J Comp Physiol B (1994) 164:55–61

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

Dietary fats, selected body temperature and tissue fatty acid composition of agamid lizards (*Amphibolurus nuchalis*)

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Accepted: 12 October 1993

Abstract. The composition of tissue and membrane fatty acids in ectothermic vertebrates is influenced by both temperature acclimation and diets. If such changes in body lipid composition and thermal physiology were linked, a diet-induced change in body lipid composition should result in a change in thermal physiology. We therefore investigated whether the selected body temperature of the agamid lizard *Amphibolurus nuchalis* (body mass 20 g) is influenced by the lipid composition of dietary fatty acids and whether diet-induced changes in thermal physiology are correlated with changes in body lipid composition. The selected body temperature in two groups of lizards was indistinguishable before dietary treatments. The selected body temperature in lizards after 3 weeks on a diet rich in saturated fatty acids rose by 2.1 °C (photophase) and 3.3 °C (scotophase), whereas the body temperature of lizards on a diet rich in unsaturated fatty acids fell by 1.5 °C (photophase) and 2.0 °C (scotophase). Significant diet-induced differences were observed in the fatty acid composition of depot fat, liver and muscle. These observations suggest that dietary lipids may influence selection of body temperature in ectotherms via alterations of body lipid composition.

Key words: Dietary lipids – Fatty acids – Behavioural thermoregulation – Reptiles – Lizard, *Amphibolurus nuchalis*

Introduction

Ectothermic organisms alter the lipid composition of tissues and membranes during cold acclimation (Hazel 1988). Such alterations occur in a number of lipids, but the most consistent change in lipid composition during cold acclimation appears to be an increase of UFA and PUFA (Hazel 1988). It is likely that this increase in UFA increases the fluidity of membrane and tissue lipids at low T_b, which may partially explain how physiological functions can be maintained during cold exposure (Hochachka and Somero 1984; Cossins and Bowler 1987; Hazel 1988).

Although this compositional change of lipids in tissues and membranes seems to provide a convenient modulator of cellular physiology at low T_b the animals are faced with the problem of how to obtain PUFA. While vertebrates are able to synthesize MUFA, which have been shown to significantly increase the fluidity of cellular membranes and lower the melting point of tissue fats (Irving et al. 1957; Hazel 1988), they are unable to synthesize the essential fatty acids linoleic acid (C18:2) and linolenic acid (C18:3). These fatty acids are required as precursors for the production of most long-chain PUFA, which appear to be important particularly in those ectotherms that are active at low T_b (Hazel 1988). Thus, the PUFA concentration in the body of vertebrates can only be raised through incorporation of a diet containing essential FA.

This study investigates the effect of a diet rich in PUFA (10% sunflower oil) and a diet rich in SFA (10% sheep fat) on the selected T_b of the insectivorous agamid lizard *Amphibolurus nuchalis*. In a previous study on the largely herbivorous skink *Tiliqua rugosa* the selected T_b was found to be influenced by the lipid composition of the diet (Geiser et al. 1992). However, in that study, the lipid composition of tissues was not investigated and the question remained of how the FA composition of depot fat, liver and muscle was affected by diet and if these changes were correlated with those in thermal physiology.

Abbreviations: bm, body mass; FA, fatty acid(s); MUFA, monounsaturated fatty acids; PUFA polyunsaturated fatty acids; SFA, saturated fatty acids; T_a, air temperature; T_b, body temperature; UFA, unsaturated fatty acids

Material and methods

Twelve central-netted dragons *Amphibolurus nuchalis* (syn. *Ctenophorus nuchalis*; Agamidae) were caught in January 1991 near

Fowler's Gap Station (about 100 km north of Broken Hill), New South Wales. They were transported to the University of New England, Armidale, and were held in large terraria under an artificial photoperiod of LD 12:12, light from 06:00 to 18:00 hours. Ceramic heat lamps (100 W) were on throughout the photophase and heated the sand surface under the lamps to 44 °C; T_a during the scotophase was 25±1 °C. Animals were maintained on water and a diet of Reptile food (Wombaroo, Adelaide) mixed with apples and water and Friskies Go-Cat soaked in water. On 18 March, the 12 individuals were divided into two groups of matched bm and sex ratio. The selected T_b in these individuals was measured on 20 March (pre-feeding). Two days before this initial measurement animals were fed, by syringe, 10% of their bm a diet consisting of 40% Reptile food, 60% water and 6 drops Pentavite per 50 g food.

For measurements of selected T_b animals were placed in a 1.20 m × 0.17 m thermal gradient with substrate (sand) temperatures ranging from 17 to 58 °C. The temperatures in the gradient were kept high because this species selects very high T_bs in the wild (Bradshaw and Main 1968; MacMillen et al. 1989) and because soil surface temperatures at the site and time of capture approached 60 °C. Fine thermocouples (38 gauge) were inserted 3 cm into the cloaca of each animal, the wires taped to the tail, and T_b was monitored to the nearest 0.1 °C over 1 day at 15-min intervals with an Electronic Services Unit (Armidale, New South Wales) thermocouple data logger. Photoperiod during measurements was LD 12:12. After this initial measurement animals were fed once a week, by syringe, 10% of their bm. Water was always available to the animals when they were held in the terraria. The diet consisted of 40% Reptile food, 60% water, and 10% addition by weight of (1) sunflower seed oil ("unsaturated" diet; $n = 6$; bm 20.6±7.7 g SD) or (2) sheep lard ("saturated" diet; $n = 6$; bm 20.4±6.6 g). The water, fat and oil were warmed to 50 °C to ensure an even mixing of the diets. Six drops Pentavite were added to 55 g of the diet mixture. The selected T_b was measured 2 days after feeding as previously described after the animals had been on their respective diets in the first, second and third week. Body mass in both diet groups did not change significantly during the experimental period. In the third week on the respective diets, bm was 22.5±8.2 g in animals on the unsaturated diet and 21.4±7.4 g in animals on the saturated diet.

The mean selected T_b was calculated from all measurements during the photophase (lights on) and scotophase (lights off). Measurements during the first 30 min after animals were placed in the gradient were excluded from calculations. As the selected T_b changed during both the photophase and scotophase, the mean selected T_b maxima (14:00–17:00 hours) and the mean selected T_b minima (03:00–06:00 hours) were also calculated and compared.

The total lipid FA composition of the experimental diets differed substantially (Table 1). Differences were particularly pronounced in the content of the fatty acids C14:0, C18:0 and C18:2. These differences in the FA composition of the two diets were reflected in the SFA/UFA ratio which differed by a factor of 5, the n6/n3 FA ratio which differed by a factor of 9 and the PUFA content which differed by a factor of 8.6.

Animals were decapitated after they had been on the diets for 4 weeks. Depot fat (intraperitoneal), liver and muscle (upper hind leg) were immediately removed and frozen at −30 °C. Total lipid FA of diets and tissues were extracted and methylated using the method of Lepage and Roy (1986). Methyl esters were extracted in hexane and analyses were performed with a computer-controlled Hewlett Packard Series II gas chromatograph using a 30 m capillary FFAP column (Alltech, Deerfield, Ill., USA). Data were analysed using the Delta Chromatography Data System (Digital Systems, Brisbane). Standards for all 21 FA methyl esters that were identified were purchased from Larodan Fine Chemicals (Malmö, Sweden) and from Sigma (Castle Hill, Australia).

Numerical values in the results are expressed as mean ± 1 standard error (SE). Differences in the selected T_b between diet groups and fatty acid composition were determined using a two-tailed t-test and a one-way ANOVA. Repeated measures ANOVA was applied when comparing the selected T_b of the two groups before feeding and after animals had been on the diets for 3 weeks. Percentage values were arcsine-transformed before testing. Linear regressions were fitted using the method of least squares.

Table 1. Percent fatty acid composition of the two diets fed to *Amphibolurus nuchalis*

Fatty acid	Sheep fat diet "saturated"	Sunflower oil diet "unsaturated"
10:0	0.4	0.3
12:0	0.4	0.3
14:0	3.5	1.6
14:1	0.3	0.2
15:0	0.9	0.5
16:0	22.3	12.4
16:1	1.7	0.6
17:0	1.9	0.1
18:0	28.1	6.6
18:1	30.0	26.9
18:2n6	4.3	47.7
18:3n3	1.0	1.4
20:0	0.2	0.2
20:1	1.2	0.3
20:2n6	0.1	–
20:4n6	0.1	–
22:0	0.2	0.9
22:1	0.1	–
24:0	0.2	–
22:6n3	0.2	–
SFA	58.8	22.9
UFA	39.0	77.1
SFA/UFA	1.5	0.3
PUFA	8.6	32.0
n6	4.5	47.7
n3	1.2	1.4
n6/n3	34.1	3.8

Number of carbon atoms and number of double bonds of fatty acids are shown. The percentage values represent means of two diet preparations. SFA, sum of saturated fatty acids; UFA, sum of unsaturated fatty acids; PUFA, sum of polyunsaturated fatty acids; n6, sum of n6 fatty acids; n3, sum of n3 fatty acids

Results

Dietary fats and the selected T_b

The daily fluctuation of T_b in *A. nuchalis* was affected by the composition of dietary FA. The time-course of T_b was similar in the two experimental groups before feeding experiments, with relatively high T_bs during the photophase and relatively low T_bs during the scotophase (Fig. 1a,b). In the third week on their respective diets the mean T_b of animals on the saturated diet was well above that of most corresponding pre-feeding measurements, whereas most of the T_bs in animals on the unsaturated diet were well below those of pre-feeding measurements at the respective time of day (Fig. 1a,b).

The selected T_b of the two diet groups was indistinguishable before feeding (Fig. 2; $P>0.1$; ANOVA). Changes in the selected T_b that occurred within the 4 weeks of measurements differed between diet groups. In the animals on the saturated diet the selected T_b during the scotophase increased more or less linearly through-

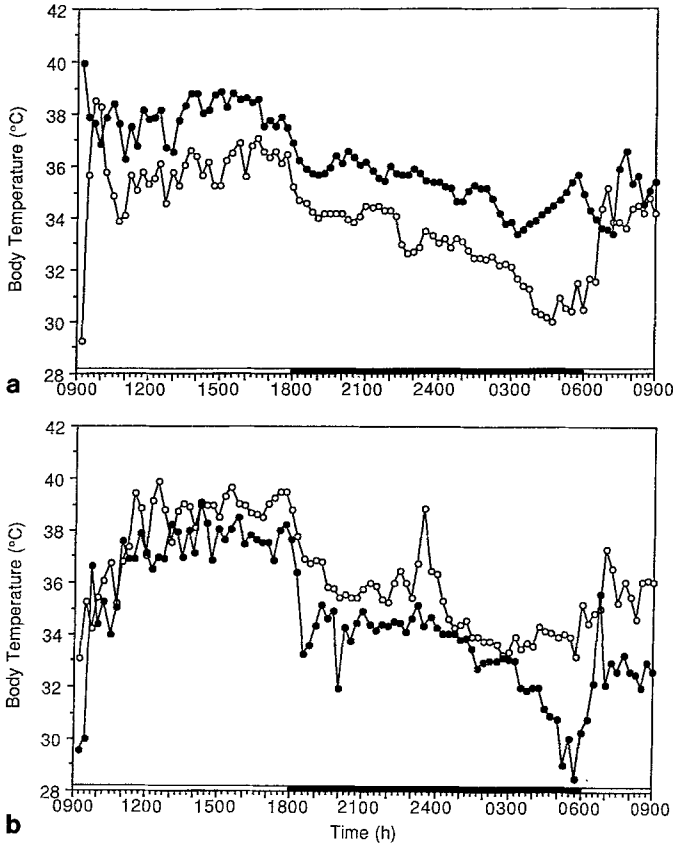

Fig. 1a,b. Daily variation of the selected T_b of *Amphibolurus nuchalis* before the dietary manipulations (*open symbols*) and after the animals had been on (**a**) saturated diet or (**b**) unsaturated diet for 3 weeks (*closed symbols*). Mean T_b was calculated for the six individuals. The *black bar* indicates the period of darkness. ○ Pre-feeding; ● Saturated diet

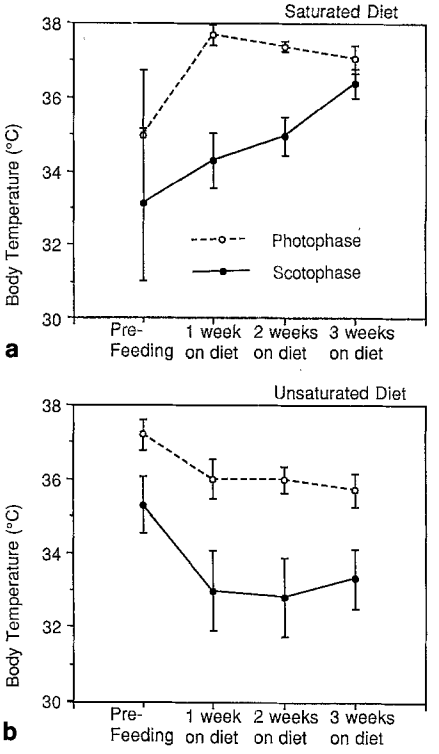

Fig. 2a,b. The change of the selected T_b of *Amphibolurus nuchalis* over a 4-week period. Values represent means ± 1 SE of six individuals on (**a**) saturated diet or (**b**) unsaturated diet during the photophase (*open symbols*) and scotophase (*closed symbols*)

out the experimental period; during the photophase selection of relatively high T_bs occurred within the first week of feeding and was maintained at this level throughout the rest of the experiment (Fig. 2a). In animals on the unsaturated diet the decrease in the selected T_b was most pronounced during the first week on the diet and relatively low T_bs were maintained throughout the rest of the experimental period (Fig. 2b). The selected T_b of the two diet groups changed significantly over the 4-week experiments (repeated measures ANOVA; $P<0.01$). In the third week on the respective diets the selected T_b differed between animals on the saturated diet (photophase $T_b = 37.0 \pm 0.4$ °C; scotophase $T_b = 36.4 \pm 0.4$ °C) and animals on the unsaturated diet (photophase $T_b = 35.7 \pm 0.4$ °C; scotophase $T_b = 33.3 \pm 0.8$ °C) ($P<0.05$ photophase; $P<0.01$ scotophase; t-test).

The change in the selected T_b from pre-feeding to the third week on the diets also differed significantly between the diet groups ($P<0.05$; t-test; Fig. 3). Animals on the saturated diet showed a rise in the selected T_b ($+2.1 \pm 1.5$ °C photophase; $+3.3 \pm 2.0$ °C scotophase), whereas animals on the unsaturated diets showed a drop in the selected T_b (-1.5 ± 0.7 °C photophase; -2.0 ± 0.5 °C scotophase).

Significant effects of dietary lipids were also observed when the mean selected T_b maxima during the photophase (14:00–17:00 hours) and mean T_b minima during the scotophase (03:00–06:00 hours) were compared. The pre-feeding selected T_b maxima and minima were indistinguishable between groups (unsaturated group: photophase $T_b = 38.8 \pm 0.7$ °C, scotophase $T_b = 33.8 \pm 2.8$ °C; saturated group: photophase $T_b = 36.1 \pm 6.8$ °C, scotophase $T_b = 31.1 \pm 4.2$ °C) (ANOVA; $P>0.1$). The selected T_b maxima and minima of the two diet groups changed significantly over the 4-week experiment (repeated measures ANOVA; $P<0.01$). After 3 weeks on the two diets the selected T_b maxima and minima differed beween animals on the unsaturated diet (photophase $T_b = 37.7 \pm 1.5$ °C, scotophase $T_b = 30.9 \pm 1.4$ °C) and animals on the saturated diet (photophase $T_b = 38.5 \pm 0.9$, scotophase 34.1 ± 1.9 °C) (ANOVA; $P<0.01$).

Dietary fats and tissue fatty acid composition

The FA composition of the depot fat total lipids was affected by the diets (Table 2). Of the 20 FA that were identified, 10 differed significantly between the two diet groups. A further 7 FA were considered to differ between diet groups, as they were detected in small amounts in one of the diet groups, but not in the other. Thus, only 3 FA in the depot fat did not differ between diet groups. Compositional differences were particularly pronounced for C18:0, C18:1 and C18:2 FA, reflecting differences in the diet composition (Table 1). The sums of SFA, UFA,

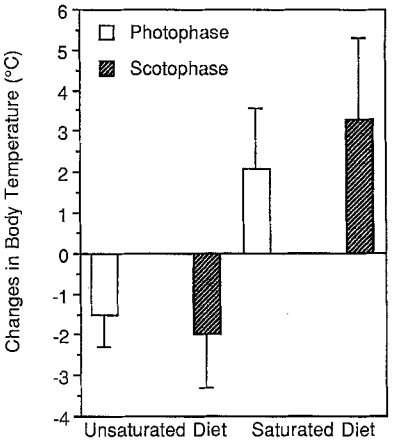

Fig. 3. The difference in selected T_b of *Amphibolurus nuchalis* from before feeding to 3 weeks on the diets. Values represent means ± 1 SE of six individuals

the SFA/UFA ratio, PUFA, n6 FA and the n6/n3 FA ratio also differed significantly between diet groups. The SFA/UFA ratio was 2-fold greater and the PUFA content was 3.5-fold smaller in animals on the saturated diet in comparison to animals on the unsaturated diet.

Fatty acids of liver total lipids were also affected by the diets (Table 3). Of the 17 FA that were identified, 6 differed significantly between diets and a further 3 were detected in one diet group but not in the other; compositional differences were particularly pronounced in the C18:0, C18:1 and C18:2 fatty acid. The remaining 8 FA were indistinguishable. However, the sums of FA and their ratios differed significantly between diet groups, with the exception of the n3 FA. The SFA/UFA ratio was 1.7-fold greater and the PUFA content was 2.9-fold smaller in animals on the saturated diet in comparison to those on the unsaturated diet.

Muscle total lipid FA also differed between diet groups (Table 4). Of the 19 FA that were identified, 8 differed significantly and a further 2 were detected in one diet group but not in the other; pronounced differences were observed for the C18:1, C18:2 and C18:3 FA. The remaining 9 FA did not differ. The FA sums and ratios differed significantly between the two diet groups with the exception of the SFA. Differences were particularly pronounced in the content of MUFA, PUFA, n6 and n3 FA.

Discussion

The present study suggests that the selected T_b of *A. nuchalis* is affected by the composition of dietary FA. A

Table 2. Percent fatty acid composition of depot fat total lipids of *Amphibolurus nuchalis* maintained on different lipid diets

Fatty acid	Saturated fat diet ($n=4$)	Unsaturated oil diet ($n=5$)	t-test $P<$
12:0	0.3±0.05	0.2±0.04	ns
14:0	3.1±0.20	1.9±0.09	0.0005
14:1	0.3±0.05	0.1±0.04	0.05
15:0	0.5±0.05	0.3±0.00	0.001
16:0	19.1±0.40	14.6±0.80	0.01
16:1n9	5.5±0.65	3.0±0.36	0.01
17:0	0.8±0.05	0.3±0.00	0.0001
18:0	11.2±1.05	5.9±0.54	0.005
18:1	45.3±0.95	35.8±1.48	0.005
19:0	0.5±0.05	–	–
18:2n6	8.5±0.50	34.7±2.06	0.00001
18:3n3	1.3±0.15	1.3±0.18	ns
20:1n11	1.2±0.05	0.6±0.00	0.00001
20:1n9	0.3±0.05	–	–
20:2n6	–	0.4±0.04	–
20:4n6	–	0.2±0.00	–
22:0	–	0.5±0.04	–
22:1n9	0.1±0.05	–	–
22:2n6	0.2±0.00	0.1±0.04	ns
24:0	–	0.2±0.13	–
SFA	35.4±1.05	23.7±1.03	0.001
UFA	63.6±1.2	76.0±1.07	0.0001
SFA/UFA	0.56±0.04	0.31±0.02	0.0005
PUFA	9.8±0.60	36.6±2.19	0.00001
MUFA	52.9±1.25	39.4±1.61	0.001
n6	8.6±0.50	35.3±2.06	0.00001
n3	1.3±0.15	1.3±0.18	ns
n6/n3	7.0±0.69	28.22±2.25	0.0001

Fatty acid concentrations are shown as the mean percentage±SEM of the number of individuals investigated. SFA, saturated fatty acids; UFA, unsaturated fatty acids; PUFA, polyunsaturated fatty acids; MUFA, monosaturated fatty acids; –, Fatty acid not present or statistical test not performed, ns = $P>0.05$

Table 3. Percent fatty acid composition of liver total lipids of *Amphibolurus nuchalis* maintained on different lipid diets

Fatty acid	Saturated fat diet ($n=4$)	Unsaturated oil diet ($n=5$)	t-test $P<$
14:0	1.6±0.20	1.4±0.09	ns
14:1	0.3±0.10	0.3±0.09	ns
15:0	0.2±0.05	–	–
16:0	20.3±0.35	18.0±0.45	0.005
16:1n9	10.1±1.10	8.6±1.43	ns
17:0	0.5±0.05	–	–
18:0	7.0±0.35	3.5±0.36	0.0005
18:1	43.8±1.55	32.9±1.07	0.001
18:2n6	9.0±0.70	30.7±1.39	0.00001
18:3n3	1.3±0.15	1.1±0.09	ns
20:1n11	1.3±0.10	0.7±0.04	0.001
20:1n9	0.2±0.10	–	–
20:2n6	0.2±0.00	0.7±0.13	0.05
20:4n6	1.1±0.25	1.0±0.27	ns
22:0	0.9±0.15	0.7±0.18	ns
24:0	0.2±0.05	0.1±0.04	ns
22:6n3	0.3±0.05	0.2±0.09	ns
SFA	30.9±0.65	23.6±0.67	0.0001
UFA	67.5±0.45	76.1±0.63	0.00001
SFA/UFA	0.46±0.01	0.31±0.01	0.00001
PUFA	11.7±1.15	33.6±1.74	0.00001
MUFA	55.8±1.55	42.3±2.06	0.005
n6	10.3±1.00	32.4±1.65	0.00001
n3	1.4±0.15	1.2±0.09	ns
n6/n3	7.59±0.38	27.61±1.85	0.00001

Fatty acid concentrations are shown as the mean percentage±SE of the number of individuals investigated. SFA, saturated fatty acids; UFA, unsaturated fatty acids; PUFA, polyunsaturated fatty acids; MUFA, monosaturated fatty acids; –, Fatty acid not present or statistical test not performed; ns = $P>0.05$

diet containing high amounts of SFA raised the selected T_b, one rich in UFA lowered the selected T_b.

Changes in T_b selection following dietary lipid supplementation observed here for the agamid *A. nuchalis* differed somewhat from those observed in the skink *T. rugosa* (Geiser et al. 1992). While the T_b of *T. rugosa* on unsaturated diet fell, the T_b in individuals on the saturated diet did not change. These differences could be attributed to species-specific ideosyncrasies in the response to the diets. They also could be due to differences in the FA composition of the diets that were fed to the animals. Compositional differences of the diet in the present study were greater than in the previous study (Geiser et al. 1992) because of the relatively greater content of added fat or oil. It is also possible that at different times of the year reptiles respond in a different way to dietary lipids as they do to photoperiod (Rismiller and Heldmaier 1988). The *T. rugosa* were studied in November/December (early summer), whereas the *A. nuchalis* were studied in March/April (autumn). The *T. rugosa* in summer had already a relatively high selected T_b before feeding of the two diets (Firth et al. 1989; Geiser et al. 1992) and therefore may not have raised T_b any further despite feeding of saturated diet. By contrast, the selected T_b of the *A. nuchalis* in autumn before dietary manipulations were somewhat low in comparison to summer active field values (Licht et al. 1966; MacMillen et al. 1989), although they were high in comparison to the T_bs experienced in winter.

Diet-induced differences in thermal physiology have also been observed in hibernating mammals (Geiser and Kenagy 1987; Florant et al. 1993). Hibernators on an unsaturated diet showed longer torpor bouts and lower minimum T_bs (at which T_b is metabolically defended during torpor) than individuals on a saturated diet. In the two lizard species studied to date the diet-induced differences in the selected T_b between diet groups of lizards were somewhat more pronounced than differences in the minimum T_b of hibernators (Geiser et al. 1992; present study). As unsaturated dietary lipids resulted in a reduction of T_b in both hibernating mammals and lizards it is likely that similar thermoregulatory mechanisms are involved in ectotherms and heterothermic endotherms. However, it appears that both the seasonal change in body lipid composition (Aloia 1988; Hazel 1988) and the diet-induced change in thermoregulation are less pronounced in mammalian hibernators than in ectotherms.

A direct comparison of the selected T_b of lizards and the minimum T_b of torpid hibernators may invite criticism because of the differences in thermoregulatory mechanisms between ectotherms and endotherms. The T_b of lizards is regulated predominantly by behaviour (Huey 1982; Heatwole and Taylor 1987), whereas the minimum T_b during torpor is defended by endogenous heat production (Heller and Hammel 1972). However, there are well established parallels between ectothermic and endothermic thermoregulation. For example, during fever T_b rises in both ectotherms and endotherms in response to the

Table 4. Percent fatty acid composition of muscle total lipids of *Amphibolurus nuchalis* maintained on different lipid diets

Fatty acid	Saturated fat diet ($n=4$)	Unsaturated oil diet ($n=5$)	*t*-test $P<$
14:0	0.7±0.05	0.6±0.09	ns
15:0	0.2±0.00	0.2±0.09	ns
16:0	12.7±0.30	11.1±0.45	0.05
16:1n9	2.5±0.40	1.4±0.22	0.05
17:0	0.6±0.05	0.2±0.04	0.05
18:0	14.5±0.90	14.1±0.31	ns
18:1	27.2±1.70	18.3±0.45	0.001
18:2n6	19.7±1.80	34.0±1.21	0.0005
18:3n3	1.5±0.05	0.6±0.09	0.0005
20:0	0.3±0.10	0.5±0.04	ns
20:1n11	1.0±0.05	0.6±0.04	0.001
20:1n9	0.2±0.10	–	–
20:2n6	0.8±0.10	0.8±0.04	ns
20:4n6	8.6±0.55	8.1±0.36	ns
22:0	1.8±0.20	1.1±0.04	0.005
22:2n6	–	0.6±0.18	–
22:4n6	0.4±0.05	0.5±0.09	ns
24:0	1.3±0.10	1.4±0.13	ns
22:6n3	2.0±0.20	1.9±0.18	ns
SFA	31.9±1.05	29.1±0.67	ns
UFA	63.7±2.20	66.7±0.63	0.05
SFA/UFA	0.48±0.05	0.43±0.01	0.05
PUFA	32.9±2.45	46.5±1.16	0.005
MUFA	30.8±2.05	20.3±0.67	0.001
n6	29.5±2.25	43.9±1.25	0.001
n3	3.5±0.20	2.5±0.18	0.01
n6/n3	9.25±0.05	17.79±1.42	0.001

Fatty acid concentrations are shown as the mean percentage±SE of the number of individuals investigated. SFA, saturated fatty acids; UFA, unsaturated fatty acids; PUFA, polyunsaturated fatty acids; MUFA, monosaturated fatty acids; – Fatty acid not present or statistical test not performed, ns = $P>0.05$

same exogenous stimulus (Firth et al. 1980; Cabanac 1990). Thus, a comparison of diet-induced differences in thermoregulation between the two groups may be justified.

Diet-induced changes in the selected T_b of individual *A. nuchalis* observed here correlated with changes in the FA composition of their tissues. In the third week on the diets, the mean selected T_b during the scotophase was positively correlated with the SFA/UFA ratio (a reliable indicator of lipid fluidity) of depot fat (linear regression: $r^2 = 0.54$; $P<0.02$), liver ($r^2 = 0.60$; $P<0.01$) and muscle ($r^2 = 0.58$; $P<0.01$). Correlations between the mean selected T_b during the photophase and the SFA/UFA ratio were less distinct (depot fat, $r^2 = 0.46$, $P<0.05$; liver $r^2 = 0.15$, $P>0.05$; muscle $r^2 = 0.52$, $P<0.02$). As the variation of the tissue SFA/UFA ratio explained between 45 and 60% of the variation in the selected T_b of individuals (with the exception of the mean selected T_b during the photophase and liver SFA/UFA ratio), it appears reasonable to assume that tissue FA composition and T_b selection and regulation are functionally linked.

The data on the time-course of T_b change during the experimental period may shed further light on possible regulatory mechanisms. The selected T_b changed most dramatically within the first week on the diet (i.e. only 2 days after experimental diets were first administered). This suggests the involvement of relatively fast mechanisms. It is thus possible that digestibility of fat may influence selection of T_b of lizards. Unsaturated fats may be easy to digest at low T_b, whereas saturated fats may require selection of high T_b so they can be digested and absorbed. However, some changes in body lipid composition may have occurred within 2 days, as this species selects very high T_bs similar to those of mammals. A relatively fast lipid turnover is therefore likely. The involvement of body composition in determination of the selected T_b is supported by the observation that selected T_b during the scotophase changed gradually over the 4 weeks of experimentation in animals on the saturated diet. This gradual change in T_b selection is likely to be caused by a gradual change in body lipid composition. A gradual change of the selected T_b was also observed in *T. rugosa* on an unsaturated diet, which decreased the selected T_b over a 2-week period (Geiser et al. 1992). Thus, both digestibility of dietary fats and body lipid composition may play a role in the selection of T_b in lizards.

How could body lipid composition affect the selected T_b of animals? Compositional differences of FA in body tissues may affect access to fat stores which may be difficult to mobilise when they are in a rigid state. Large amounts of MUFA and PUFA in fat stores may allow regulation at a low T_b without negative effects on energy balance. As tissue FA composition was significantly affected by dietary lipids it is likely that cellular membranes

were also influenced (McMurchie 1988; Geiser 1990). Enrichment of MUFA and PUFA in cellular membranes appears to be a general requirement for maintenance of physiological function at low temperatures (Hazel 1988). Moreover, it is well documented that the thermal response of mitochondrial membrane-associated enzymes are affected by the membrane FA composition (McMurchie 1988). Therefore, ATP production and energy metabolism may be influenced by the FA composition of mitochondrial membranes and high amounts of PUFA may improve mitochondrial function at low temperatures and thus allow selection of low T_b. An alternative possibility is that membrane permeability is directly influenced by the content of PUFA and this may influence cellular metabolism at low T_b (Hulbert and Else 1989). Furthermore, it has been demonstrated that the lipid environment surrounding neural receptors affects receptor binding activity (Loh and Law 1980). Thus, diet-induced changes in thermoregulation may be explained by changes in the FA composition of tissues and cellular membranes.

Acknowledgements. This work was supported by a grant from the Australian Research Council to F.G. Collection permits were granted by the New South Wales National Parks and Wildlife Service. We would like to thank Paul Else for sharing information on collecting sites, Steve Trémont for help collecting animals, Denise Gosper, Barbara Learmonth and Susan Wyborn for technical assistance, Bronwyn McAllan for comments on the manuscript and the University of New South Wales for accomodation at Fowler's Gap.

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