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Polyunsaturated dietary lipids lower the selected body temperature of a lizard

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Summary. Cold acclimation lowers the selected body temperature (T_b) in many ectothermic vertebrates. This change in behavioural thermoregulation is accompanied by an increase in the proportion of polyunsaturated fatty acids in tissues and cellular membranes. We investigated how diets containing different fatty acids, known to significantly alter the fatty acid composition of animal tissues and membranes, affect the selected T_b of the lizard *Tiliqua rugosa*. Lizards on a diet containing many polyunsaturated fatty acids (10% sunflower oil) showed a 3–5 °C decrease in T_b, whereas T_b in animals on a diet containing mainly saturated fatty acids (10% sheep fat) did not change. Our study suggests that the composition of dietary lipids influences thermoregulation in ectothermic vertebrates and may thus play a role in the seasonal adjustment of their physiology.

Key words: Fatty acids – Diet – Behavioural thermoregulation – Reptiles – Lizard – *Tiliqua rugosa*

Introduction

Terrestrial vertebrates have to cope with diurnal and annual fluctuations of environmental temperatures. Homeothermic mammals and birds avoid fluctuations of body temperature (T_b) by maintaining thermal homeostasis via internal heat production. A thermally constant internal milieu promotes metabolic efficiency and independence from external temperature change. In contrast, cellular function in ectothermic vertebrates is subject to variations in the thermal environment, but many species are able to impart some control of T_b by behavioural thermoregulation (Huey 1982).

To adjust for seasonal changes in environmental temperature many ectothermic vertebrates lower the selected T_b during winter (Hazel and Prosser 1974; Case 1976; Rismiller and Heldmaier 1988). This seasonal alteration in the selected T_b requires biochemical alterations of cellular components to maintain normal function at the lower T_b. Such modifications seem to be achieved predominantly by changes in the lipid composition of tissues and cell membranes (Cossins et al. 1977; Hazel 1988). Cold acclimation increases the concentration of polyunsaturated fatty acids in tissue fats and phospholipids of cellular membranes of ectotherms which seems important for maintenance of suitable fluidity and permeability of membranes at low T_b (Cossins and Bowler 1987; White and Somero 1982). However, the polyunsaturated fatty acids linoleic acid (C18:2) and linolenic acid (C18:3) are essential in the diet of vertebrates and are required for production of most longer chain polyunsaturated fatty acids (Lehninger 1982). Therefore an increase in the proportion of polyunsaturated fatty acids in body lipids can only be achieved by either selecting a diet of appropriate composition or by the selective incorporation of these fatty acids.

Because cold acclimation increases the proportion of polyunsaturated fatty acids in tissues and cellular membranes of ectothermic vertebrates, and because dietary lipids also alter tissue and membrane lipid composition of animals (McMurchie 1988; Geiser 1990), we were interested in whether a diet rich in polyunsaturated fatty acids ("unsaturated" diet; Table 1) would lower the selected T_b of shingle-back lizards *Tiliqua rugosa*, in comparison to animals on a diet rich in saturated fatty acids ("saturated" diet; Table 1).

Materials and methods

Twelve *T. rugosa* (Scincidae) were caught in November near Murray Bridge, South Australia. They were divided into two groups of matched body mass and sex ratio and kept at a constant air temperature (T_a) of 20 °C, photoperiod 05:00–19:00 hours CST. One day after capture the selected T_b was measured (pre-feeding) for 24 h in a 1.5-m thermal gradient with substrate (sand) temperature gradually changing from 7 to 57 °C; photoperiod 05:00–19:00 h.

Abbreviations: CST, central standard time; T_a, air temperature; T_b, body temperature

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Table 1. Percent fatty acid composition of the two diets used in this study

Fatty acid	Sheep fat diet „Saturated"	Sunflower oil diet „Unsaturated"
12:0	2.5	trace
14:0	7.4	5.8
14:1	4.0	1.5
16:0	23.6	22.1
16:1	4.6	0.8
18:0	14.5	8.2
18:1	26.3	23.6
18:2	5.2	29.9
18:3	3.4	1.4
20:0	1.5	0.8
21:0	1.5	–
22:0	1.6	3.7
22:5	–	0.7
UI	55.5	93.4
PUFA	8.6	32.0

Number of carbon atoms and number of double bonds of fatty acids are shown. Unsaturation index (UI) is the sum of the percentage of unsaturated fatty acids multiplied by their number of double bonds. PUFA is the sum of polyunsaturated fatty acids

Flexible 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 at 10-min intervals with a Fluke data logger. After this initial measurement, animals in the two groups were fed with two diets that differed substantially in the fatty acid composition (Table 1). The diets were: (1) reptile supplement (Wombaroo; Adelaide) containing 55% protein, 22% fat, 12% carbohydrate and vitamins and minerals with addition by weight of 10% sheep lard (saturated diet), and (2) reptile supplement with 10% sunflower seed oil (unsaturated diet). The unsaturation index of the unsaturated diet was almost double and the content of polyunsaturated fatty acids was 3.7-fold that of the saturated diet. Differences were particularly pronounced in the content of linoleic acid (C18:2). Animals were fed 20 ml of the diet mixed with 50% water with a syringe every 2 days. T_b was measured as outlined above after the animals had been on their diets for 6 and 14 days.

Fatty acids of total lipids of the two diets were extracted and methylated using the method of Lepage and Roy (1986). Methyl esters were extracted in hexane and analyses were performed in a computer-controlled Hewlett Packard 5890 Series II gas chromatograph using a 30 m capillary FFAP column (Alltech, Deerfield, ILL.). Data were analysed using the Delta chromatography data system (Digital Systems, Brisbane).

Results

The daily variation in T_b of lizards in the two groups was similar before the dietary manipulations (Fig. 1a). The selected T_b gradually decreased in both groups after lights off and increased again after lights on. After the lizards had been on their respective diets for 14 days the mean selected T_b of individuals on the unsaturated diet was always below that of individuals on the saturated diet (Fig. 1b).

The mean selected day-time and night-time T_b of the two groups of lizards was indistinguishable before the dietary manipulations ($P > 0.1$; t-test; Fig. 2). The selected day-time and night-time T_b in animals on the unsaturated diet decreased linearly over the next 14 days (Fig. 2). After 14 days on the diet the selected day-time T_b of animals on the unsaturated diet was significantly lower than that of animals on the saturated diet ($P < 0.01$; t-test). The selected T_b of animals on the saturated diet did not change (linear regression: $P > 0.1$ for both day-time and night-time).

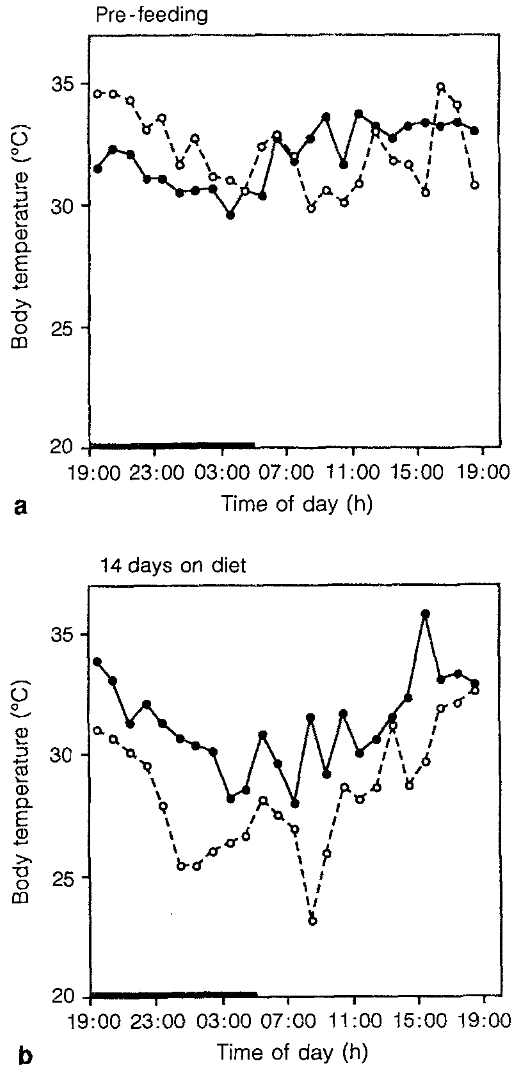

Fig. 1a, b. Daily variation of the mean selected T_b of *Tiliqua rugosa* before the dietary manipulation (pre-feeding; **a**), and after animals had been on their respective diets for 14 days (14 days on diet; **b**). Means were calculated for six individuals from each diet group. Bars indicate the period of darkness; —●— saturated, --○-- unsaturated diet

Discussion

This study demonstrates that the composition of dietary fatty acids influences the selection of T_b in the lizard *T. rugosa*. In particular, dietary unsaturated fatty acids resulted in a significant decrease in the selected T_b.

The unsaturated diet may elicit a lower selected T_b for

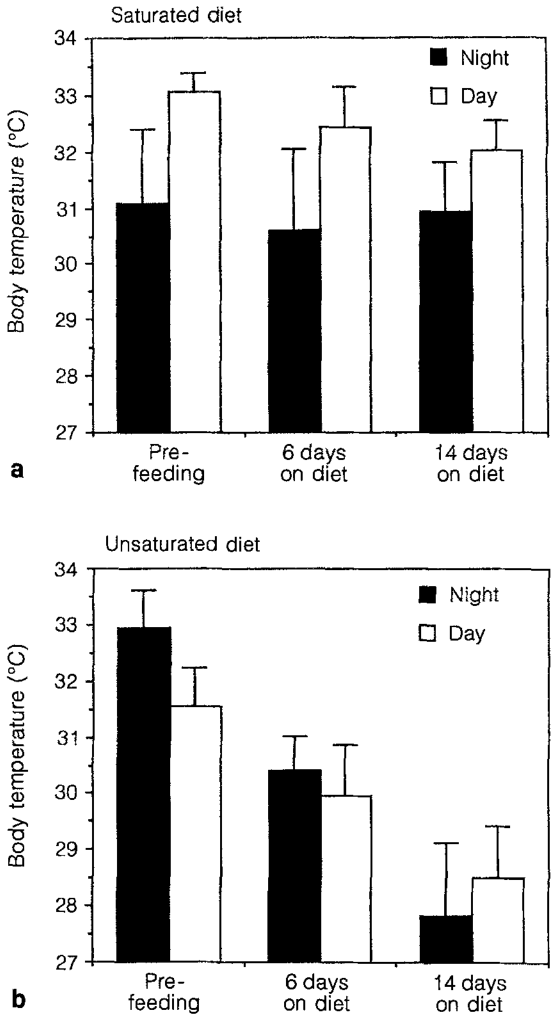

Fig. 2a, b. Mean selected body temperature (T_b with 1SE) of *T. rugosa* on saturated diet (**a**; n=6) and unsaturated diet (**b**; $n=6$). Mean selected T_b of animals was indistinguishable before the diet experiments, but selected day-time T_b differed significantly ($P<0.01$; *t*-test) after the animals had been on their respective diets for 14 days. Linear regressions for selected T_b as a function of time of animals on the unsaturated diet were: Day-time: T_b (°C) = 31.43–0.21 time (days), $P<0.01$, $r=-0.54$; Night-time: T_b (°C) = 32.79–0.36 time (days) $P<0.001$, $r=-0.71$. Regressions for selected T_b of animals on saturated diet were not significant ($P>0.1$)

several reasons. It is known that dietary lipids change the composition of animal cellular membranes (McMurchie 1988). Animals on a diet high in polyunsaturated fatty acids might therefore be able to manufacture cell membranes with a composition able to maintain the physical properties that are required for function at low temperature (Cossins and Bowler 1987; Hazel 1988). A correlation between reduction of selected T_b and diet-induced increase in unsaturated fatty acids in membrane phospholipids would suggest a direct involvement of membrane lipid composition in the regulation of T_b.

However, dietary lipids also affect the composition of animal tissues. For example, depot fat largely reflects the ingested fatty acids (Geiser 1990). Saturated fats solidify at relatively high temperature, therefore negating or reducing access to lipid stores when T_b falls below the melting point of the fat. Lipid stores in the form of unsaturated fatty acids, which remain fluid over a wide range of temperatures, would therefore provide fuel for the animals at low temperatures.

High quantities of stored or dietary polyunsaturated fatty acids also could be used for synthesis of prostaglandins which have been shown to be involved in thermoregulation (Lin 1984). Thus, the increase of polyunsaturated fatty acids in the body could influence T_b indirectly via hormone production. However, as prostaglandins seem to be predominantly involved in raising T_b of ectothermic and endothermic vertebrates (Cabanac 1990), and unsaturated fatty acids cause a decrease of the selected T_b, the influence of prostaglandins in the present study seems unlikely.

A further possibility that has to be considered is the digestibility of dietary fats. As for stored fats, the high melting point of saturated triglycerides may slow their uptake at low temperatures. Digestion of saturated dietary fats may therefore require selection of high T_b. The digestive system should be able to process unsaturated dietary fats with low melting points at relatively low selected T_b, and their uptake should be possible even at relatively low environmental temperatures.

Whatever the reasons for the diet-induced changes in thermoregulation, they have important implications for nutritional ecology and seasonal adjustment of physiology of vertebrates. Because of their inability to synthesize most polyunsaturated fatty acids from saturated or monounsaturated fatty acids, the seasonal changes in body lipid composition and thermoregulation of ectothermic vertebrates may require selective feeding of diets of appropriate lipid composition. However, because invertebrates and plants, the main diet of the species investigated here (MacMillen et al. 1989), both increase their content of polyunsaturated fatty acids in the cold (Fast 1970; Raison et al. 1982), seasonal changes of dietary fatty acid intake and consequently body lipid composition may occur incidentally and without diet selection.

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