staggered over days as not all animals could be processed at the same time. Females that were provided with larvae *ad libitum* after the initial feed were treated as controls for the temperature selection group only.

Males and females were tested separately for the effect of nutritional status on mass. For males, a profile analysis was performed on five repeated measure dependent variables associated with days (pre-fed, then 1, 5, 21 and 42 days after feeding). For females, a similar profile analysis was conducted except that nutritional status (fed *ad libitum* and starved) was the grouping variable. A *post hoc* test using simple effects analysis was then conducted to examine the mean differences between adjacent days. For each analysis there were no univariate or multivariate within-cell outliers at $\alpha = 0.001$. Results of evaluation of assumptions of normality, homogeneity of variance-covariance matrices, linearity, and multicollinearity were satisfactory for the non transformed data. All repeated measures test results are given using Wilk's criterion.

For the effects of nutritional status and sex on RMR, mass was first tested for its adjustment of overall $\dot{V}O_2$ to utilise the allometric relationship between RMR and animal body size (Section 3.1). All correlations between mass and $\dot{V}O_2$ for both sexes, and each day, and temperature were non significant ($P > 0.05$). The results are not presented here because of their large volume. The size range within each sex was judged to be too narrow, therefore covariate analysis was abandoned. Instead, two profile analyses were performed, one on overall $\dot{V}O_2$, and the other on mass-specific $\dot{V}O_2$. The analyses were conducted on fifteen repeated measure dependent variables at two levels associated with days (pre-fed, then 1, 5, 21 and 42 days after feeding) and the temperature at which $\dot{V}O_2$ was measured (20, 30 and 40°C). The grouping variable was sex. *Post hoc* tests using simple effects analyses were then conducted to examine parallelism between

the sexes in the profiles of $\dot{V}O_2$ on each day. For each analysis there were no univariate or multivariate within-cell outliers at $\alpha = 0.001$. Results of evaluation of assumptions of normality, homogeneity of variance-covariance matrices, linearity, and multicollinearity were satisfactory for the non-transformed data. All multivariate repeated measures test results are given using Wilk's criterion.

For the effect of nutritional status and sex on Q_{10}, a profile analysis was conducted on ten repeated measure dependent variables at two levels associated with days (pre-fed, then 1, 5, 21 and 42 days after feeding) and the temperature ranges at which $\dot{V}O_2$ was measured (20-30 and 30-40°C). The grouping variable was sex. All multivariate repeated measures test results are given using Wilk's criterion.

Males were not fed *ad libitum* for the effects of nutritional status on temperature selection, so to avoid unevenness in the designs of the analyses, males and females that were starved and females that were fed *ad libitum* were compared as three categories under the one grouping variable. Three profile analyses were performed on twenty-five repeated measure dependent variables at two levels associated with days (pre-fed, then 1, 5, 21 and 42 days after feeding) and the time periods: 15-18:00 h, 18-21:00 h, 21-24:00 h, 24-03:00 h and 03-06:00 h. The grouping variable was groups (females fed, females starved and males starved). The three analyses separately examined average, maximum and minimum selected temperature. For each analysis there were no univariate or multivariate within-cell outliers at $\alpha = 0.001$. Results of evaluation of assumptions of normality, homogeneity of variance-covariance matrices, linearity, and multicollinearity were satisfactory for the non-transformed data. All multivariate repeated measures test results are given using Wilk's criterion. *Post hoc* tests using simple effects analyses were then conducted to examine parallelism between the three groups in the profiles of selected temperature on each day.

The effect of nutritional status on scorpion activity was analysed using profile analysis. The test was performed on twenty five repeated measure dependent variables at two levels associated with days (pre-fed, then 1, 5, 21 and 42 days after feeding) and the time periods: 15-18:00 h, 18-21:00 h, 21-24:00 h, 24-03:00 h and 03-06:00 h. The grouping variable was groups (females fed, females starved and males starved). There were no univariate or multivariate within-cell outliers at $\alpha = 0.001$. Results of evaluation of assumptions of normality, homogeneity of

variance-covariance matrices, linearity, and multicollinearity were satisfactory for the non-transformed data. All repeated measures test results are given using Wilk's criterion. *Post hoc* tests using simple effects analyses were then conducted to examine parallelism between the three groups in the profiles of selected temperature on each day. The profiles of activity of each group were calculated for each day of feeding and/or starvation as the proportion of active animals every 15 min.

6.3 Results

All scorpions had eaten by the next morning and they were either resting well back under their shelter or still eating at the entrance of the shelter. In all cases observed, the scorpions had started feeding from the anterior end of the larvae. 41% of females consumed all three larvae, the remainder all consuming two. 50% of the males consumed two larvae, the others consuming a single larva. None of the fed females ate during the five days after the initial meal, but three of them recommenced feeding after 9 days and all animals had consumed one additional mealworm by 15 days (pers. obs.).

Scorpion mass was affected by feeding and starvation (Figure 6.1). Mass changes were not attributed to water gain or loss because all animals had access to water. Female mass increased with feeding from 1.35 (± 0.06) to 1.60 (± 0.06) g and the males increased from 0.59 (± 0.04) to 0.73 (± 0.04) g. With the use of Wilk's criterion, there was a significant effect of day on female mass after the initial meal, $F(4, 11) = 170.28$, $P < 0.001$, $\eta^2 = 0.98$. The trend of mass over the days differed between the two nutritional groups, $F(4, 11) = 5.42$, $P < 0.05$, $\eta^2 = 0.66$. Females that were continuously provided with prey had greater masses 21 and 42 days after the initial meal than females that were starved after the initial meal. After 21 days, the fed females had a mass of 1.63 (± 0.08) g and starved females a mass of 1.53 (± 0.07) g. This difference was significant, $F(1, 14) = 20.15$, $P < 0.001$. After 42 days the mass of the fed females was 1.63 (± 0.09) g and that of the starved females was 1.48 (± 0.07) g and these masses were also significantly different,

F(1, 14) = 20.15, P < 0.01. Starved male mass after 21 days was 0.68 (± 0.04) g which decreased to 0.64 (± 0.04) g after 42 days. The change in male mass over the 42 days was best described by polynomial contrasts as quadratic, F(1, 7) = 34.04, P < 0.001.

6.3.1 Oxygen Consumption

Both overall and mass-specific $\dot{V}O_2$ increased with increasing temperature regardless of the nutritional state or sex of the scorpions (Figures 6.2 and 6.3). Female overall $\dot{V}O_2$ (Figure 6.2a) was greater than that of the males (Figure 6.3a). The difference in overall $\dot{V}O_2$ between the sexes was highly significant, F(1, 14) = 67.85, P < 0.001. Male mass-specific $\dot{V}O_2$ (Figure 6.3b) was significantly greater than that of the females, F(1, 14) = 5.06, P < 0.05 (Figure 6.2b). The nutritional status of the animals had a significant effect at all temperatures for both overall $\dot{V}O_2$, F(8, 7) = 14.57, P < 0.001 and mass-specific $\dot{V}O_2$, F(8, 7) = 9.62, P < 0.01.

A large increase in both overall and mass-specific female $\dot{V}O_2$ occurred at all temperatures with feeding. At 30°C for example, overall $\dot{V}O_2$ increased from 91.43 (± 5.43) to 186.45 (± 8.54) µl O_2 h^{-1} (Figure 6.2a) and mass-specific $\dot{V}O_2$ increased from 70.15 (± 6.60) to 119.14 (± 8.30) µl O_2 g^{-1} h^{-1} (Figure 6.2b). Male $\dot{V}O_2$ did not increase to the same extent as female $\dot{V}O_2$. At 30°C, male overall $\dot{V}O_2$ increased from 60.63 (± 6.51) to 79.65 (± 3.34) µl O_2 h^{-1} (Figure 6.3a) and mass-specific $\dot{V}O_2$ increased from 105.58 (± 9.55) to 116.86 (± 9.73) µl O_2 g^{-1} h^{-1} (Figure 6.3b). The increase in overall $\dot{V}O_2$ over all temperatures was significantly greater in females than males, F(1, 14) = 29.77, P < 0.001, as was the increase in mass-specific $\dot{V}O_2$, F(1, 14) = 9.74, P < 0.01.

The drop in overall $\dot{V}O_2$ between the first and fifth days after feeding was greater in females (Figure 6.2a) than males (Figure 6.3a), but the drop in mass-specific $\dot{V}O_2$ was not different between the sexes (Figures 6.2b and 6.3b). Female $\dot{V}O_2$ at 30°C decreased from 186.45 (± 8.54) to 110.20 (± 15.82) µl O_2 h^{-1} and that of males decreased from 79.65 (± 3.34) to 66.59 (± 7.99) µl O_2 h^{-1} after five days. The drop in overall $\dot{V}O_2$ between the sexes was significant, F(1, 14) = 9.23, P < 0.01, but not for mass-specific $\dot{V}O_2$, F(1, 14) = 1.99, P > 0.05. The profiles of male and female for both measures of $\dot{V}O_2$ were the same between 5 and 42 days of starvation with $\dot{V}O_2$ the

lowest at 21 days and then back up to pre-feeding levels at 42 days. Taking mass-specific $\dot{V}O_2$ at 30°C as an example, females decreased to 53.63 (± 3.82) after 21 days then increased to 63.32 (± 4.00) µl O_2 g^{-1} h^{-1} and males decreased to 62.65 (± 6.16) then increased to 82.88 (± 12.53) µl O_2 g^{-1} h^{-1} after 42 days of starvation.

Q_{10} decreased with feeding and increased back to pre-feeding levels after 42 days of starvation (Table 6.1). Although $\dot{V}O_2$ differed between females and males, Q_{10} did not and their values were combined for Table 6.1. Female and male Q_{10} over all days and temperatures were not significantly different, $F(1, 14) = 3.17$, $P > 0.05$, and sex did not interact with the nutritional status of the scorpions, $F(1, 14) = 1.2$, $P > 0.05$. The overall Q_{10} from 20 to 30°C was not significantly different than from 30 to 40°C and the effect of nutritional status was the same between the high and low temperature Q_{10}'s. Between 30 and 40°C, Q_{10} decreased with feeding from 2.01 (± 0.12) to 1.64 (± 0.08) and remained depressed up to 21 days after the meal (1.68 ± 0.08). After 42 days of starvation, Q_{10} for the upper range rose back to pre-feeding value (1.92 ± 0.10). The effect of nutritional status on both upper and lower Q_{10}'s was significant, $F(4, 11) = 4.85$, $P < 0.05$.

6.3.2 Temperature Selection

Feeding resulted in a reduction of overall average selected temperature, which then increased back to the initial temperatures with starvation in males (Figure 6.4a) and females (Figure 6.4b). Continual provision of food kept selected temperatures depressed for females (Figure 6.4c). Mean temperature selected by all animals during the first 3 hours of dark decreased with feeding from 33.3 (± 0.9) to 24.7°C (± 0.9) and remained low after 5 days without feeding (24.2°C ± 1.01). After 21 days without food, female selected temperatures in the same 3 hour period increased to 30.8°C (± 1.8) and then to 33.2°C (± 1.5) after 42 days. Starved males selected similar temperatures of 31.3°C (± 2.6) after 21 days and 34.5°C (± 1.6) after 42 days. Females that were fed *ad libitum* continuously selected lower temperatures up to 42 days (24.1°C ± 1.7). The change in selected temperature over the days was significantly different from flatness, $F(4, 13) = 16.26$, $P < 0.001$, $\eta^2 = 0.83$, but was not affected by sex or the provision of food,

$F(8, 26) = 1.69$, $P > 0.05$, despite the lower selected temperatures with continual food provision. *Post hoc* testing revealed that the decreases in temperature with feeding were significant, $F(3, 16) = 20.19$, $P < 0.001$, as well as the increase from day 5 to day 21, $F(3, 16) = 9.84$, $P < 0.001$ (Table 6.2). Temperatures the day after the initial meal and then 5 days later were not significantly different, $F(3, 16) = 0.49$, $P > 0.05$, nor were temperatures selected on days 21 and 42, $F(3, 16) = 1.22$, $P > 0.05$. The profiles of average selected temperature over the 3 hour periods were characteristic of *U. manicatus* and were independent of nutritional status and sex. Temperature increased with the onset of the scotophase and decreased with each successive 3 hour period during the night. The profiles deviated significantly from flatness, $F(4, 13) = 25.99$, $P < 0.001$, $\eta^2 = 0.89$, but were parallel with regards to day, $F(8, 26) = 1.69$, $P > 0.05$, and category of animal, $F(8, 26) = 0.89$, $P > 0.05$. *Post hoc* testing revealed that each adjacent period was significantly different, the greatest difference occurring before and after the commencement of the scotophase (Table 6.2).

The results of maximum temperatures recorded in the gradient were the same as average selected temperature with feeding restricting the extent that scorpions travelled into the warm end of the gradient. With subsequent starvation in males (Figure 6.5a) and females (Figure 6.5b) the maximum temperatures increased back to pre-feeding levels. Continual provision of food saw females avoid the high temperatures (Figure 6.5c). Maximum temperatures decreased below equivalent average temperatures with feeding. The mean maximum temperature recorded for all animals during the first 3 hours of dark decreased with feeding from 38.3 (± 0.7) to 29.4°C (± 0.9) and remained low after 5 days without food (28.4°C ± 1.3). As with average temperature, the pattern of lower temperatures of the continually fed females over days was not significantly different than the starved females and males, $F(8, 26) = 1.34$, $P > 0.05$. *Post hoc* testing revealed that the decreases in temperature with feeding were significant, $F(3, 16) = 15.27$, $P < 0.001$, as well as the increase from day 5 to day 21, $F(3, 16) = 5.33$, $P < 0.01$ (Table 6.2). *Post hoc* testing revealed that each adjacent period averaged over all days and groups was significantly different and that the changes in temperature were more pronounced than for average temperature (Table 6.2).

Patterns in the minimum temperatures recorded also generally reflected that of average (and maximum) temperatures (Figure 6.6) except that the profiles of the means of each 3 hour period

were flatter with only a small rise in temperature associated with the onset of the scotophase (Table 6.2). After feeding, scorpions travelled further into the cooler part of the gradient. Subsequent starvation in males (Figure 6.6a) and females (Figure 6.6b) resulted in scorpions retreating from the cooler temperatures. Females that were allowed to continue feeding also continued to move further into the cooler temperatures (Figure 6.6c). Mean minimum temperature selected by all animals during the first 3 hours of dark decreased with feeding from 27.2 (± 1.3) to 19.3°C (± 1.1) and remained low after 5 days without feeding (18.8°C ± 1.1). After 21 days without food, female temperatures in the same 3 hour period increased to 24.2°C (± 1.8) and then to 28.6°C (± 1.7) after 42 days. Starved males experienced a similar change in temperature of 25.1°C (± 3.0) after 21 days and 28.3°C (± 2.3) after 42 days. Females that were continuously provided with food selected lower temperatures up to 42 days (15.7°C ± 2.6) during the first period of the scotophase. The profile of day was significantly different from flatness, $F(4, 13) = 17.48$, $P < 0.001$, $\eta^2 = 0.84$. Unlike average or maximum temperatures, there was a significant effect of category of animals on the profile of day, $F(8, 26) = 2.55$, $P < 0.05$, due to the lower temperatures of the continually fed females. *Post hoc* testing revealed that the difference was due to the change in temperature 21 days after the initial meal, $F(2, 16) = 6.44$, $P < 0.01$.

6.3.3 Activity

The pre-feeding activity profiles were typical for *Urodacus manicatus* showing an increase in activity with the onset of the scotophase and then decreasing towards the end of the night, thus reflecting changes in temperature selection. Male activity (Figure 6.7) was slightly greater later in the scotophase than the female starvation group (Figure 6.8) and the female fed group (Figure 6.9). Mean activity for all animals between 18:00 and 21:00 h was 5.22 (± 0.27) turns. Male activity between 24:00 and 03:00 h was 4.14 (± 0.99) turns compared to female activity of 2.31 (± 0.45) turns. Feeding reduced the response of increased activity to the onset of the scotophase in the female starvation group (Figure 6.8b). However, the response was less for both the feeding female group (Figure 6.9b) and the males in which the increase in activity preceded

18:00 h (Figure 6.7b). Mean activities, though, were similar between 18:00 and 21:00 h for all groups, with a combined mean of 3.86 (± 0.30) turns. By day 5 both starved groups showed lower and more uniform activity during the scotophase (Figures 6.7c and 6.8c) and remained this way after 21 days of starvation (Figures 6.7d and 6.8d). The response to the scotophase by the fed females after 5 days (Figure 6.9c) and 21 days (Figure 6.9d) of feeding was more variable than that of the starved groups, but they were not more active. Mean activity between 18:00 and 21:00 h after 21 days without food was 3.25 (± 0.25) turns for females and 4.38 (± 0.26) turns for males and 3.63 (± 0.50) turns for fed females. After 42 days without food, males and females had increased in their response to the onset of the scotophase (Figures 6.7e and 6.8e) above that of the fed females (Figure 6.9e). Mean activities between 18:00 and 21:00 were 6.00 (± 0.66) and 6.25 (0.41) turns for starved females and males respectively and 3.88 (± 0.44) turns for the fed females.

Activity profiles between 15:00 and 06:00 h, when averaged across all groups and days, were significantly different from flatness, $F(4, 11) = 19.79$, $P < 0.001$, $\eta^2 = 0.88$. Day profiles from pre-feeding to day 42, when averaged over all time periods, however, did not significantly differ from flatness, $F(4, 11) = 1.43$, $P > 0.05$. Sex and nutritional status did not have a significant effect on either the time period profiles, $F(8, 22) = 1.28$, or the day profiles, $F(8, 22) = 0.82$. A marginally significant difference was found between the three groups, $F(2, 14) = 3.77$, $P < 0.05$, with males slightly more active than females.

6.4 Discussion

The present study clearly demonstrates a profound effect of nutritional state on temperature selection, activity and metabolic rate of *Urodacus manicatus*. Feeding resulted in the selection of lower temperatures for at least 5 days, a finding contrary to the response of many terrestrial ectothermic vertebrates. Elevation of RMR with feeding indicated was associated with assimilation (Bradley 1982). Starvation for six weeks had no effect on the thermoregulatory behaviour of *U. manicatus*.

The degree to which animals select different temperatures after feeding is associated with their ecology (Sievert 1989). Increases in selected temperature have been reported for amphibians (Heller et al. 1978) and reptiles (Bradshaw et al. 1980, Lysenko and Gilles 1980, Slip and Shine 1988), a greater body temperature resulting in greater assimilation rates. Other studies on reptiles show no clear elevation in selected temperature (Mullens and Hutchison 1992, Sievert 1989, Touzeau and Sievert 1993, Tu and Hutchison 1995), but the maintenance of a normally high active body temperature in these species may exclude elevation of temperature (Sievert 1989, Tu and Hutchison 1995). This argument, however, does not explain the observed reduction of selected temperature by *Urodacus manicatus* after feeding. The selection of cooler temperatures and the concomitant decrease in foraging activity by *U. manicatus* following a meal was not associated with predator avoidance because of the "door-keeping" foraging behaviour of this species. Snakes avoid predation by selecting shelters and basking less often in the open resulting in a reduction of body temperature because their mobility is restricted after a large meal (Hammerson 1987, Lysenko and Gilles 1980). The 19% and 24% respective increases in the masses of female and male *U. manicatus* would have decreased their locomotor capacity after a meal and thus, their ability to evade capture by a predator if they were surface foragers. Feeding decreased foraging behaviour in the surface foraging scorpion *Paruroctonus utahensis* for up to 20 days after a meal because the scorpions could then "afford" the avoidance of cannibalism or predation (Bradley 1982). *U. manicatus*, however, rarely leaves the burrow and presumably has a low risk of predation at all times while within the burrow.

Fed *Urodacus manicatus* reduced their active selected temperature below that of their inactive temperatures when initially starved for 21 days (Figure 6.6). The scorpions would presumably not seek further prey after attaining their maximum capacity for food uptake after a large meal. Southcott (1954) observed that *U. manicatus* would ignore passing prey if they were "bloated" with food. The selection of high body temperatures when foraging aided prey detection and capture behaviour, but were not required during the time of no foraging activity after feeding. A lower body temperature also reduced energy expenditure, thus conserving metabolic stores during the period of no foraging activity. In this study, foraging activity in *U. manicatus* was reduced for at least 21 days. The time until predatory behaviour recommences in scorpions may depend upon the species, previous nutritional state, microhabitat temperature and the size of the

meal ingested. For example, the scorpion, *E. flavicaudis*, is a "door-keeping" forager that will sometimes resume its foraging position at the entrance in the same night after a meal (Benton 1992).

Urodacus manicatus that were continuously provided with food maintained lower temperatures and attained a greater mass than the starved animals at the conclusion of the experiment. The continuous presence of potential prey items in close proximity to the scorpion may have affected the observed foraging patterns in the gradient. Scorpions that continued to feed did not maintain low activity levels as when after the first meal perhaps due to the continual disturbance of the scorpions by the *Tenebrio* larvae as the larvae moved about the scorpions' containers. Stimulation of foraging behaviour by the presence of prey may also account for the fact that individuals of *U. manicatus* consumed two or more prey items during the night in captivity instead of becoming less active following the ingestion of a single prey item.

Feeding had an immediate effect of increasing the RMR of *Urodacus manicatus* which was presumably due to assimilation (Bradley 1982, Hanski 1976). The effect of feeding on the actual metabolic rates of the scorpions was determined by calculating mass-specific $\dot{V}O_2$'s at the active selected temperatures with the use of the Q_{10}'s from Table 6.1. Before feeding, the respective mass-specific $\dot{V}O_2$'s of females and males were 84.68 and 142.70 µl O_2 g^{-1} h^{-1}. The reduction in active selected temperature with assimilation resulted in female and male $\dot{V}O_2$'s of 87.92 and 75.63 µl O_2 g^{-1} h^{-1} respectively. After 5 days, the $\dot{V}O_2$'s of females and males were 44.50 and 73.14 µl O_2 g^{-1} h^{-1}. Therefore, females did not change in their metabolic expenditure associated with assimilation, whereas actual male RMR dropped down to similar values for females during assimilation and remained unchanged for 5 days. Female expenditure decreased by half after 5 days.

Assimilation time at 25°C for *Urodacus manicatus* must have been greater than 12 h, but less than 5 days because the RMR of both sexes had returned to pre-feeding levels after 5 days. This time period is similar to the digestion times reported for other scorpion species (Bradley 1982, Quinlan et al. 1993, Sinha 1982). For the desert species *Paruroctonus utahensis*, assimilation time was 6 h at 20°C (Bradley 1982). The syntopic species *Urodacus armatus* and *U. novaehollandiae* (Quinlan et al. 1995) belong to the same species group as *U. manicatus*

(Koch 1977) and their digestion was complete after 3 days at room temperature (Quinlan et al. 1993). Sinha (1982) reported an assimilation time of greater than 24 h in *Buthus tamulus*.

The RMR associated with digestion was 70% above the pre-feeding rate for females, but only 31% above for males at 30°C. The reason for this difference was because male RMR before feeding was elevated, but the RMR of assimilation was the same for both sexes per mass. The elevated RMR of males may have been due to the commencement of the experiment at the time of when their roving activity had peaked during mid to late spring (Crawford and Riddle 1975, Riddle 1978, Smith 1966, Willmer 1957). The RMR of males collected in spring (Chapter 3) did not exhibit an elevation of RMR, however, their $\dot{V}O_2$ was measured earlier in the season before courtship and mating behaviours commenced.

Urodacus manicatus reduced its absolute RMR and Q_{10} at high temperatures as a means of conserving metabolic stores when food was not available for 21 days. However, the importance of metabolic depression in scorpions as a means of surviving long periods without food, has not been resolved. The desert surface forager *Paruroctonus utahensis*, exhibited metabolic depression at high temperatures after starvation for 6 weeks which Riddle (1978) suggested was a lowering in the energetic cost of *P. utahensis* as it utilised warmer parts of its habitat. Dejours and Ar (1991), however, found that the RMR of another desert species *Leiurus quinquestriatus* was not altered by the lack of both food and water. The detection of metabolic depression may be time dependent because the RMR of female *U. manicatus* in this study returned to pre-feeding levels after 42 days without food. In the study of Dejours and Ar (1991), the time at which the $\dot{V}O_2$ of *L. quinquestriatus* was measured was not given and metabolic depression may have gone unnoticed. The onset and duration of metabolic depression, if any, may depend on the species of scorpion and the temperatures under which the animals are maintained. After 42 days, the RMR of male *U. manicatus* increased from 21 days, but remained below pre-feeding levels. Their RMR at this time may have been associated with the cessation of roving activity.

Strong seasonality exists in food availability for scorpions (McCormick and Polis 1990, Polis and Farley 1979b) with there being long periods of infrequent feeding. Some species hibernate over these periods by sealing their burrows and not feeding at all (Smith 1983). There are two possible strategies for dealing with irregular feeding: reduce energy expenditure to conserve metabolic

stores or be highly efficient in storing nutrients for continual activity. Metabolic depression may occur in animals in which feeding is usually regular and/or they have a smaller capacity for metabolic reserves. *Urodacus manicatus* did not reduce its RMR over normal activity temperatures nor did it select lower temperatures to facilitate energy reduction when starved. The storage capacity of *U. manicatus* was large enough to carry the scorpions through long periods of irregular or no feeding. The capacity of a single specimen of *U. manicatus* to survive for 17 months with only a single meal of a housefly after 8 months (Southcott 1954) supports this view.

Most species of scorpions show a remarkable ability to survive long periods of even more than a year without food (Bender 1959, Cloudsley-Thompson 1955, Smith 1983, Southcott 1954, Vachon 1953). This remarkable ability is due to the combination of the large capacity of the hepatopancreas as a storage organ (McCormick and Polis 1990, Quinlan et al. 1993), a low metabolic rate (Sinha 1982, Sinha and Kanungo 1967), and the enormous proportion of time spent being inactive (Polis 1988). The hepatopancreas is composed of two tissues: digestive diverticulae (containing basophilic cells that produce exoenzymes and digestive cells that ensure intracellular digestion and store glycogen, lipids and mineral salts and metabolic wastes in the lumen of diverticulae) and interstitial tissue (which stores glycogen and lipids) (Goyffon and Martoja 1983). The concentration of glycogen in the hepatopancreas is high and it is utilised from the onset of starvation, increasing back to normal levels within four days after a meal (Sinha 1982, Sinha and Kanungo 1967). Haemolymph glucose levels remain unchanged as glucose converted from glycogen is released from the hepatopancreas (Padmanabhanaidu 1966a). As glycogen levels decrease, gluconeogenesis causes amino acid and protein levels to fall also. Neither starvation nor feeding affected the water content of the hepatopancreas or leg muscles (Sinha 1982, Sinha and Kanungo 1967). The lowering of the respiratory quotient (ratio of CO_2 produced per O_2 consumed) with starvation indicates that scorpions utilise lipid reserves (Dresco-Derouet 1964).

The size difference between males and females suggests that females have a greater capacity for storage in the hepatopancreas, principally for reproduction. The extra capacity of the hepatopancreas may also benefit the females over periods of few feeding opportunities after parturition. Unlike females, however, adult males require energy for increased activity associated

with courtship and mating (Polis and Farley 1979a). Adult male foraging patterns are therefore similar to that of adult females and both are correlated with insect abundance unlike the foraging activity patterns of immature scorpions (Polis 1980b). Male *Urodacus manicatus* ate the same proportion of food per body mass as females and thus their foraging patterns in the field were probably the same. The size of a species of scorpion influences the size of the prey, for example, the larger *Urodacus novaehollandiae* consumes larger prey than the smaller conspecific *U. armatus* (Quinlan et al. 1995). However, it is not known whether sexual dimorphism in size (females were larger than males) affects prey size preference in *U. novaehollandiae* and *U. armatus* (Quinlan et al. 1995). Although male *Paruroctonus mesaensis* ate a wider variety of food types than females (which are also larger) they generally fed on similar prey. As such, there was no sexual dimorphism in the requirements of reproduction in scorpions (Polis 1986).

Urodacus manicatus is a sit-and-wait ambush predator like many species of scorpions (Enders 1975), staying within the burrow entrance with only the pedipalps slightly protruding unlike surface foragers which usually locate their prey then pursue it (Alexander 1972, Brownell 1979). Differences in the effects of the "door-keeping" and surface foraging strategies on nutritional status are not known, but would depend on many factors. Many surface foragers are desert dwellers. Sand is a good propagator of compressional and surface waves (Brownell 1977) that are detected by the tarsal mechanosensory hairs and basitarsal slit sensillum respectively when hunting on the sand's surface (Brownell and Farley 1979). Large prey items may be detected up to 30 cm away when they are in contact with the substrate, but go undetected when only 2 cm away in the air (Brownell 1979). Surface foragers orientate themselves with respect to the prey by the temporal pattern of activation of the slit sensilla of each leg and mark the distance by the spatial pattern of stimulation of the tarsal mechanosensory hairs. *U. manicatus* occupies regions of fine black clays and loams that may not have the same properties of surface vibration propagation as the sands of many surface foragers do and is therefore not useful as a means of detecting prey at a distance. The ground surface is usually uneven and covered with grasses, sedges and small herbaceous plants which would obstruct the transmission of surface vibrations originating from potential prey. The additional vegetation, however, has the benefit of there being a greater abundance of prey species associated with it at ground level due to the greater number of microhabitats formed by the plants. The dock wall inhabiting *Euscorpius flavicaudis* in

England forages from within the entrance of its crack in the wall where distant prey location is not possible, but its main prey species, the woodlouse *Pocellio scaber*, is abundant (Benton 1992).

The number of prey species of scorpions can be large (95 prey species recorded for *Paruroctonus mesaensis* (Polis 1979)) reflecting the potentiality of any suitably sized animal in the vicinity of a scorpion's home site of becoming prey. As such, other arthropods rarely occupy the same space as scorpions (Zinner and Amitai 1969). However, only a few species form the bulk of the diet of scorpions (Benton 1992, Polis 1979). The size range of prey can vary enormously, but is generally related to the size and age of the individual. Many prey species are seasonally dependent, but a few are annual such as cockroaches and conspecifics. Feeding in *Urodacus manicatus* was typical of scorpions, with prey consumed head-first as orientated by the scorpion (Alexander 1972, Polis 1979, Quinlan et al. 1995, Southcott 1954). This behaviour might be to avoid disruption of feeding by the large posterior legs of some orthopterans, to quickly subdue the prey by destroying the brain first or avoiding chemical defences most often found at the rear end of some insects (Bub and Bowerman 979). The prey of *U. manicatus* at Black Mountain were frequently the most abundant arthropods that occupied a similar niche to the scorpions. The most abundant arthropods were cockroaches and scolopendromorph centipedes. Ants were also abundant, but there was no evidence to suggest that they formed a part of the diet of *U. manicatus*. On several occasions, scorpions were observed in the field to be consuming tenebrionid larvae which leave few remains. Prey remains of *U. manicatus* at both Black Mountain and Dubbo were always found in the living area of the burrow and not near the entrance. Surface foragers ate prey wherever it was caught (Hadley and Williams 1968) whereas "door-keeping" species usually retreat with their prey back into the burrow.

The "door-keeping" strategy for predation in *Urodacus manicatus* excludes cannibalism as an important food source for this species. Cannibalism has not been observed in the field for *U. manicatus* although it has occurred in the laboratory when animals were maintained together (this study and Southcott (1954)). Early instars during their dispersal and home site selection may encounter and be consumed by larger individuals (Smith 1966). On no occasions were more than one scorpion found beneath a rock or log even under adverse conditions (c.f. McAlister (1966), Polis and Lourenço (1986)). Surface foragers on the other hand have numerous encounters with individuals both of the same and different species. In these scorpions cannibalism and inter-

specific predation are population regu ating and stabilising features as a source of food (Polis 1980a, 1981 and 1988, Polis and Farl y 1979b, Polis and McCormick 1987, Polis et al. 1989). In autumn, growth rates are high for *Par uroctonus mesaensis* due to cannibalism and inter-specific predation (Polis and Farley 1979b).

Another effect of the sedentary mode of foraging of *Urodacus manicatus* is the exclusion of scavenging as an additional means of acquiring food. The incidence of scavenging has been found to increase during starvation in surface foraging scorpions (Krapf 1986). During normal maintenance of *U. manicatus* dead and half eaten prey were never consumed and always had to be removed from the scorpion's containe to avoid contamination. Yet another source of nutrition is the resorption of embryos which is common in scorpions (Rosin and Shulov 1963, Shorthouse 1971) and can act as an additional reserve if food becomes too scarce (Polis 1980a, Shorthouse and Marples 1982). It is not known what the nutritional status of a gravid *U. manicatus* must be before resorption takes place.

Urodacus manicatus can survive long periods without food because of the large capacity of the hepatopancreas, their low RMR and the large proportion of time they spend being inactive. Therefore, short-term starvation does not affect their physiology or behaviour. Feeding, however, does have a short term affect of increasing RMR with assimilation and decreasing selected temperatures with a decrease in foraging activity. Further studies on the effects of differing amounts of prey ingestion on the dura ion of decreased foraging activity would determine whether inactivity after a meal was due to the maximum capacity of the hepatopancreas, predator avoidance, or a short term conservation of energy. A comparative study on surface and "door-keeping" foragers in the same locality would further our knowledge on the benefits and costs of the different foraging behaviours.

Female *U. manicatus* need to have enough metabolic reserves after parturition to survive limited feeding opportunities during the cooler months. The effect of gravidity on the nutritional status and foraging behaviour of adult females is examined in the next chapter.

Table 6.1. The effect of nutritional status on combined adult female and male temperature coefficients (Q_{10}) calculated for each increment in the temperature range from $\dot{V}O_2$ (n = 16). Feeding significantly reduced Q_{10} between 30 and 40°C ($P < 0.05$).

Temperature range (°C)	Pre-feeding	Fed previous night	5 days starved	21 days starved	42 days starved
20-30	2.07 ± 0.11	1.86 ± 0.09	2.10 ± 0.13	1.82 ± 0.10	1.94 ± 0.11
30-40	2.01 ± 0.12	1.64 ± 0.08	1.75 ± 0.16	1.68 ± 0.08	1.92 ± 0.10

Values are means ± SE.

Table 6.2. *Post hoc* evaluation of the significant results of flatness and parallelism. Tests are one-way within-subjects ANOVAs examining the mean differences in average, maximum and minimum temperatures between repeated dependent variables.

Tests	Period contrasts	df	Univariate F		
			Average	Maximum	Minimum
Period (flatness)	l1-d1	3,16	42.44***	98.56***	4.79*
	d1-d2	3,16	15.94***	34.96***	2.50
	d2-d3	3,16	6.72**	11.43***	0.31
	d3-d4	3,16	6.88**	18.88***	0.47
Days (flatness)	D0-D1	3,16	20.19***	15.27***	20.44***
	D1-D5	3,16	0.49	0.92	0.94
	D5-D21	3,16	9.84***	5.33**	14.67***
	D21-D42	3,16	1.22	1.56	1.23

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

D0 = pre-fed, D1 = day 1 after feeding, etc.

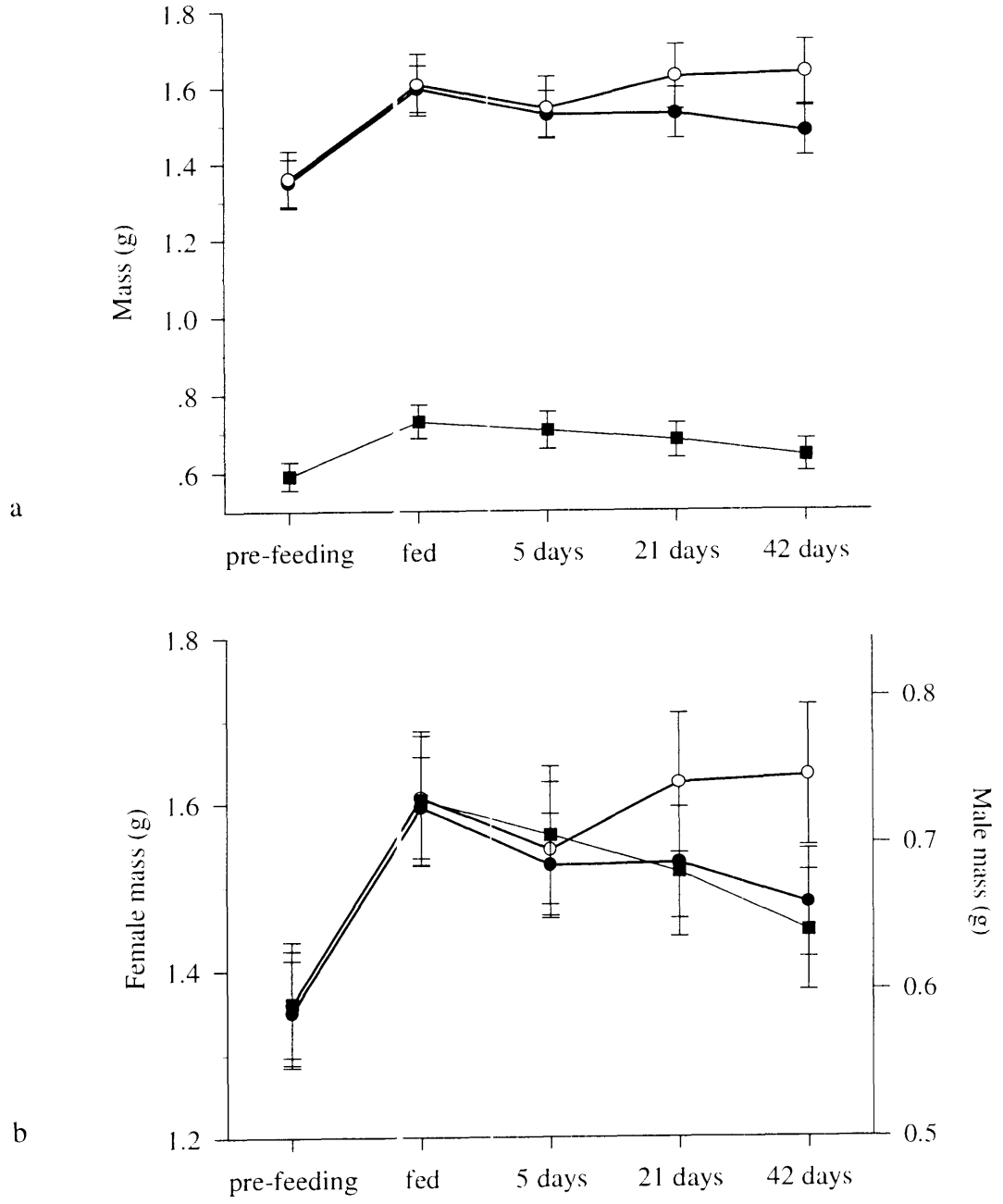

Figure 6.1. Effect of nutritional status on (a) absolute wet body mass (g) and (b) relative wet body mass (g) over the course of the feeding experiment. Females fed *ad libitum* (open circles; $n = 8$), females starved after single feed (closed circles; $n = 16$) and males starved after single feed (closed squares; $n = 16$). Water was provided *ad libitum* throughout experiment. Points represent mean values ± SE. Differences in starved and fed female masses after 21 and 42 days are not significant.

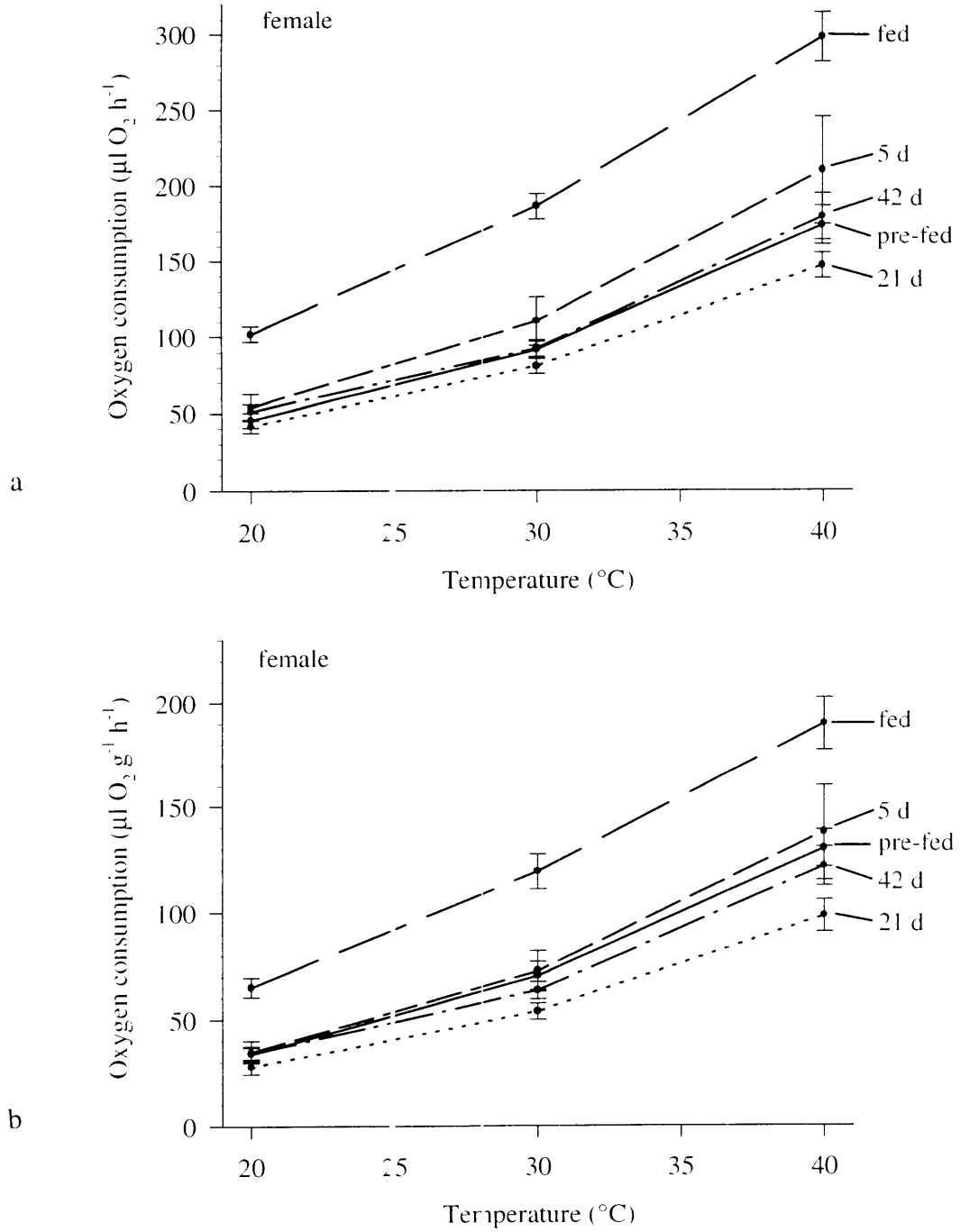

Figure 6.2. Effect of nutritional status on female RMR as a function of temperature (°C) presented as (a) whole animal oxygen consumption rate (µl O_2 h^{-1}) and (b) mass-specific oxygen consumption rate (µl O_2 g^{-1} h^{-1}). Pre-feeding (solid lines; n = 16), fed (long dashes; n = 16), 5 days after feeding (short dashes; n = 16), 21 days (dots; n = 16) and 42 days (dash-dots; n = 16).

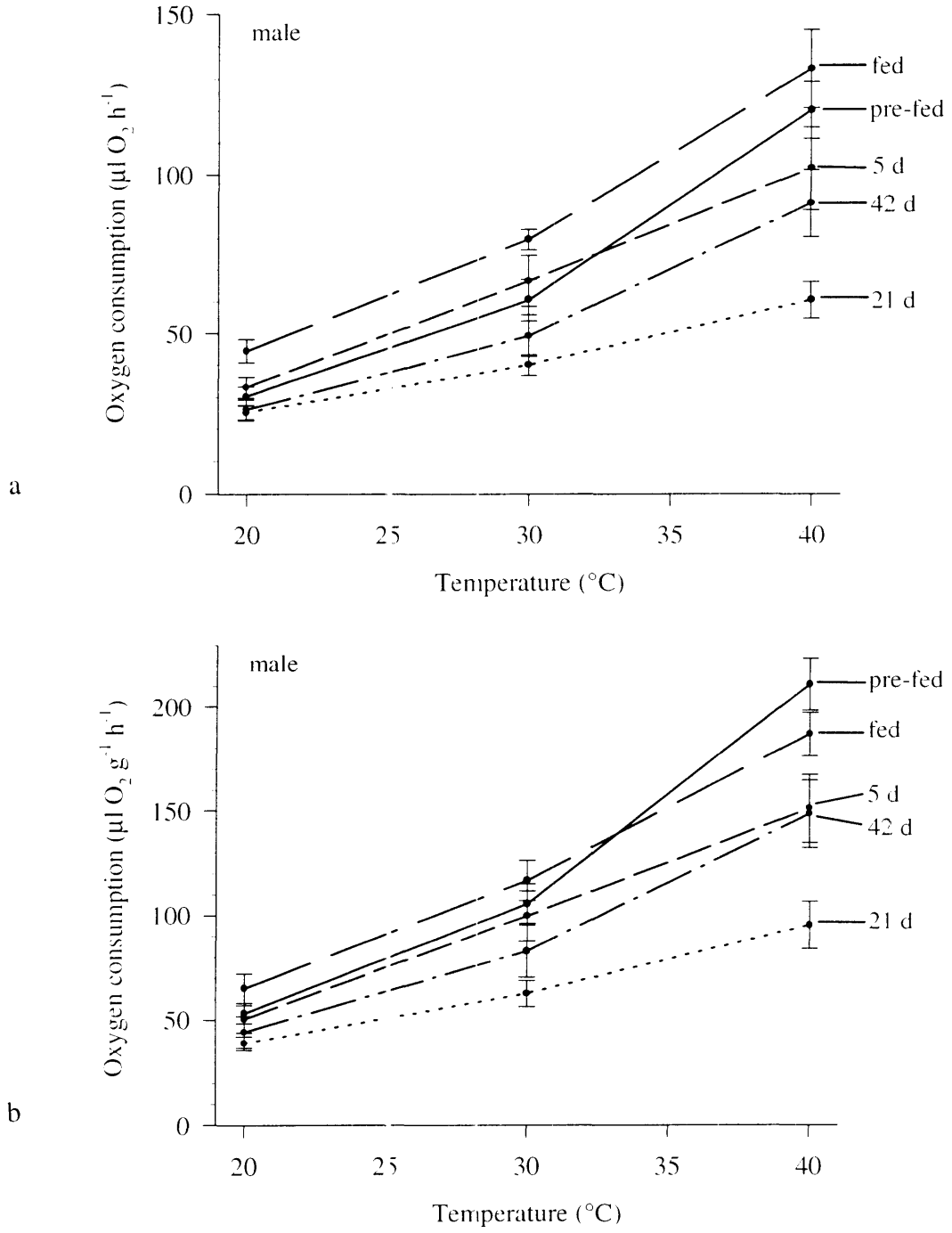

Figure 6.3. Effect of nutritional status on male RMR as a function of temperature (°C) presented as (a) whole animal oxygen consumption rate (µl O_2 h^{-1}) and (b) mass-specific oxygen consumption rate (µl O_2 g^{-1} h^{-1}). Pre-feeding (solid lines; n = 16), fed (long dashes; n = 16), 5 days after feeding (short dashes; n = 16), 21 days (dots; n = 16) and 42 days (dash-dots; n = 16).

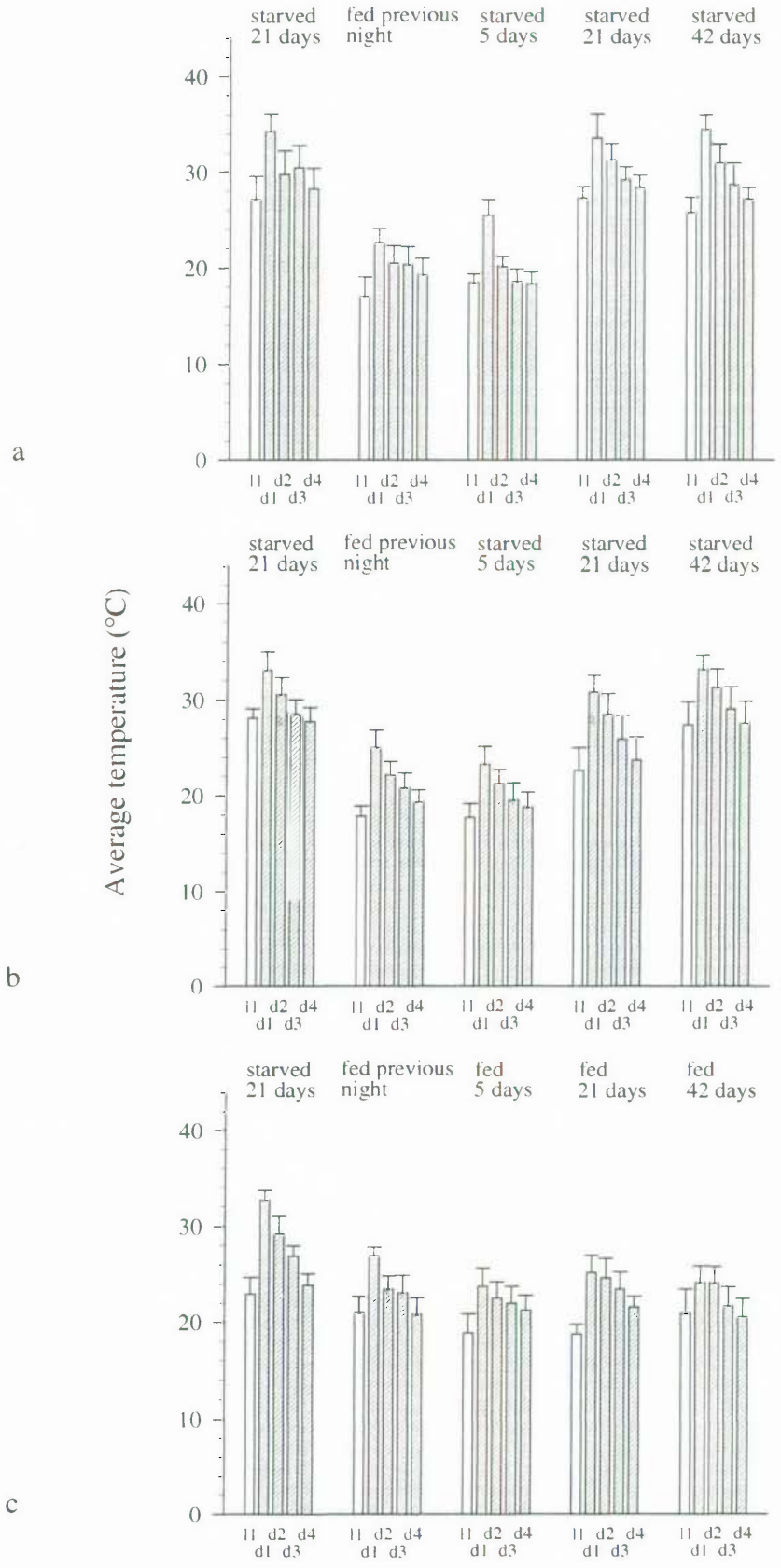

Figure 6.4. Effect of nutritional status on the profiles of average selected temperatures (°C) of (a) adult males fed then starved, (b) adult females fed then starved, and (c) adult females fed then continuously provisioned with larvae. Averages are of 12 measurements per animal within the 3 hour periods of 15-18:00 h (l1), 18-21:00 h (d1), 21-24:00 h (d2), 24-03:00 h (d3) and 03-06:00 h (d4). Bars represent mean values ± SE. For all cases $n = 8$. Shaded bars highlight the scotophase periods.

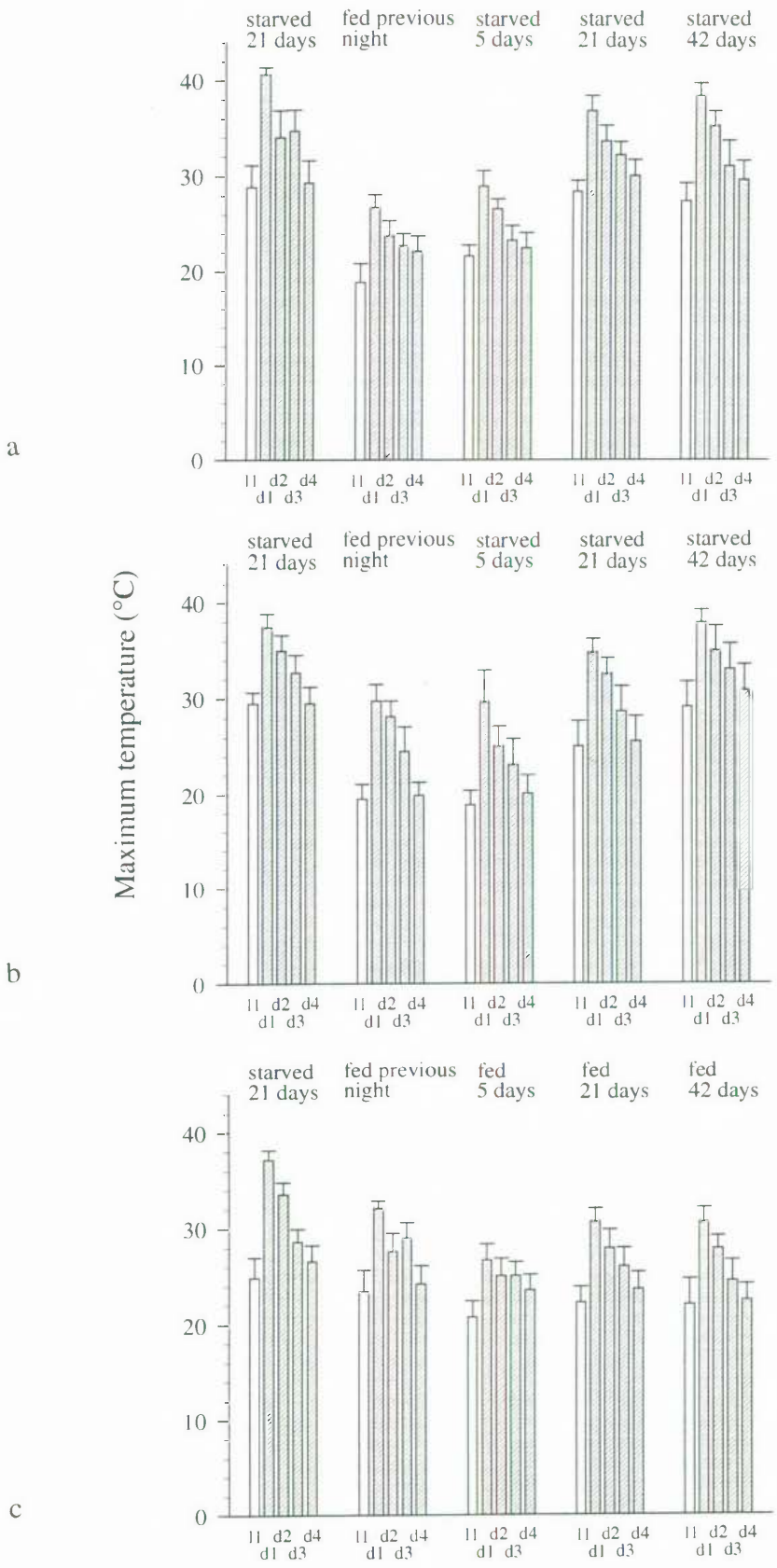

Figure 6.5. Effect of nutritional status on the profiles of maximum temperature (°C) recorded in the gradient of (a) adult males fed then starved, (b) adult females fed then starved, and (c) adult females fed then continuously provisioned with larvae. Maxima are from 12 measurements per animal within the 3 hour periods of 15-18:00 h (l1), 18-21:00 h (d1), 21-24:00 h (d2), 24-03:00 h (d3) and 03-06:00 h (d4). Bars represent mean values ± SE. For all cases $n = 8$. Shaded bars highlight the scotophase periods.

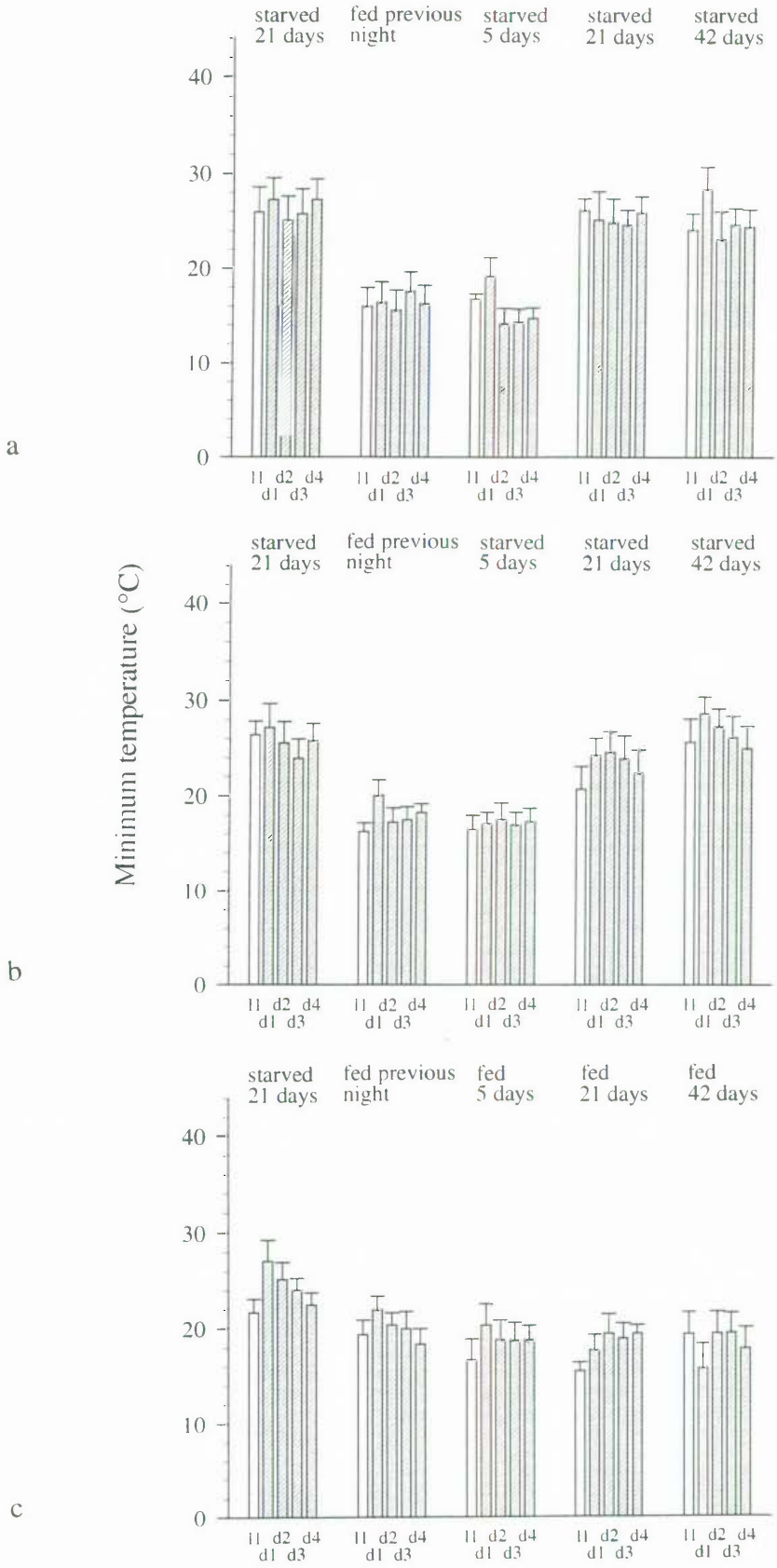

Figure 6.6. Effect of nutritional status on the profiles of minimum temperature (°C) recorded in the gradient of (a) adult males fed then starved, (b) adult females fed then starved, and (c) adult females fed then continuously provisioned with larvae. Minima are from 12 measurements per animal within the 3 hour periods of 15-18:00 h (l1), 18-21:00 h (d1), 21-24:00 h (d2), 24-03:00 h (d3) and 03-06:00 h (d4). Bars represent mean values ± SE For all cases $n = 8$. Shaded bars highlight the scotophase periods.

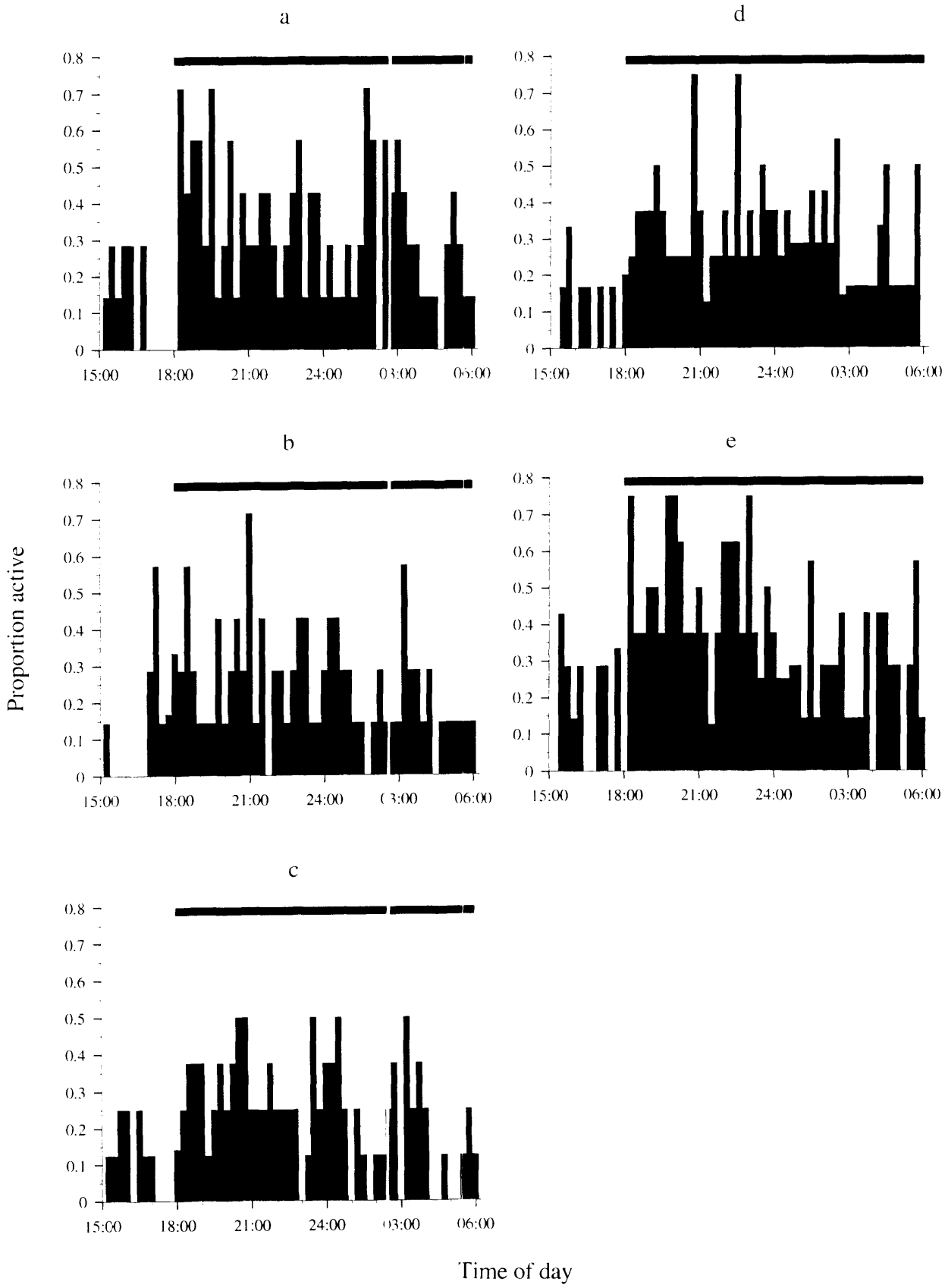

Figure 6.7. Activity profiles of adult males (a) initially starved for 21 days, (b) 1 day after feeding, (c) starved for 5 days, (d) starved for 21 days, and (e) starved for 42 days. Each bar represents the proportion of animals that had turned in the gradient resulting in a 5°C or greater change in selected temperature from the preceding temperature. Temperature was measured every 15 min. Horizontal bars represent scotophase from 18:00 to 06:00 hours. For all cases $n = 8$.

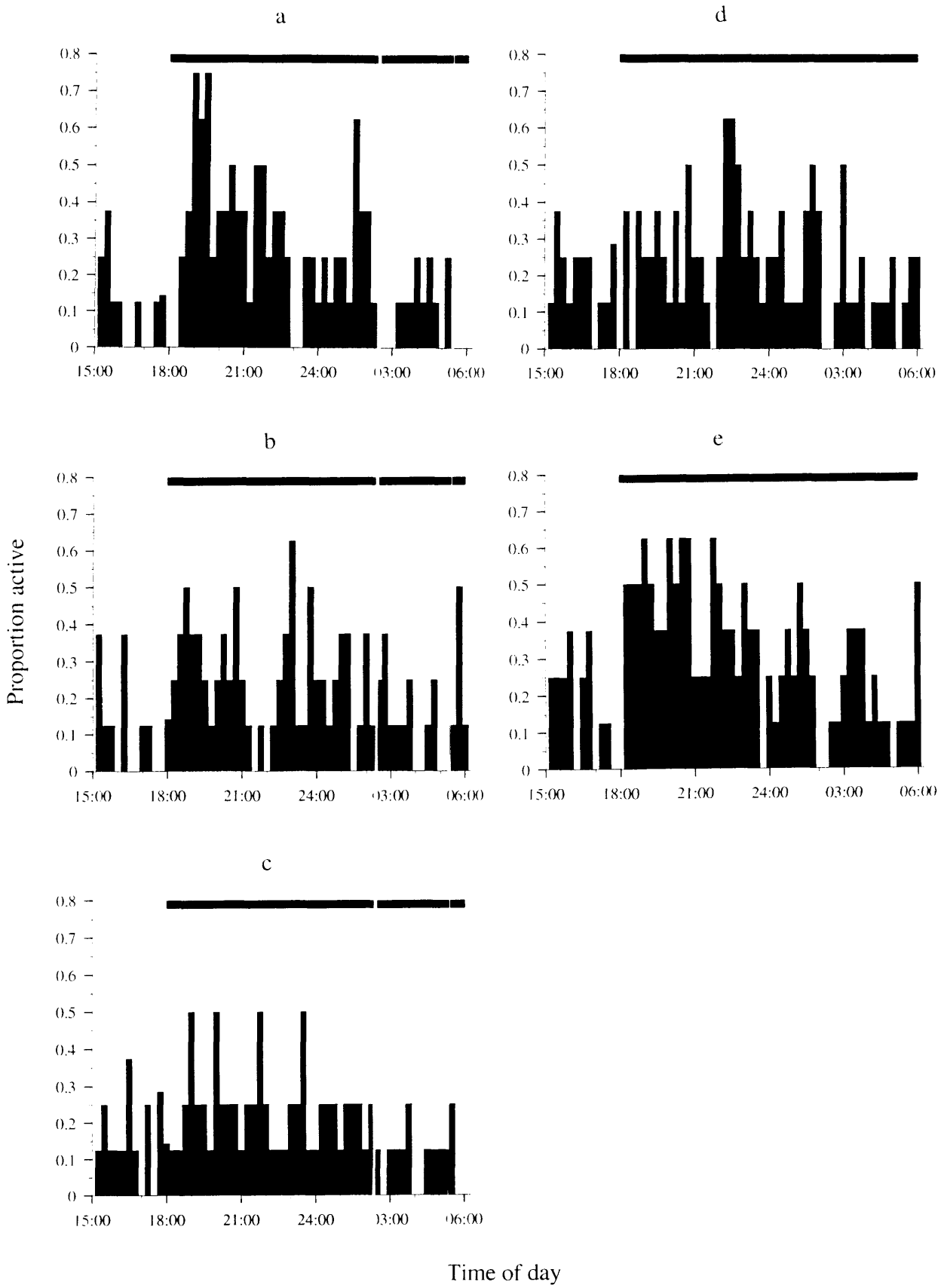

Figure 6.8. Activity profiles of adult females (a) initially starved for 21 days, (b) 1 day after feeding, (c) starved for 5 days, (d) starved for 21 days, and (e) starved for 42 days. Each bar represents the proportion of animals that had turned in the gradient resulting in a 5°C or greater change in selected temperature from the preceding temperature. Temperature was measured every 15 min. Horizontal bars represent scotophase from 18:00 to 06:00 hours.
For all cases $n = 8$.

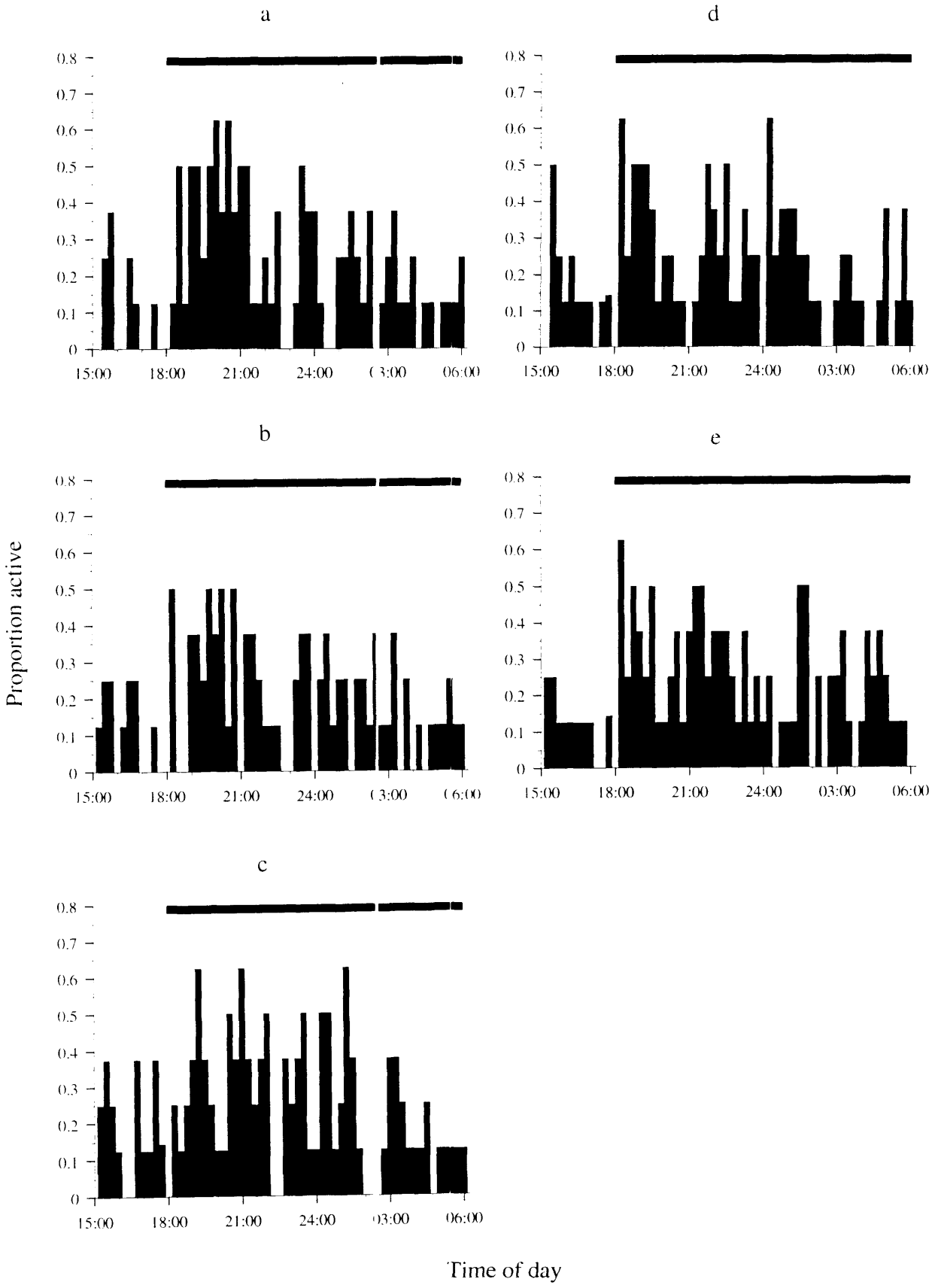

Figure 6.9. Activity profiles of adult females (a) initially starved for 21 days, (b) 1 day after feeding, (c) fed for 5 days, (d) fed for 21 days, and (e) fed for 42 days. Each bar represents the proportion of animals that had turned in the gradient resulting in a 5°C or greater change in selected temperature from the preceding temperature. Temperature was measured every 15 min. Horizontal bars represent scotophase from 18:00 to 06:00 hours. For all cases $n = 8$.