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## Daily rhythm of oxygen consumption and thermoregulatory responses in some European winter- or summer-acclimatized finches at different ambient temperatures

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**Abstract** The oxygen consumption of European finches, the siskin (*Carduelis spinus*), the brambling (*Fringilla montifringilla*), the bullfinch (*Pyrrhula pyrrhulla*), the greenfinch (*Carduelis chloris*) and the hawfinch (*Coccothraustes coccothraustes*), was recorded continuously while ambient temperature was decreased stepwise from +30 down to -75 °C. The oxygen consumption, body temperature (telemetrically), and shivering (integrated pectoral electromyography) of greenfinches were measured simultaneously at ambient temperatures between +30 and -75 °C. Maximum heat production, cold limit, lower critical temperature, basal metabolic rate and thermal conductance (of the greenfinch) were determined. The diurnal variation of oxygen consumption of siskins and greenfinches was recorded at thermoneutrality and below the thermoneutral zone in winter- and summer-acclimatized birds. The diurnal variation of body temperature and thermal conductance of greenfinches were also determined. The diurnal variation of heat production was not seasonal or temperature dependent in the siskin and in the greenfinch. Nocturnal reduction of oxygen consumption saved 15–33% energy in the siskin and greenfinch. Body temperature of the greenfinch was lowered by 2.5–3.4 °C. The nocturnal reduction of thermal conductance in the greenfinch was 39–48%. The basal metabolic rate was lowest in the largest bird (hawfinch) and highest in the smallest bird (siskin). The values were in the expected range. The heat production capacity of finches in winter was 4.7 times basal metabolic rate in the siskin, 4.2 times in the brambling, 3.5 times in the greenfinch and 2.9 times in the bullfinch and hawfinch. The heat production capacity of the

siskin and greenfinch was not significantly lower in summer. The cold limit temperatures (°C) in winter were -61.2 in the siskin, -41.3 in the greenfinch, -37.0 in the bullfinch, -35.7 in the brambling and -28.9 in the hawfinch. The cold limit was 14.3 °C higher in summer than in winter in the siskin and 8.7 °C in the greenfinch. Thermal insulation of the greenfinch was significantly better in winter than in summer. The shivering of the greenfinch increased linearly when ambient temperature was decreased down to -40 °C. Maintenance of shivering was coincident with season. In severe cold integrated pectoral electromyography did not correlate with oxygen consumption as expected. The possible existence of non-shivering thermogenesis in birds is discussed. It is concluded that the acclimatization of European finches is primarily metabolic and only secondly affected by insulation.

**Key words** Thermoregulation · Metabolism · Daily rhythm · Shivering · European finches

**Abbreviations** *AAT* avian adipose tissue · *bm* body mass · *BMR* basal metabolic rate · *C<sub>t</sub>* thermal conductance · *EMG* electromyogram · *HP* heat production · *HP<sub>max</sub>* maximum heat production · *MR* metabolic rate · *NST* non-shivering thermogenesis · *RMR* resting metabolic rate · *RQ* respiratory quotient · *T<sub>a</sub>* ambient temperature · *T<sub>b</sub>* body temperature · *T<sub>c</sub>* colonic temperature · *T<sub>lc</sub>* lower critical temperature · *TNZ* thermoneutral zone · *T<sub>st</sub>* shivering threshold temperature · *VO<sub>2</sub>* oxygen consumption

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### Introduction

The finches (Fringilidae) used in the present study are typical European residents. They live in boreal and temperate climatic zones where minimum *T<sub>a</sub>* is around -30 °C in winter and around 0 °C during cold summer nights. The greenfinch (*Carduelis chloris*) and the siskin

(*Carduelis spinus*) are distributed up to latitudes 65–66° N in Fennoscandia, living between longitudes 10° W and 57° E. The northern boundary of the distribution is more northern (70° N) in the brambling (*Fringilla montifringilla*) and slightly more southern (60° N) in the hawfinch (*Coccothraustes coccothraustes*) than in the Carduelinae. The winter quarters of the bullfinch (*Pyrrhulla pyrrhulla*) are between longitudes 10° W and 140° E. The habitats of these Fringilidae birds are the forests of lowland and mountains (the Carduelinae and the hawfinch) and the tall-growing or dark taiga of spruce and fir forests (the bullfinch and the brambling) (Dement'ev and Gladkov 1954; Voous 1960).

The permanent avian residents in these subarctic regions have different strategies for responding to low  $T_a$ . Large birds like the black grouse (*Lyrurus tetrix*, with a bm of 1 kg) and the capercaillie (*Tetrao urogallus*, bm 2–5 kg) compensate for the increased cold load mainly by seasonal improvement of thermal insulation and increase their heat production only in severe cold (Hissa et al. 1983; Rintamäki et al. 1983). Due to the minor significance of thermal insulation, the  $T_{lc}$  of small birds (with a bm < 50 g) is relatively high. Maintenance of high  $T_b$  in the cold and seasonal improvement of cold tolerance is mainly dependent on HP and is thus associated with a metabolic form of acclimatization (Dawson et al. 1983a; Dawson and Marsh 1989; Marsh and Dawson 1989).

The thermogenic capacity of north European finches must be sufficient to endure the lowest  $T_a$  which may occur in winter. Previous studies in this field have mainly concentrated on  $T_{lc}$  and on the slope of  $O_2$  consumption. Our special interest focused on changes in  $HP_{max}$  and on the thermogenic capacity of finches during seasonal acclimatization. The thermogenic capacity of birds is mainly dependent on muscle activity for shivering HP (Marsh and Dawson 1989). During cold exposure shivering is evoked when  $T_a$  is lowered below  $T_{lc}$ . Thermogenesis in a shivering muscle is based firstly on hydrolysis of extramitochondrial ATP and ion transports to provide energy for involuntary actomyosin contractions of shivering, and secondly on oxidative reactions regenerating ATP and inorganic phosphate within mitochondria (Hochachka 1974).

The studies by Hart (1962) and West (1965) show that there is a direct relationship between electrical activity (raw EMG peak-to-peak) in the pectoral muscle of birds and reduced  $T_a$ . However, there is no seasonal adaptation of shivering in small wild birds (Hart 1962; West 1965) or in the dynamics of onset of shivering in the pigeon (Saarela et al. 1984). Unfortunately the relationship between shivering and HP was not studied in this connection. Consequently, using continuous recording devices in winter and in summer, we investigated simultaneously the effect of cold on the EMG and on  $\dot{V}O_2$  of greenfinches (bm 25 g).

Thermoregulatory and behavioral adjustments of birds to fluctuating environmental conditions allow

survival under extremes of  $T_a$ , daylength and food availability as found in Arcticum and at higher latitudes. As an adaptation to food scarcity some small birds enter into torpor or nocturnal hypothermia during inactivity to save energy (Steen 1958; Chaplin 1976; Prinzing et al. 1981; Reinertsen 1983). Proper timing of response to seasonal fluctuation of environmental conditions is essential. Because finches may tolerate reduced  $T_b$  better than the willow tit, *Parus montanus* (Reinertsen and Haftorn 1983),  $T_b$  was recorded continuously (telemetrically).

The existence and the possible role of nocturnal hypothermia in greenfinches and siskins for the maintenance of diurnal energy balance was also studied. The diurnal variation of HP and  $T_b$  (only for greenfinch) were recorded at thermoneutrality and in the cold.

## Materials and methods

### Experimental birds and housing conditions

Adult birds of greenfinch (ten males, six females), siskin (four males and four females), brambling (two males, two females), hawfinch (two males, one female) and one male bullfinch were captured in the Marburg area (51° N, West Germany) from their respective habitats during winter (December–March). Each bird was used once per experiment. The mean bm ( $\pm$  SEM) of the birds recorded before the cooling experiment were: greenfinch  $26.6 \pm 0.68$  g, siskin  $13.2 \pm 0.22$  g, brambling  $21.2 \pm 0.83$  g, hawfinch  $51.0 \pm 1.13$  g and bullfinch 22.9 g. The birds were kept in outdoor aviaries (2 m  $\times$  4 m  $\times$  2 m) between experiments. The aviaries were covered with plastic plates (1 m wide) with a wind break on the north side but with the south, east and west sides open, allowing exposure to natural changes in temperature and photoperiod. The birds were maintained in the aviary for at least 1 week before the experiments were conducted. Water and food were supplied in the cages *ad libitum*. During winter the water was prevented from freezing by means of a heating device. A commercial premix of seeds (sunflower, millet, etc.) for forest small birds was given. Shrub or tree vegetation, flower and leaf buds of bushes, were also available from spring to autumn.

### Apparatus and measurement in metabolic chambers

Maximum thermal heat production was measured as  $\dot{V}O_2$ . Small plastic boxes (3 l) were used as metabolic chambers. Air was sucked at  $1 \text{ l} \cdot \text{min}^{-1}$  through the boxes into gas analysers: a paramagnetic  $O_2$ -analyser Oxytest-S (Hartmann and Braun) and an infrared  $CO_2$ -analyser Uras 2T (Hartmann and Braun), or an oxygen analyser (Applied Electrochemistry Model S-3A).

HP was calculated from  $\dot{V}O_2$  ( $\text{ml } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) and RQ. The regression lines for increasing  $\dot{V}O_2$  versus decreasing  $T_a$  were calculated in each experiment using the three lowest plateau values of each temperature step (RMR). Regression lines were used to calculate the cold limit and  $T_{lc}$  of each bird. Additional details are available elsewhere (Heldmaier and Steinlechner 1981; Saarela and Heldmaier 1987).

The  $T_c$  of all birds was measured prior to and after the experiments by means of a thermistor probe (AMR thermophil, accuracy  $\pm 0.1$  °C). The  $T_b$  of greenfinches was continuously recorded in winter (for five birds) and in summer (for seven birds) by temperature transmitters (Mini Mitter, Model X, weight 1.2 g, sensitivity  $\pm 0.5$  °C), which were implanted into the abdominal cavity 2 weeks

prior to the experiments.  $C_t$  ( $\text{m W} \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ ) of the greenfinches was calculated according to the equation:

$$C_t = \frac{\text{HP}}{T_b - T_a} \quad (1)$$

The EMG of the pectoral muscle of greenfinches was measured in different experiments both in winter ( $n = 9$ ) and in summer ( $n = 6$ ) to estimate the role of shivering in HP. It was recorded by bipolar stainless steel electrodes fixed on a resin plate (UHU plus glue). The electrode length was 2 mm and the distance between electrodes was 3 mm. The electrodes were connected to the top of the metabolic cuvette by a slip-ring system to allow the free movement of the bird. The EMG signal was fed into a differential amplifier and band-pass filter (Hellige Recorder 130T with BIO-AC preamplifier; low and high cut-off frequencies 5.3 and 1000 Hz, respectively). For details see Saarela and Heldmaier (1987).

### Procedure

BMR,  $\text{HP}_{\text{max}}$  and the cold limit of all birds were measured in winter (December–March) and in greenfinches and siskins again in summer (July–September). The procedure for measuring  $\text{HP}_{\text{max}}$  and cold limit was as follows: the gas analysers were calibrated every morning. The birds were weighed and placed into the plastic boxes in a dark climatic chamber (Weiss 500 SD/500-60 DU). The birds were kept first at  $+30^\circ\text{C}$  for about 2 h to obtain their RMR. The first readings of every test were taken at about 1100 hours. The gas analysis was performed continuously at 1-min intervals. After stabilization of  $\dot{V}\text{O}_2$ ,  $T_a$  of the climatic chamber was lowered stepwise for the subsequent 8 h until the birds had reached their  $\text{HP}_{\text{max}}$ .  $T_a$  steps were:  $+30$ ,  $+25$ ,  $0$ ,  $-20$ ,  $-40$  and  $-60^\circ\text{C}$ . For siskins a  $T_a$  step of  $+35^\circ\text{C}$  was added on the upper end and  $-70$  and  $-75^\circ\text{C}$  on the lower end of  $T_a$ .  $\dot{V}\text{O}_2$  was measured continuously from the top of the metabolic chamber with a thermocouple.  $\dot{V}\text{O}_2$  stabilized at a given temperature step usually within 45 min, and the last 15 min of stable values were used for calculations of RMR. Additional details are available elsewhere (Saarela and Heldmaier 1987).

To determine TNZ and BMR,  $\dot{V}\text{O}_2$  was measured for four greenfinches at  $T_a$  between  $+33$  and  $+15^\circ\text{C}$ . In this experiment  $T_a$  was lowered in steps of  $3^\circ\text{C}$ .

### Diurnal rhythm of metabolic rate and $T_b$

The diurnal rhythm of  $\dot{V}\text{O}_2$  of greenfinches and siskins was measured in winter and in summer. The first 25 hourly recordings were performed at  $T_a = +26^\circ\text{C}$  in greenfinches and at  $T_a = +29^\circ\text{C}$  in siskins under natural photoperiod. To study the effect of cold on the diurnal energy expenditure the recordings were repeated 1 week later at  $T_a = 0^\circ\text{C}$ . The diurnal rhythm of  $T_b$  could be registered only in greenfinches. The  $\text{bm}$  of birds was measured before and after each experiment. The birds were placed into the metabolic chamber just before sunset or shortly after sunrise. Throughout the experiment the bird had free access to water.

Statistical significance was tested by Student's *t*-test.

## Results

### Basal metabolic rate

The winter BMR of greenfinch, siskin, brambling, hawfinch and bullfinch are given in Table 1. The lowest BMR was found in the largest bird, i.e. the hawfinch ( $51.0 \pm 1.13$  g), and the highest BMR was found in the smallest species, i.e. the siskin ( $13.2 \pm 0.22$  g). The BMR of the greenfinch was 13.2% higher in summer than in winter ( $P < 0.05$ ). The BMR of the siskin did not differ between winter and summer.

Table 1 shows that all birds measured in winter exhibit virtually the expected BMR (Aschoff and Pohl 1970), but essentially higher BMR than expected when compared to the equation of Bennett and Harvey (1987). Respectively, the summer BMR of greenfinches were 121 and 189% of that expected. The RMR of siskins and greenfinches were obtained from the 25 h recordings of  $\dot{V}\text{O}_2$ . The mean nighttime value was 132% of the expected winter BMR in siskins and 119% in greenfinches [ $P < 0.05$ ;  $\text{BMR} = 114.8 \text{ bm}^{0.726}$ ;

**Table 1** Means ( $\pm$  SEM) of basal metabolic rate (BMR) and means of maximum heat production ( $\text{HP}_{\text{max}}$ ) indicated as oxygen consumption ( $\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ). Heat production capacity ( $\text{HP}_{\text{max}}/\text{BMR}$ ) ( $\text{bm}$  body mass, *w* winter, *s* summer, *n* number of birds). Percent values (%) are calculated according to allometric equations  $\text{BMR} = 140.9 \text{ bm}^{0.704}$ ,  $\text{BMR} = \text{kcal} \cdot 24 \text{ h}^{-1} \cdot \text{bird}^{-1}$ ,  $\text{bm} = \text{kg}$  (Aschoff and Pohl 1970);  $\text{BMR} = 0.778 \text{ bm}^{0.67}$ ,  $\text{BMR} = \text{kcal} \cdot 24 \text{ h}^{-1} \cdot \text{bird}^{-1}$ ,  $\text{bm} = \text{g}$  (Bennett and Harvey 1987)

Species	<i>n</i>	Body mass (g)	BMR	%Aschoff and Pohl	%Bennett and Harvey	$\text{HP}_{\text{max}}$	$\text{HP}_{\text{max}}/\text{BMR}$
Siskin (w)	8	$13.2 \pm 0.22$	$4.5 \pm 0.33$	102	156 <sup>2</sup>	$20.6 \pm 0.81$	$4.7 \pm 0.27$
Siskin (s)	3	$12.8 \pm 0.37$	$4.7 \pm 0.33$	106	162 <sup>2</sup>	$19.6 \pm 0.46$	$4.4 \pm 0.04$
Brambling (w)	4	$21.2 \pm 0.83$	$3.2 \pm 0.43$	84	130	$12.7 \pm 1.40$	$4.2 \pm 0.44$
Bullfinch (w)	1	22.9	3.1	83	129	8.9	2.9
Greenfinch (w)	16	$26.6 \pm 0.68$	$3.8 \pm 0.17$	105	165*	$11.7 \pm 0.89$	$3.5 \pm 0.20$
Greenfinch (s)	14	$27.1 \pm 0.63$	$4.3 \pm 0.18$	121***	189*	$13.7 \pm 0.55$	$3.3 \pm 0.16$
Hawfinch (w)	3	$51.0 \pm 1.13$	$2.9 \pm 0.17$	98	157**	$8.2 \pm 0.66$	$2.9 \pm 0.11$

BMR winter vs. summer: Si n.s., Gf  $P < 0.05$

BMR winter: Si vs. Br, Gf, Hf;  $P < 0.05$

BMR: \*  $P < 0.001$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.05$ , between observed and predicted values

$\text{HP}_{\text{max}}$  winter vs. summer: Si n.s., Gf n.s.

$\text{HP}_{\text{max}}$ : Si vs. Gf, Br, Hf;  $P < 0.001$ ; Br vs. Hf;  $P < 0.05$ ,

$\text{HP}_{\text{max}}/\text{BMR}$ : Si vs. Gf, Hf;  $P < 0.001$

The lowest value around  $+30^\circ\text{C}$  was taken as BMR

**Table 2** Lower critical temperature ( $T_{lc}$ ), shivering threshold (of the greenfinch,  $T_{st}$ ) and the cold limit of the tested birds. The values for BMR,  $HP_{max}$ ,  $T_{lc}$  and the cold limit are calculated from regression lines obtained from each  $\dot{V}O_2$  values plotted against  $T_a$  ( $n$  see Table 1).

Species	$T_{lc}$ (°C)	Cold limit (°C)	$T_a$ of $\dot{V}O_2$ or EMG minimum; Shilow (1973)
Siskin (w)	+ 28.0 ± 0.76	- 61.2 ± 2.17	+ 30.4 + 30
Siskin (s)	+ 31.6 ± 0.55	- 46.9 ± 3.30	+ 28.7 + 30
Brambling (w)	+ 27.3 ± 2.20	- 35.7 ± 5.15	+ 26.5
Bullfinch (w)	+ 22.8	- 37.02 ± 5.8	+ 20
Greenfinch (w)	+ 23.3 ± 1.32	- 41.3 ± 2.29	+ 30.3 + 30
Greenfinch (s)	+ 24.9 ± 0.65	- 32.6 ± 3.93	+ 25.3 + 30
Greenfinch (w)	+ 26.6 ± 1.51 <sup>a</sup>		+ 29.6
Greenfinch (s)	+ 26.2 ± 1.15 <sup>a</sup>		+ 36.0
Hawfinch (w)	+ 21.1 ± 1.91	- 28.9 ± 0.27	+ 20.3

<sup>a</sup> Shivering threshold temperature ( $T_{st}$ ) calculated from respective regression lines (see Table 3)

Difference between  $T_{lc}$  and  $T_{st}$  not significant

$T_{lc}$ : Si: winter vs. summer  $P < 0.05$ ; Gf winter vs. summer n.s.; Si vs. Gf  $P < 0.05$ ; Si vs. Hf  $P < 0.01$

Cold limit: Si: winter vs. summer  $P < 0.01$ ; Gf winter vs. summer n.s.; Si vs. Gf, Br, Hf  $P < 0.001$ ; Gf vs. Hf  $P < 0.05$

Aschoff and Pohl (1970)]. Respective summer values were 122 and 101% of expected (ns).

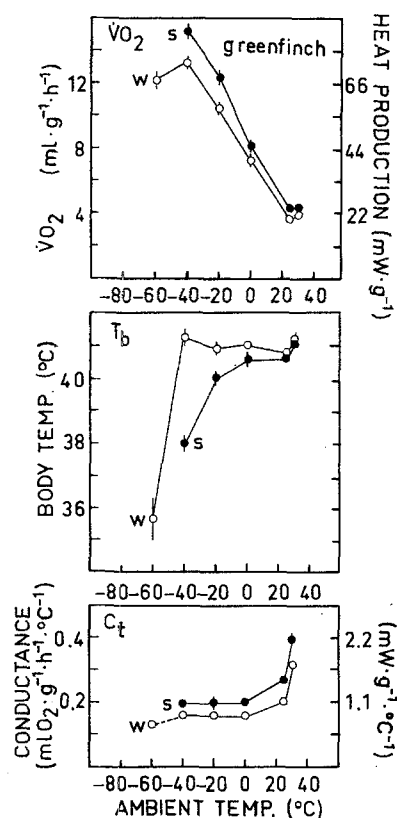
#### Lower critical temperature and cold limit

In winter the  $T_{lc}$  was lowest (+21.1 ± 1.91 °C) in the hawfinch and highest in the siskin (Table 2). In the siskin  $T_{lc}$  was significantly lower in winter than in summer (+28.0 ± 0.76 and +31.6 ± 0.55 °C, respectively;  $P < 0.05$ ). The  $T_{lc}$  of the greenfinch did not differ significantly in winter and summer (+23.3 ± 1.32 and +24.9 ± 0.65 °C, respectively).

The cold limit is the lowest  $T_a$  at which the birds can maintain their  $T_b$ . Table 2 shows that cold resistance was best in the bird with the highest capacity for HP (Table 1). Winter acclimatization of the siskin improved the cold limit from -46.9 to -61.2 °C ( $P < 0.01$ ).

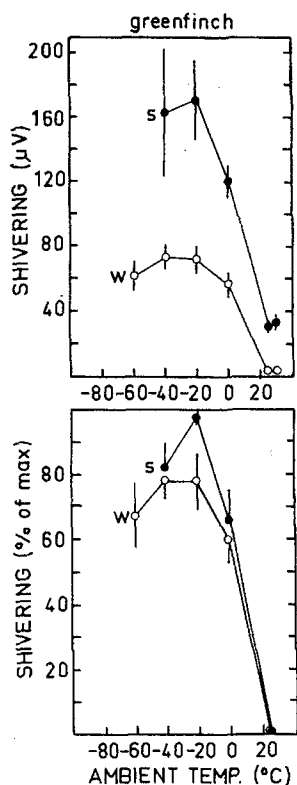
#### Heat production

The RMR of summer greenfinches was above that of winter greenfinches at thermoneutrality. Furthermore, RMR of greenfinches at each temperature step was significantly higher in summer than in winter ( $P < 0.05$ ; Fig. 1). This higher level of RMR correlated with the higher EMG activity of summer greenfinches (Fig. 2). The maximum EMG activity was reached at -20 °C in summer. Winter greenfinches maintained their high EMG activity between  $T_a$  of 0 and -60 °C.  $HP_{max}$  was reached in summer greenfinches at -40 °C, and was followed by a sudden decrease of  $\dot{V}O_2$  when the metabolic chamber was further cooled. Winter greenfinches were also able to increase their HP down to -40 °C, and could maintain a high metabolic rate down to -60 °C.  $HP_{max}$  was  $76.6 \pm 3.08 \text{ mW} \cdot \text{g}^{-1}$  in summer and  $65.4 \pm 4.98 \text{ mW} \cdot \text{g}^{-1}$  in winter (difference ns). The

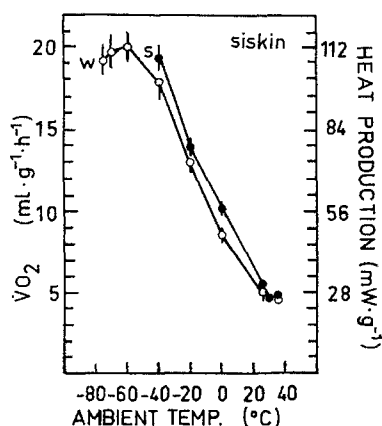


**Fig. 1** The mean of changes in oxygen consumption ( $\dot{V}O_2$ ), body temperature ( $T_b$ ) and thermal conductance ( $C_t$ ) of the greenfinch during stepwise lowering of ambient temperature ( $T_a$ ). Open circles refer to winter (w) and closed circles refer to summer (s). Standard errors larger than symbol diameter are indicated by vertical bars. Number of birds were (1)  $\dot{V}O_2$ : 8 in winter and 11 in summer; (2)  $T_b$ : 5 in winter and 7 in summer; (3)  $C_t$ : 5 in winter and 7 in summer; the last point is the mean of 3 birds

factors describing the increase in  $HP_{max}$  above BMR ( $HP_{max}/BMR$ ) were  $3.5 \pm 0.20$  in winter- and  $3.3 \pm 0.16$  in summer-acclimatized greenfinches (ns, Table 1).



**Fig. 2** The relationship between shivering and ambient temperature ( $T_a$ ) of the greenfinch. The pattern of shivering was continuous. Values are means of integrated EMG activity of the pectoral muscle. In the lower panel shivering is indicated by means of the per cent values from each individual maximum. Number of birds was nine in winter and six in summer. For other explanations see Fig. 1



**Fig. 3** The mean changes in oxygen consumption ( $\dot{V}O_2$ ) of the siskin during stepwise lowering of ambient temperature  $T_a$ . w refers to winter and s refers to summer. For other explanations see Fig. 1

Figure 3 shows that the RMR of summer siskins tended to be higher at each  $T_a$  than the RMR of winter siskins. The  $HP_{max}$  of summer siskins was reached at  $-40^\circ\text{C}$ , and HP decreased rapidly when  $T_a$  was lowered further. Winter siskins, however, were able to increase HP down to  $-60^\circ\text{C}$  and maintained a high

MR even at  $-75^\circ\text{C}$ .  $HP_{max}$  ( $115.0 \pm 4.52 \text{ mW} \cdot \text{g}^{-1}$ ) and HP capacity ( $HP_{max}/BMR$ ,  $4.7 \pm 0.27$ ) were significantly higher ( $P < 0.001$ , Table 1) in the siskin weighing 13.2 g.  $HP_{max}$  for a winter siskin is thus 1.52 W, for a winter brambling (21.2 g) 1.50 W, for a winter bullfinch (22.9 g) 1.14 W, for a winter greenfinch (26.6 g) 1.74 W and for a winter hawfinch (51.0 g) 2.34 W.

Table 3 gives the equations for tested birds describing the relationship between increase in HP and decrease in  $T_a$ . It appears that the increase in  $\dot{V}O_2$  in tested birds varies between 2.2 and 2.6% when  $T_a$  decreases by  $1^\circ\text{C}$ .

#### Body temperature and conductance of greenfinches

Greenfinches were able to maintain a higher  $T_b$  in winter than in summer (Fig. 1). At  $T_a -20^\circ\text{C}$ , winter-acclimatized greenfinches maintained  $T_b$   $0.8^\circ\text{C}$  above that of summer greenfinches ( $P < 0.01$ ). At  $-40^\circ\text{C}$  their  $T_b$ s were  $3.2^\circ\text{C}$  higher in winter than in summer ( $+41.2 \pm 0.24^\circ\text{C}$  and  $+38.0 \pm 0.27^\circ\text{C}$ , respectively) ( $P < 0.001$ ). Greenfinches became hypothermic ( $T_b = +35.6 \pm 0.67^\circ\text{C}$ ) in winter at  $T_a$ s not higher than  $-60^\circ\text{C}$ . The curves of conductance show that the insulation of greenfinches was significantly ( $P < 0.01$ ) better (by 20%) in winter than in summer.

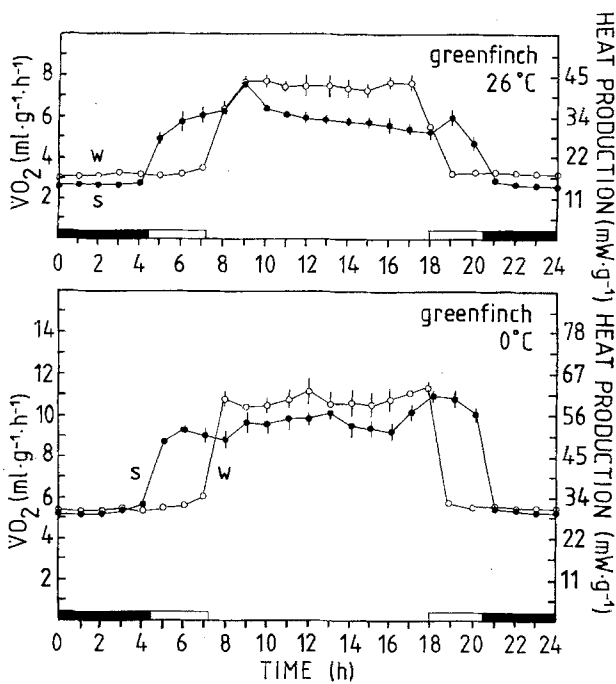
#### Diurnal variation of oxygen consumption, body temperature and conductance in greenfinches

Greenfinches show a diurnal cycle of metabolic rate (Fig. 4), whereby daytime values are about twice the nighttime values. This pattern was observed in summer as well as in winter, and at thermoneutrality or during cold exposure only small differences were observed between summer- and winter-acclimatized greenfinches. The rate of reduction of bm in the course of an experiment lasting 25 h was lowest in winter: 6.8–7.5% during both day and night at  $T_a 0^\circ\text{C}$ . In summer bm decreased by 8.9–11.6% during the day and 12.0–13.6% at night. During short photophase (10 h light:14 h dark) in winter the elevated levels of MR were adjusted for a shorter period of time as compared to the prolonged activity hours in summer-acclimatized finches. The means of day and night  $\dot{V}O_2$  are given in Table 4. During the day RMR at  $+26^\circ\text{C}$  was 25.0% higher, and night values were 18.5% higher, in winter greenfinches than in summer greenfinches. During the day  $\dot{V}O_2$  was increased by 44.0% in winter and by 63.3% in summer when  $T_a$  was lowered to  $0^\circ\text{C}$ . Elevated  $\dot{V}O_2$  was maintained at night. The mean reduction of  $\dot{V}O_2$  at night was 57% in winter and 55% in summer at  $+26^\circ\text{C}$ , and 52% in winter and 47% in summer at  $0^\circ\text{C}$ . Furthermore, in winter MR was slightly higher (10.2%) during daytime, whereas nighttime values were not significantly different.

**Table 3** Regression equations describing relation of oxygen consumption ( $\dot{V}O_2$ ) or shivering (of greenfinches) to ambient temperature ( $T_a$ ) in siskin, brambling, bullfinch, greenfinch and hawfinch.  
 $\dot{V}O_2 = \text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , mean of individual regression lines,  $T_a = ^\circ\text{C}$ ,  $r =$  mean of correlation coefficients

Species	n	Regression equations	r	Increase in $\dot{V}O_2$ on decreasing $T_a$ by 1°C	
				$\dot{V}O_2$	%
<i>This work</i>					
Siskin (w)	8	$\dot{V}O_2 = 9.52 - 0.182 T_a$	0.973	0.18	2.3
Siskin (s)	3	$\dot{V}O_2 = 10.43 - 0.197 T_a$	0.996	0.19	2.2
Brambling (w)	4	$\dot{V}O_2 = 7.18 - 0.150 T_a$	0.987	0.15	2.6
Bullfinch (w)	1	$\dot{V}O_2 = 5.29 - 0.097 T_a$	0.991	0.10	2.3
Greenfinch (w)	16	$\dot{V}O_2 = 7.10 - 0.141 T_a$	0.975	0.14	2.5
Greenfinch (s)	14	$\dot{V}O_2 = 8.48 - 0.170 T_a$	0.988	0.17	2.5
Greenfinch (w)	7	$y = 42.64 - 1.439 T_a$	0.974		
Greenfinch (s)	6	$y = 115.4 - 3.301 T_a$	0.982		
Hawfinch (w)	3	$\dot{V}O_2 = 5.08 - 0.107 T_a$	0.945	0.10	2.5
<i>Shilow (1973)</i>					
Siskin (w)	47	$\dot{V}O_2 = 11.4 - 0.221 T_a$	0.984		
Siskin (s)	17	$\dot{V}O_2 = 11.83 - 0.136 T_a$	0.973		
Bullfinch (w)	6	$\dot{V}O_2 = 7.15 - 0.100 T_a$	0.881		
Greenfinch (w)	20	$\dot{V}O_2 = 7.62 - 0.103 T_a$	0.953		
Greenfinch (s)	6	$\dot{V}O_2 = 10.49 - 0.234 T_a$	0.972		

<sup>1</sup> Calculated from Shilow's (1973) data (mean values of oxygen consumption obtained at  $T_a$ s between +5 and +33°C)



**Fig. 4** Diurnal variation of oxygen consumption ( $\dot{V}O_2$ ) of the greenfinch at +26 and 0°C in winter (w, open circles) and in summer (s, closed circles). Each symbol represents the mean value of 1-h moving average picked up with every 1-min recording. Number of greenfinches was six in winter and four in summer. Horizontal bars indicate scotophase, black for summer and black and white for winter

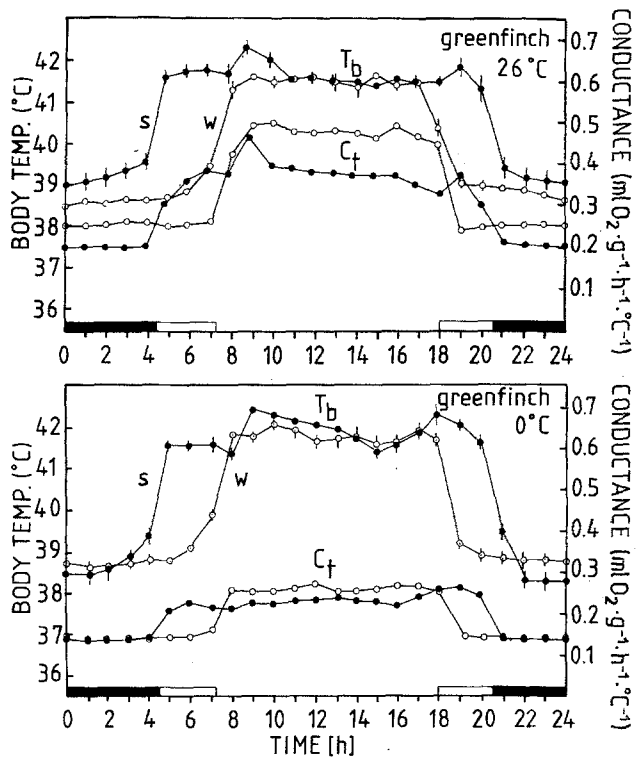
Figure 5 shows the diurnal variation in  $T_b$  and  $C_i$  of greenfinches. Mean day and night values are given in Table 5. The daily average  $T_b$  was +41.5°C both in winter and in summer at  $T_a$  +26°C, and +41.7°C and

**Table 4** Means of day and night values of  $\dot{V}O_2 = (\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1})$  of greenfinches and siskins (w winter, s summer, 0 = 0°C, 26 = +26°C, 29 = +29°C)

	Greenfinch				Siskin			
	w26	s26	w0	s0	w29	s29	w0	s0
Day	7.5	6.0	10.8	9.8	9.5	8.0	14.5	15.5
Night	3.2	2.7	5.2	5.2	4.3	4.0	7.9	8.3
Reduction (%)	57	55	52	47	55	50	46	46

+41.8°C at  $T_a$  0°C, respectively.  $T_b$  decreased early in the dark phase and eventually reached a plateau of low nocturnal values (about +38.5°C) within 1 h of sunset. Low nocturnal values were maintained for several hours, and the anticipatory warmup accompanied by the increase in  $\dot{V}O_2$  began about 2 h before sunrise. After sunrise a sharp rise in  $T_b$  to normothermic values of +41.5°C was observed, accompanied by a sharp rise in  $\dot{V}O_2$ . In summer the minimum  $T_b$  was again in the middle of the scotophase and the increase in  $T_b$  again started 2 h before sunrise. Normal  $T_b$ , however, was reached immediately after sunrise and was again accompanied by a sharp rise in  $\dot{V}O_2$ .

$C_i$  at  $T_a$  0°C at noon were about the same as  $C_i$  in the TNZ at night (Fig. 5, Table 5). The mean nightly  $C_i$  was reduced by 44% in winter and by 39% in summer in the cold. Similarly, the difference between mean  $C_i$  at night was 48% lower in winter and 47% lower in summer at +26°C.  $\dot{V}O_2$  and  $C_i$  were about 20% higher both at noon and at night than the respective values in summer. Thus, although greenfinches maintain a higher level of HP and have a higher  $C_i$  they



**Fig. 5** Diurnal variation of body temperature ( $T_b$ ) and thermal conductance ( $C_i$ ) of the greenfinch at  $+26$  and  $0^\circ\text{C}$ . For other explanations see Fig. 4

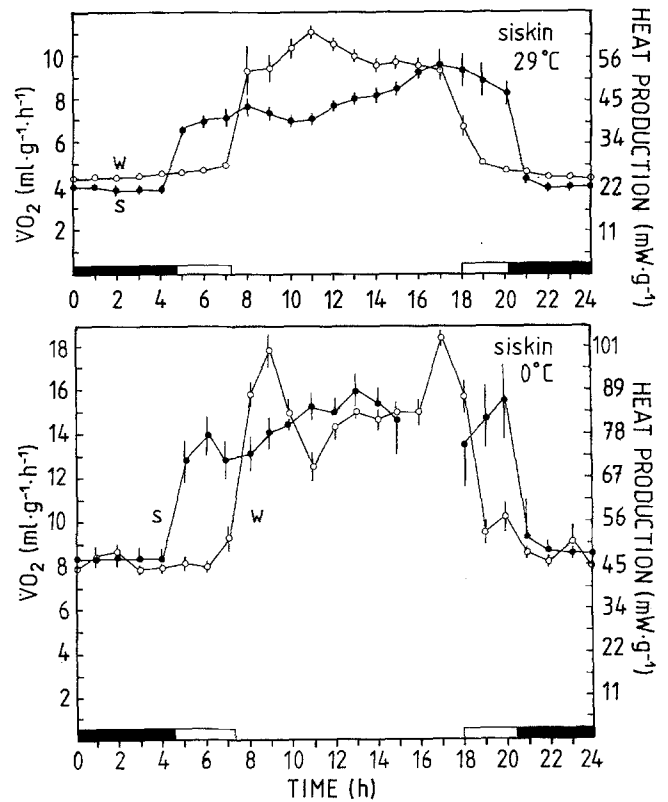
**Table 5** Means of day and night values of  $T_b$  ( $^\circ\text{C}$ ) and thermal conductance ( $C_i$ ) ( $\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ ) in greenfinches. Reduction of  $T_b$  ( $^\circ\text{C}$ ) and  $C_i$  (%) is also indicated (w winter, s summer, 0 =  $0^\circ\text{C}$ , 26 =  $+26^\circ\text{C}$ )

	Body temperature				Thermal conductance			
	w26	s26	w0	s0	w26	s26	w0	s0
Day	41.5	41.5	41.7	41.8	0.48	0.38	0.25	0.23
Night	38.5	39.0	38.6	38.4	0.25	0.20	0.14	0.14
Reduction	3.0	2.5	3.1	3.4	48	47	44	39

maintain a similar  $T_b$  at noon, but a lower  $T_b$  (by  $0.5^\circ\text{C}$ ) at night.

#### Diurnal variation of oxygen consumption in siskins

The diurnal variation in  $\dot{V}\text{O}_2$  in the TNZ ( $T_a +29^\circ\text{C}$ ) and in the cold ( $T_a 0^\circ\text{C}$ ) was also studied in the siskin in winter and in summer (Fig. 6). The mean loss of bm at  $+29^\circ\text{C}$  was 11.4% in winter and 17.4% in summer in the course of an experiment lasting 25 h. The increase in  $\dot{V}\text{O}_2$  in the morning and the decrease in  $\dot{V}\text{O}_2$  in the evening were cued directly by sunrise and sunset, respectively. The  $\dot{V}\text{O}_2$  of winter siskins exceeded that of



**Fig. 6** Diurnal variation of oxygen consumption ( $\dot{V}\text{O}_2$ ) of the siskin at  $+29$  and at  $0^\circ\text{C}$ . For other explanations see Fig. 4. Number of birds was six in winter and four in summer

summer siskins. The mean day and night  $\dot{V}\text{O}_2$  are given in Table 4. The mean reduction of HP at night was 55% in winter and 50% in summer at  $+29^\circ\text{C}$ . At  $0^\circ\text{C}$  the reduction in  $\dot{V}\text{O}_2$  was 46% both in winter and in summer.

The response of  $\dot{V}\text{O}_2$  was biphasic in winter siskins at  $0^\circ\text{C}$ , with a first peak in the morning and a second in the late afternoon. The average day values of RMR at  $0^\circ\text{C}$  were  $14.5 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  in winter and  $15.5 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  in summer. The night values of  $\dot{V}\text{O}_2$  were  $7.9 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  in winter and  $8.3 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  in summer. The energy expenditure of summer siskins in the cold ( $T_a 0^\circ\text{C}$ ) was 5.1% higher during the inactive night period and 6.9% higher during the active day period than the energy expenditure of winter siskins.

## Discussion

### Basal metabolic rate

The BMR of birds depends on bm and the time of the day (Aschoff and Pohl 1970; Bennett and Harvey 1987). Steen (1958) reported that the BMR of the greenfinch at

night was  $3.1 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  and  $3.3 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  in the brambling. The values agree well with our respective night values in winter of  $3.2 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  for the greenfinch and  $3.2 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  day value for the brambling. Table 1 shows that our observed BMR values are within the predicted range. Also, avian BMR correlates with climate, i.e. birds from cold climates show a 1% higher BMR per degree change in latitude than expected from the bird's bm (Weathers 1979). The elevation in BMR theoretically improves the total thermogenic capacity, extends the TNZ to lower  $T_{as}$  and by this decreases  $T_{lc}$  (Heldmaier et al. 1989). Birds resident at high latitudes would therefore have a higher BMR in winter than in summer in order to reduce the thermal burden. However, some of our results show that both siskins and greenfinches tend to have a higher BMR in summer than in winter (Table 1).

There are contradictory reports of seasonal changes in the BMR of small birds, and only a small fraction of birds acclimatized to northern winter conditions show increases in BMR [reviews: Saarela (1980); Dawson and Marsh (1989)]. The adaptive value of such shifts in general is not clear, and at least in animals with high metabolic capacity the elevated BMR is only of minor significance (Heldmaier et al. 1989). Recently, Lindström et al. (1993) found that metabolic rate was 111% higher in bluethroats (*Luscinia svecica*, bm 17 g) and 106% higher in redpolls (*Carduelis flammea*, bm 13 g) during peak molt intensity when compared to premolt BMR. This may partly explain the opposing reports in literature since species with relatively high BMR for their size also have fairly high costs of feather production (Lindström et al. 1993).

#### Thermal insulation, cold limit and thermogenic capacity

Thermal insulation increases with body size, suggesting that large birds should tolerate cold much better than their smaller counterparts (Aschoff 1981). Furthermore, birds tend to have better insulating plumage in winter than in summer (Barnett 1970; Dawson et al. 1983a; Swanson 1991). However, our results (Table 2) show that the cold limit of smaller sized birds is highly dependent on their metabolic capacity. The average cold limit of winter-acclimatized birds was  $-61.2^\circ\text{C}$  in the siskin (13 g) and  $-28.9^\circ\text{C}$  in the hawfinch (51 g). Cold tolerance was further improved by the development of moderate hypothermia. The siskin seemed to tolerate hypometabolism very well and some siskins survived when  $T_a$  was lowered stepwise down to  $-75^\circ\text{C}$ , although they attained  $\text{HP}_{\max}$  at  $-50^\circ\text{C}$ . The increased cold tolerance in siskins was obviously related to their greater capacity for HP, being 4.7 times BMR in the siskin and 2.9 times BMR in the hawfinch (Table 1).

#### Thermoregulatory differences between summer- and winter-acclimatized birds

In the greenfinch the cold limit was  $8.7^\circ\text{C}$  lower ( $14.3^\circ\text{C}$  in the siskin) in winter than in summer (Table 2). Winter-acclimatized greenfinches maintained their HP at the high level down to  $T_a - 60^\circ\text{C}$  and winter-acclimatized siskins down to  $T_a - 75^\circ\text{C}$ . However, HP in summer-acclimatized birds fell suddenly after the increase in  $\text{HP}_{\max}$ . In winter the ratio of  $\text{HP}_{\max}$  to BMR was 4.7 in siskins and 3.5 in greenfinches when compared to respective values of 4.4 and 3.3 in summer (Table 1). These values are similar to those recorded for other passerines (Dawson and Marsh 1989). The seasonal improvement of thermogenic capacity in greenfinches and siskins is not unprecedented. Dawson and Carey (1976) found that winter-acclimatized American goldfinches (*Carduelis tristis*) tolerated exposure to severe cold ( $T_a - 70^\circ\text{C}$ ) for 6–8 h, while summer-acclimatized goldfinches became hypothermic within 1 h. Improved cold tolerance has also been observed in evening grosbeaks, *Hesperiphona vespertina* (Hart 1962), house sparrows, *Passer domesticus* (Barnett 1970) and starlings, *Sturnus vulgaris* (Lustick and Adams 1977) in winter. However, house finches (*Carpodacus mexicanus*) are only slightly more resistant to cold in winter than in summer (Dawson et al. 1983b).

$C_t$  in greenfinches was significantly ( $P < 0.001$ ) greater in summer than in winter between  $T_a + 20$  and  $-40^\circ\text{C}$  (Fig. 1). At  $T_{as}$  lower than  $0^\circ\text{C}$   $C_t$  was at its minimum in winter and in summer. This means that heat loss is faster in summer-acclimatized than in winter-acclimatized birds because of their defective thermal insulation. Consequently, HP of greenfinches and siskins increases faster in summer than in winter to compensate the greater heat loss (Figs. 1, 3). Our telemetrical measurements of  $T_b$  of greenfinches show that heat conservation can overcome the cooling of summer-acclimatized greenfinches when  $T_a$  is lower than  $0^\circ\text{C}$  (Fig. 1). The speed of cooling was very high between  $T_a - 20$  and  $-40^\circ\text{C}$  in summer-acclimatized greenfinches. At the same time winter-acclimatized greenfinches maintained high  $T_b$  down to  $T_a - 40^\circ\text{C}$ . The  $\text{HP}_{\max}$  of winter-acclimatized greenfinches was also reached at  $T_a - 40^\circ\text{C}$ . The maintenance of a high level of  $\text{HP}_{\max}$  could not compensate for the increase of heat loss between  $T_a - 40$  and  $-60^\circ\text{C}$ , and  $T_b$  decreased quickly to  $+35.5^\circ\text{C}$ .

#### Diurnal rhythm of heat production and body temperature

Greenfinches and siskins decreased HP by about 50% at night regardless of season or  $T_a$ . This represents daily energy savings of about 33% in winter at the TNZ and by about 18% in summer (Table 6). At  $T_a 0^\circ\text{C}$  energy saved was about 28% in winter and about 15%



**Table 6** Energy expenditure (in kcal) of greenfinches and siskins during day and night calculated from  $\dot{V}O_2$  in Table 4 (w winter, s summer, 0 = 0 °C, 26 = +26 °C, 29 = +29 °C). Photoperiod (LD) 10:14 h in winter and 16:8 h in summer. Energy expenditure derived from warmup and loss of bm were ignored in calculations

Energy (kcal)	Greenfinch				Siskin			
	w26	s26	w0	s0	w29	s29	w0	s0
24 h day level	403	334	578	535	259	218	395	413
Day	168	223	241	356	108	145	165	275
Night	103	52	177	99	68	37	126	73
Saved (%)	32.7	17.8	27.6	14.8	32.0	16.3	26.6	15.6

in summer. The longer duration of hypometabolism in winter explains the higher amount of relative energy conservation. Our results support the finding obtained previously with the willow tit (*Parus montanus*) that energy savings were smaller at lower  $T_{as}$  (Reinertsen and Haftorn 1986).

The amplitude of  $T_b$  rhythm among birds varies from 0.8 to 3.7 °C (Refinetti and Menaker 1992). Some birds develop a pronounced nocturnal hypothermia and their  $T_b$  may even decrease by 10 °C. The depth of hypothermia is dependent on feeding conditions (Steen 1958; Chaplin 1976; Bartholomew et al. 1983; Reinertsen and Haftorn 1983; 1986; Rashotte et al. 1989; Prinzinger et al. 1991). The depth of hypothermia in our greenfinches seemed to be independent of  $T_a$ . In our experiment greenfinches responded in almost the same way as the great tit, *Parus major*, and the common redpoll, *Acanthis flammea* (Reinertsen and Haftorn 1986). The  $T_b$  of winter greenfinches fell in hypothermia by 3.0 °C at  $T_a + 26$  °C at night and by 3.1 °C at  $T_a 0$  °C (Table 5). In summer-acclimatized greenfinches cold exposure induced only a 0.6 °C decrease in nocturnal  $T_b$ .

The nocturnal decrease in  $T_b$  was paralleled by a nocturnal decrease in  $C_t$ . Our greenfinches lowered their  $C_t$  by 47–48% at night at  $T_a + 26$  °C to the same minimal level as at  $T_a 0$  °C in their activity time (Table 5). At  $T_a 0$  °C  $C_t$  was reduced by 39–44% at night.  $C_t$  values, as well as the magnitude of oscillation between day and night, are in the range as obtained for birds of the same bm (Aschoff 1981).

#### Shivering and non-shivering thermogenesis

Shivering thermogenesis has been shown to be the main HP mechanism in birds (Hohtola 1982). Figures 1 and 2 show that summer greenfinches had higher RMR and higher EMG activity at all  $T_{as}$  studied. The increase in  $\dot{V}O_2$  is paralleled by an increase in EMG activity of pectoral muscle both in winter and in summer down to  $T_a - 20$  °C. The decrease in  $T_a$  to  $-40$  °C further increased HP, although EMG activity did not show any further increase. Winter greenfinches main-

tained a high level (over 60% of maximum) of shivering thermogenesis down to  $T_a - 60$  °C. The result resembles our previous finding in the Japanese quail (*Coturnix coturnix japonica*) that in the extreme cold ( $T_a$  below  $-40$  °C) there is HP independent on shivering of the pectoral muscle (Saarela and Heldmaier 1987). These results show that a pathway of NST may serve at least as an auxiliary HP mechanism in birds, as suggested previously (Saarela and Heldmaier 1987).

The difference between the  $T_a$  of  $T_{st}$  and  $T_{lc}$  is considered to prove the existence of NST. Indeed  $T_{st}$  is 10–14 °C lower than  $T_{lc}$  in pigeons acclimated to short photophase and cold (Saarela and Vakkuri 1982), in winter-acclimatized black grouse, *Lyrurus tetrix* (Rintamäki et al. 1983) and in cold-acclimated muscovy ducklings, *Anas barbarie* (Barré et al. 1985). Since  $T_{st}$  in greenfinches is about 3 °C higher than  $T_{lc}$  (Table 2) small birds respond differently to large birds in this respect. However, higher  $T_{st}$  than  $T_{lc}$  has also been found recently in a large bird: the iliotibial muscles of the bantam cock (*Gallus domesticus*), a major aerobic muscle group like the pectoralis in greenfinches, initiate shivering at 8 °C above the  $T_{lc}$  (Aulie and Tøien 1988).

Pectoral muscle EMG is considered the most representative although not exclusive thermal correlate of shivering in many bird species (Hohtola and Stevens 1986). Shivering appears to initiate with one major group of aerobic muscles, and smaller anaerobic groups are recruited in severe cold (Aulie and Tøien 1988). In this respect the house finch (*Carpodacus mexicanus*) behaves like the bantam: the shivering initiates first in aerobic muscles (the pectoralis around  $T_a + 20$  °C), while anaerobic leg muscles are recruited at around  $T_a - 10$  °C (Carey et al. 1989). Pectoral muscles represent 17% and leg muscles 2% of bm in house finches. Consequently, pectoral muscle shivering is expected to produce substantially more heat than other muscles. On the basis of mass one can speculate that besides recruitment of non-pectoral muscles, NST is necessary in severe cold at least as a complementary source of HP.

There have been many attempts to verify NST in birds but they are still considered controversial (Duchamp et al. 1993b; Marsh 1993). The existence of

NST has been proposed on the basis of a propranolol-induced reduction in the metabolism of young and cold-acclimated birds (Hissa 1988), although the source of avian NST has not yet been found. Adipose tissue may be one candidate. Contrary to Oliphant's (1983) suggestion, but supporting Johnston's (1971) findings, Saarela et al. (1986, 1989) used comparative fluorescence microscopy to show that AAT cannot be considered as mammalian-like brown adipose tissue. Since the AAT of cold-acclimated or winter-acclimatized birds has very low oxidative capacity it cannot be a thermogenic tissue either. This conclusion was supported by the finding that the tissue has also very low activity of the catabolic enzymes  $\beta$ -hydroxyacyl-CoA dehydrogenase and citrate synthase in winter-acclimatized black-capped chickadees, *Parus atricapillus* (Olson et al. 1988). Furthermore, brown fat-specific mitochondrial uncoupling protein was not detected in adipose tissue of birds (Saarela et al. 1991).

During winter acclimatization the cells of energetically significant tissues have to adapt to elevated energy demands just like in exercise training. Indeed, the oxidative capacity of skeletal muscles (pectoralis and gastrocnemius) and of the liver increases in cold-acclimated ducklings (Barré et al. 1987), and it also increases in the pectoral and heart muscles of the house sparrow (S. Saarela et al., unpublished observations). The improved oxidative capacity of shivering muscles is based on some adaptive changes during cold exposure. The amount of slow oxidative fibres (aerobic) and mitochondria increases significantly (Ballantyne and George 1978). Also, the mitochondrial protein content and cytochrome *c* oxidase activity increase (S. Saarela et al., unpublished results) just like during exercise training (Martin 1987). The permanent cold load and increased energy demands in winter also require cardiovascular adaptation but their contribution to total energy expenditure has not yet been verified.

Current research on avian thermogenesis has attempted to localize the site of NST. Connolly et al. (1989) provided some indirect evidence about the possible role of skeletal muscle in NST. Unfortunately, until now there has not been available any direct evidence, such as from blood flow studies, implicating a specific organ or tissue for avian NST. Based on the microsphere method to measure regional distribution of blood flow, Duchamp and Barré (1993) estimated that in the absence of shivering 70% of the total cold-induced NST is attributed to skeletal muscle in 6-week-old cold-acclimated muscovy ducklings (*Cairina moschata*). NST appears to be due to glucagon-induced calorogenesis localized primarily in skeletal muscles of young ducklings (Duchamp et al. 1993a). Direct blood flow measurements in adult cold-acclimated and winter-acclimatized birds of different species are needed before definite conclusions concerning avian NST can be generalized.

In conclusion, greenfinches and siskins acclimatize to winter mainly metabolically. The smallest birds in our study, the siskin and the brambling, had the greatest capacity for HP at  $T_a$  lower than  $T_{lc}$ . Siskins and greenfinches improved their cold tolerance in winter significantly. The heat loss of greenfinches was lower in winter than in summer. Greenfinches and siskins reduce their metabolism at night to save energy. However, nocturnal hypothermia or reduction of metabolism were not seasonal or temperature dependent.

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