

## Different metabolic strategies of northern birds for nocturnal survival

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**Summary.** 1. The regulation of O<sub>2</sub>-consumption and body temperature, especially the occurrence and utilization of nocturnal hypothermia, was studied in three small-sized northern species of birds occupying different ecological niches. Being sympatric, the Willow tit *Parus montanus*, the Great tit *P. major* and the Common redpoll *Acanthis flammea* encounter the same environmental conditions during the winter-time, i.e. long nights, low ambient temperatures, a snow-cover, and the possibility of periods of food shortage.

2. When fed ad libitum, neither the Great tit nor the Common redpoll utilized nocturnal hypothermia. The Willow tit lowered the body temperature to a value which was significantly correlated with that of the ambient temperature.

3. During fasting experiments the evening body weights of the birds were depleted 10–20% below the normal value. In all three bird species the O<sub>2</sub>-consumption during the night was positively correlated to the body weight of the birds. Consequently, the depth of hypothermia achieved at thermal homeostasis was inversely correlated to body weight.

4. When energy reserves in terms of body weight, are less than normal, both Willow tit, Great tit and Common redpoll utilize nocturnal hypothermia in order to make the energy reserves last throughout the night. The reason why the latter two species, in contrast to the Willow tit, do not use nocturnal hypothermia under normal conditions, may be due to differences in body size and also feeding strategies.

1970; Hainsworth et al. 1977; Hudson 1978). Daily or seasonal hypothermia, as a method for conserving energy, has already been recorded for several species of small mammals, but has been less thoroughly investigated among birds. However, during the past few decades, the number of reports of hypothermia, for a wide variety of bird species has steadily increased. Daily hypothermia, and also torpor, has now been observed in members of 8 different avian orders: Falconiformes, Columbiformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes and Passeriformes (for reviews see Dawson and Hudson 1970; Reinertsen 1983).

Thermoregulation during sleep and hibernation has been studied thoroughly in mammals, and it is now evident that the low body temperature observed during torpor and deep hibernation is not due to the absence of, or inadequacy in, the thermoregulatory process. On the contrary, the torpid animal regulates its body temperature with considerable precision (for review see Heller and Glotzbach 1977). Furthermore, Mrosovsky (1971) has suggested that the occurrence of various forms of torpor in different orders and families of mammals is an adaptation to the particular ecological niches that they occupy. He further hypothesized that the winter sleep of many, if not all, of these animals does not represent a survival of a primitive thermoregulatory system, but is a relatively recent adaptation, an adjunct to the basic mammalian physiology.

It is now generally accepted that hypothermia is a controlled condition, also in birds, during which the body temperature is precisely regulated (Wolf and Hainsworth 1972). Hypothermia has so far only been studied in a few species of small-sized northern birds (Steen 1958; Haftorn 1972; Grossman and West 1977; Reinertsen and Haftorn 1983; 1984), for which it was found to be regulated according to the particular season, time-of-day and

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### Introduction

Many small-sized homeothermic animals utilize hypothermia to reduce their energy expenditure during periods of inactivity (Dawson and Hudson

ambient temperature, and also to the physiological condition of the birds, expressed in terms of body-weight. However, the different patterns of hypothermia observed in these small northern birds have not yet been related to the differences in the ecological niches they occupy.

The aim of the present study was to compare the regulation of metabolic rate and body temperature, especially the occurrence and utilization of nocturnal hypothermia, in three small-sized northern species of birds occupying different ecological niches. The Willow tit *Parus montanus*, the Great tit *P. major*, and the Common redpoll *Acanthis flammea* provide suitable and convenient subjects for such a study. Being sympatric, all three species encounter the same environmental conditions during the winter-time, i.e. long nights, low ambient temperatures, a snow-cover, and the possibility of periods of food shortage. The Willow tit is mainly found in coniferous forests, is highly resident, and stays within a limited area of forest throughout the year. It stores a considerable amount of food for utilization in winter (Haftorn 1956). The Great tit is also a resident species, but mainly inhabits urban, or suburban, areas during the winter, and does not create food stores. In northern Scandinavia at least, the Great tit is largely dependent on man for its food supply during the winter months. In contrast to the tit species, the Common redpoll is nomadic during the winter season. Redpolls live together in flocks of various size. In winter-time large numbers may invade areas in which there is an abundance of suitable food, for example birch seeds. Before such a food resource becomes entirely depleted, most redpolls leave the area and search for a new source of food.

## Materials and methods

Willow tits, Great tits and Common redpolls were captured in Central Norway during November. The tits were captured in feeding traps, while mist nets were used to capture the redpolls. The birds were housed individually in cages (30 × 60 × 50 cm) placed in a Foster constant-temperature cabinet. The diet of the captive tits consisted of sunflower seeds, mealworms, a mixture of dried foods, and snow, while the redpolls were given a mixture of rape, poppy seeds, and Canary seed, together with a supply of snow. When given ad libitum, the body-weights of all the birds remained within the normal range of their free-living conspecifics.

The birds were kept in captivity throughout the winter. The ambient temperature varied between -30 and +20 °C. The photoperiod was kept constant at 8L:16D; the lighting was switched on at 0800 h and off again at 1600 h.

To investigate the degree of hypothermia we monitored the body temperatures, oxygen consumption rates, and body-weights of the three species while fed ad libitum, or when kept on a restricted food supply.

During the experiments, continuous records of body tem-

perature were obtained by means of a small (0.75 g) telemetry transmitter implanted into the intraperitoneal cavity. The mean length of the operating times of the transmitters was about 500 h, 450 of which were expended during each experimental series (Reinertsen 1982; Mohus 1983).

Rates of oxygen consumption were measured continuously on an open circuit system, using a S-3A Oxygen analyzer (Applied Electrochemistry, Inc.). The respirometer chambers were plexiglass cylinders, with a volume of about 2 l. Dry air was supplied at a rate of 200 ml min<sup>-1</sup> (Willow tit and Common redpoll) or 250 ml min<sup>-1</sup> (Great tit), which guaranteed an oxygen extraction rate of less than 1%. Air flow rates were measured with a calibrated respirometer. The outflowing air was dried with silica-gel, and the CO<sub>2</sub> content removed with ascarite, before the air passed into the analyzer. The O<sub>2</sub>-content of the air leaving the respirometer chamber was recorded continuously on a recorder fitted with a full scale deflection from 21 to 19.5% O<sub>2</sub>. All the oxygen consumption values were corrected to standard pressure and temperature. They were then calculated according to the equations given by Depocas and Hart (1957). Ambient temperature was controlled with a Foster constant temperature cabinet, and monitored with thermocouples.

Body-weights were measured at the beginning and end of the oxygen consumption recording periods (precision ±0.01 g). In some of the experiments a cylindrical respirometer chamber, open at the base, was placed on top of a Mettler 1120 balance. This arrangement enabled continuous measurements of the body-weight of the birds to be made throughout the experiments. A recorder, switched on automatically at pre-determined intervals by an electronic timing device, was plugged into the balance.

During the fasting experiments the birds were deprived of food from some appropriate time of day until the following morning. During the rest of the day, food was available ad libitum.

The birds were placed in the respirometer chamber between 1530 and 1600 h. At an latitude of 63°N, during midwinter, the sun sets at approximately 1400 h, so that by the time the night experiments started, it was completely dark outside, and the birds would normally have ceased feeding.

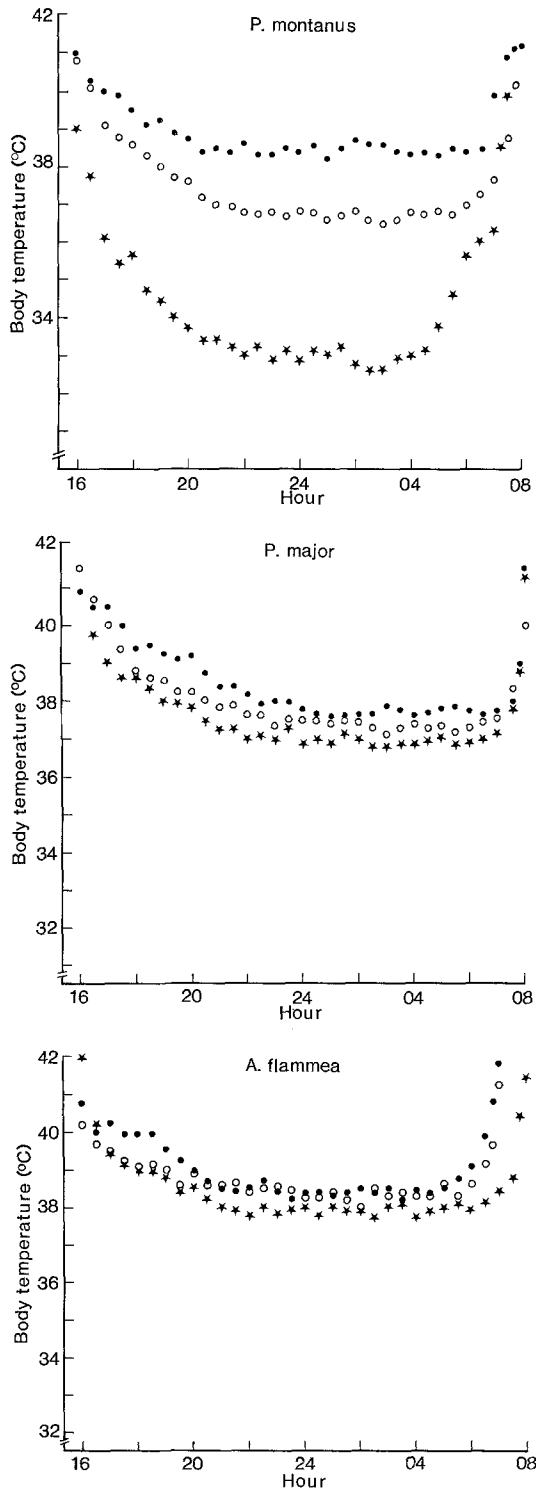
In addition to the night-time recordings, a few recordings of the oxygen consumption during daytime of resting Willow tits, Great tits, and Common redpolls, were made at ambient temperatures within and below the thermo-neutral zone (TNZ).

*Statistics.* Student's *t*-tests were used to test the statistical significance of the differences between the oxygen consumption values and the body temperatures of the normothermic and the hypothermic birds. In the figures the levels of significance are indicated as follows: \* = *P* < 0.05, \*\* = *P* < 0.01, \*\*\* = *P* < 0.001. Mean values are given ± SD (standard deviation).

## Results

### Experimental birds

From previous experiments, we had already learned that the Willow tit adapts well to conditions in captivity, and the same proved to be true for the Common redpoll. Both species spent much of their time resting on a favourite perch. They fed regularly and the Willow tit even stored surplus food items in convenient places, for example under the wire mesh of the cage or inside the roosting



**Fig. 1.** Body temperature changes of Willow tit, Great tit, and Common redpoll when entering, during, and while emerging from the deep sleep phase, acclimatized to winter photoperiod (8L:16D) and ambient temperature conditions. All three species were kept at three different, but constant, ambient temperatures ( $\bullet$  20 °C,  $\circ$  0 °C,  $*$  -20 °C) with food ad libitum. The birds were in normal condition in terms of body-weight; the mean body-weight at roosting time were as follows: Willow tit  $11.92 \pm \text{SD } 0.14$  g, Great tit  $17.17 \pm \text{SD } 0.10$  g, Common redpoll  $15.18 \pm \text{SD } 0.11$  g. (Single night recordings, the 3 curves in each diagram are from the same bird)

box. The captive Willow tits maintained their initial body-weights within narrow limits, which did not differ from the normal range for free-living Willow tits in Central Norway. Some of the Common redpolls even gained appreciably in weight.

In contrast, the Great tit proved to be surprisingly difficult to keep in captivity. Some individuals became hyper-active and had to be released after a few days. Others remained motionless, fluffed out their feathers even during the daytime, and lost weight. Only those individuals that behaved normally, i.e. successively perching quietly, making regular visits to the food tray, and flying calmly about the cage, were used in the experiments.

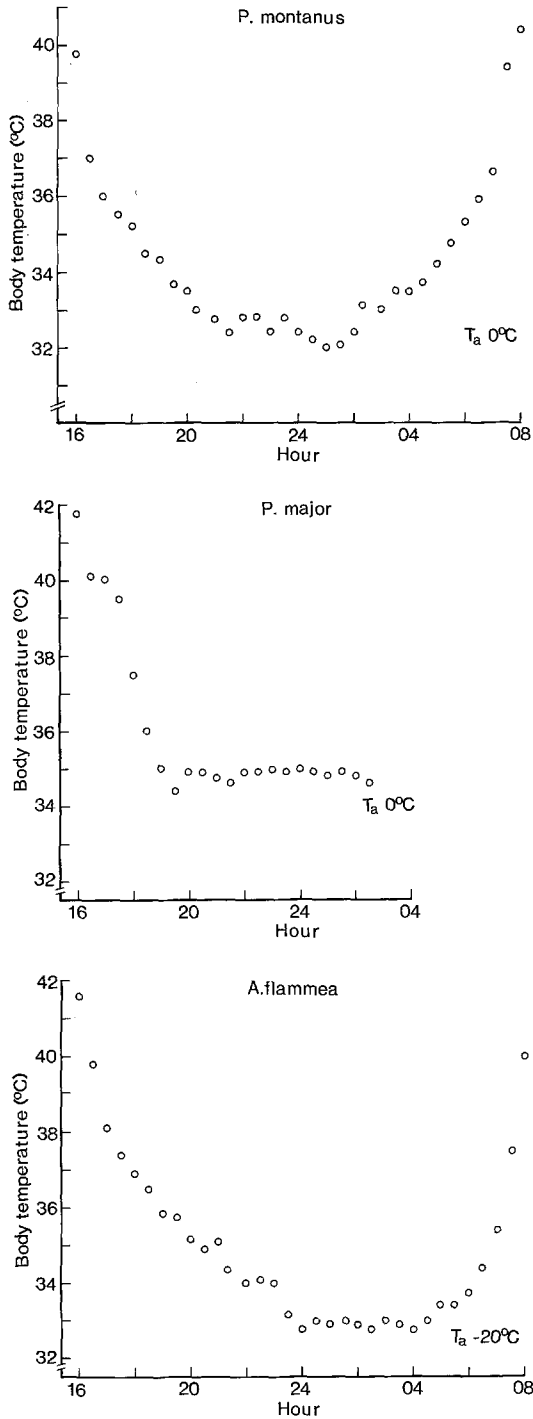
### Body temperature

The mean body temperatures in daytime of the Great tit, and Common redpoll did not differ significantly ( $41.78 \pm 0.49$ , 6 birds, and  $41.74 \pm 0.39$  °C, 4 birds), while the daytime body temperature of the Willow tit was significantly less than the values for the two other species ( $41.35 \pm 0.32$ , 8 birds,  $P < 0.001$  compared with the Great tit,  $P < 0.05$  compared with the Common redpoll).

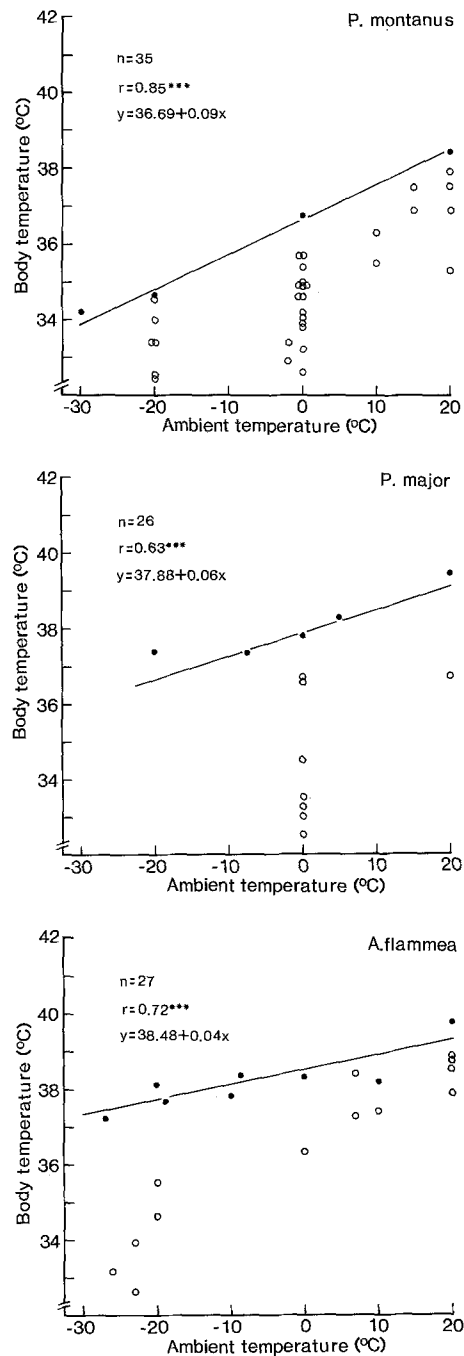
During the night-time sleep, in thermal neutrality, the  $T_b$  of the Willow tit was regulated at  $38.35 \pm 0.29$  °C ( $n=8$ , 4 birds). The corresponding value for the Great tit was  $39.39 \pm 0.75$  °C ( $n=7$ , 4 birds) and that for the Common redpoll  $39.79 \pm 0.15$  °C ( $n=9$ , 5 birds).

When the birds were exposed to ambient temperatures below the thermoneutral zone, the nocturnal body temperatures of the Willow tits always fell below the levels characteristic of the euthermic state, and the value at which the body temperature became stabilized was correlated significantly with the ambient temperature (Fig. 1A). At ambient temperatures below the TNZ, both the Great tit and the Common redpoll also regulated their nocturnal temperatures at values below the euthermic level (Fig. 1B, C). For both these species, however, this lowering of the body temperature was almost negligible compared to the nocturnal hypothermia of the Willow tit. At the lowest  $T_a$  exposed to (-20 °C), the Willow tit regulated its  $T_b$  at 32.50 °C, whereas the  $T_b$  of the two other species only declined to about 1 °C below the euthermic level.

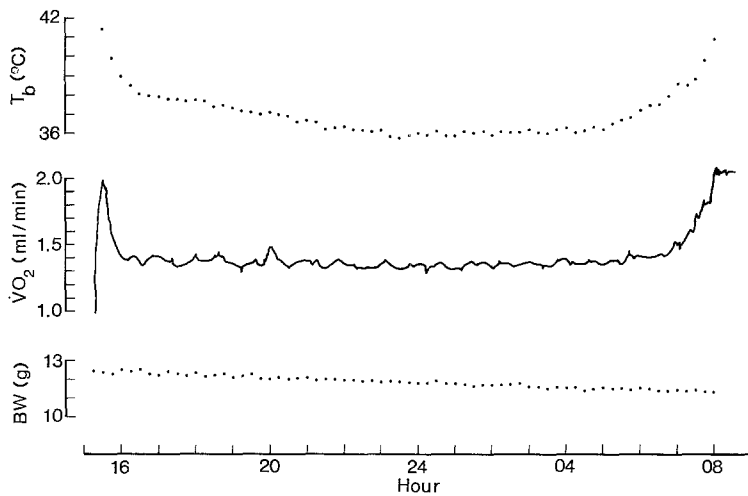
However, when deprived of food for 2-4 h before roosting time, both the Great tit and the Common redpoll also entered a state of profound hypothermia during the night-time (Fig. 2B, C), one in fact equivalent to that normally shown by the Willow tit. The degree of hypothermia achieved



**Fig. 2.** Body temperature changes of Willow tit, Great tit, and Common redpoll when entering, during, and while emerging from the deep sleep phase, acclimatized to winter photoperiod (8L:16D) and ambient temperature conditions. All three birds were kept at constant, ambient temperatures. Following a restricted food supply during the daytime, with a consequent depletion of body-reserves at roosting time. The body-weights at roosting time were as follows: Willow tit 10.75 g, Great tit 15.11 g, Common redpoll 13.80 g. (Single night recordings)



**Fig. 3.** The relationship of body temperature to ambient temperature during deep sleep of Willow tits, Great tits, and Common redpolls, when kept at constant, but different, ambient temperatures during the night. The birds were previously acclimatized to winter photoperiod (8L:16D) and ambient temperature conditions. Filled circles – data for birds fed ad libitum; each circle represents the mean value of 5–10 night body temperature measurements. Open circles – data for birds with a subnormal body-weight at roosting time; each circle represents the mean value of the body temperature during one night. The regression lines for body temperature in relation to ambient temperature are shown only for birds fed ad libitum



**Fig. 4.** Simultaneous recordings during one single night of the oxygen consumption rate, body temperature, and body-weight, of a Willow tit showing a moderate degree of nocturnal hypothermia. The ambient temperature was  $0 \pm 2.0$  °C

by all three species then depended on the ambient temperature, as well as on their body-weight at roosting time (Fig. 3 A, B, C). The lowest value at which body temperature became regulated was about 32 °C for all three species.

#### *Oxygen consumption, daytime*

In daytime, under conditions of thermal neutrality, the resting  $\dot{V}_{O_2}$  of the Willow tit (mean body-weight  $11.13 \pm 0.65$  g,  $n=12$ , 7 birds) was  $5.43 \pm 0.66$  ml  $g^{-1} \cdot h^{-1}$ , the corresponding mean value for the Great tit (mean weight  $16.75 \pm 0.51$  g,  $n=7$ , 3 birds) was  $5.92 \pm 0.62$  ml  $g^{-1} \cdot h^{-1}$  and for the Common redpoll (mean weight  $14.55 \pm 0.99$  g,  $n=11$ , 4 birds)  $5.43 \pm 0.61$  ml  $g^{-1} \cdot h^{-1}$ . These values are significantly higher than those predicted on the basis of body-weight (Aschoff and Pohl 1970).

#### *Oxygen consumption, night-time*

During the night-time all three species showed the same pattern of metabolism and thermoregulation. At roosting time,  $\dot{V}_{O_2}$  first decreased and then levelled off within 30 min, and was then maintained at this lowered value throughout the night until 2 h before the normal time of daybreak, when it steadily increased to its usual daytime level. Body temperature also decreased at roosting time, but did not become stable until ca. 2100–2200 hours, i.e. much later than the  $\dot{V}_{O_2}$  value. On the following morning the rise in body temperature to the normal daytime value paralleled the rise in the  $\dot{V}_{O_2}$ -level (Fig. 4).

**Euthermia.** At night-time, under conditions of thermal neutrality, the resting  $\dot{V}_{O_2}$  of the Willow tit (mean weight  $11.60 \pm 0.87$  g,  $n=8$ , 3 birds) was

$4.25 \pm 0.36$  ml  $g^{-1} \cdot h^{-1}$ , the corresponding mean value for the Great tit (mean weight  $16.45 \pm 0.50$  g,  $n=2$ , 2 birds) was  $3.81 \pm 0.23$   $g^{-1} \cdot h^{-1}$  and for the Common redpoll (mean weight  $14.66 \pm 1.01$ ,  $n=11$ , 3 birds)  $4.23 \pm 0.21$  ml  $g^{-1} \cdot h^{-1}$  (Fig. 5). All these mean values were about 20% lower than the daytime mean values, but higher than those predicted on the basis of body-weight (Aschoff and Pohl 1970).

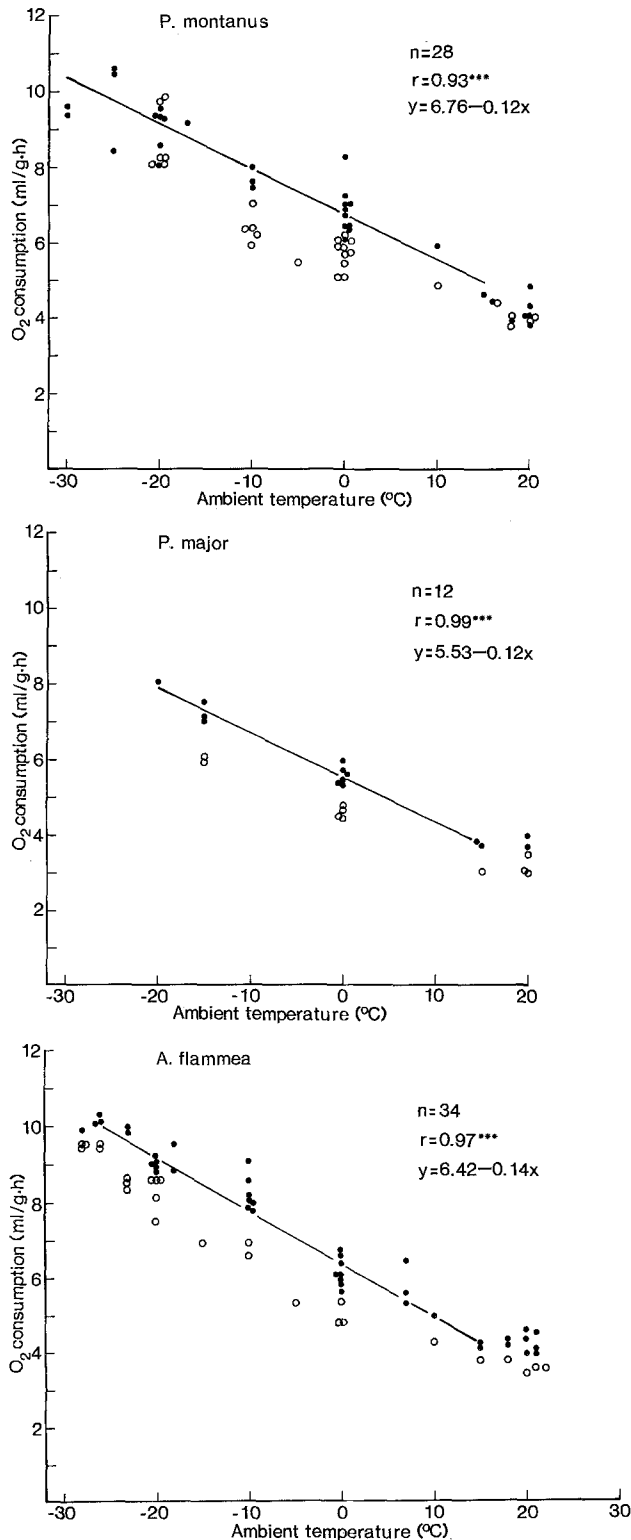
Thermal conductance  $C_t$  was calculated by dividing the measured  $\dot{V}_{O_2}$  values by the difference between the measured values of body temperature and ambient temperature, using the equation

$$C_t = \frac{\dot{V}_{O_2}}{T_b - T_a} \quad (1)$$

For the Common redpoll the mean value of  $C_t$ , calculated using Eq. (1) for simultaneous measurements of  $\dot{V}_{O_2}$ ,  $T_b$  and  $T_a$  at  $T_a$  below TNZ (Fig. 5C), was  $0.16 \pm 0.01$  ml  $O_2/(g \cdot h \cdot ^\circ C)$ . Within the thermoneutral zone, the mean value of  $C_t$  was  $0.22 \pm 0.04$  ml  $O_2/(g \cdot h \cdot ^\circ C)$ , i.e. higher than it was below conditions of thermal neutrality.

For the Great tit, during its state of nocturnal euthermia, the  $C_t$  value, calculated from Eq. (1), was  $0.15 \pm 0.01$  ml  $O_2/(g \cdot h \cdot ^\circ C)$ , once again lower than the  $C_t$  value ( $0.20 \pm 0.01$  ml  $O_2/(g \cdot h \cdot ^\circ C)$ ) in the thermoneutral zone.

**Hypothermia.** In all three species the oxygen consumption rates recorded when the birds were kept at a constant ambient temperature during the night-time were significantly lower in hypothermic than in euthermic birds, and a positive correlation with body-weight at roosting time was found (Fig. 5). Their metabolism exhibited the normal diurnal pattern, but subsequently attained corre-



**Fig. 5.** The relationship of the oxygen consumption of Willow tits, Great tits, and Common redpolls to the ambient temperature during the deep sleep phase. Filled circles – data for birds fed ad libitum; open circles data for birds with a subnormal body weight at roosting time. Each circle represents the mean value of the oxygen consumption during one night. The regression lines for  $\dot{V}_{O_2}$  in relation to ambient temperature below the lower critical temperature are shown for birds fed ad libitum only

spondingly lower values with decreasing body-weight. A positive correlation was found with the depth of hypothermia achieved at thermal homeostasis (Fig. 3). Using Eq. (1) for the simultaneous measurements of  $\dot{V}_{O_2}$ ,  $T_b$ , and  $T_a$ , the mean thermal conductance below the TNZ was  $0.17 \pm 0.02$  ml  $O_2$ /(g·h·°C) for the Willow tit,  $0.14 \pm 0.01$  ml  $O_2$ /(g·h·°C) for the Great tit, and  $0.15 \pm 0.02$  ml  $O_2$ /(g·h·°C) for the Common redpoll. For the latter two species, these values are slightly lower than those recorded during the state of euthermia below the TNZ; no corresponding euthermic values are available for the Willow tit, since it is always hypothermic at low ambient temperatures at night-time during winter. However, the minimum thermal conductance of the Willow tits fed ad libitum, decreased slightly at ambient temperatures below zero (Reinertsen and Haftorn 1983, Table 1).

#### Body-weight

The mean body-weight at roosting time of the Willow tits fed ad libitum was  $12.31 \pm 0.32$  g. When the birds were experimentally deprived of food, at different times of the day, their body-weights at roosting time varied between 11.50 and 10.00 g. The mean weight of the Great tits fed ad libitum was  $17.43 \pm 0.98$  g and their body-weights varied between 14.70 and 16.20 g when they were deprived of food. The Common redpoll had a mean body-weight of  $15.13 \pm 0.87$  g, and the weights for starved birds varied between 12.07 and 13.90 g. During the normal nocturnal fast, the body-weight of all three species decreased linearly from roosting time until the following morning. The mean values of the roosting time and morning body-weights have been used in the calculations of oxygen consumption.

## Discussion

### Hypothermia

The best documented cases of avian hypothermia have been obtained either during prolonged fasting in nature, or under conditions of experimentally reduced food availability in the laboratory. Passerines normally lower their body temperature by 1–2 °C at night. During nocturnal hypothermia the body temperature may fall by a further 3–10 °C (Steen 1958; Chaplin 1976; Biebach 1977; Bucher and Worthington 1982; Reinertsen and Haftorn 1983, 1984). In our experiments with the Willow tit, Great tit, and Common redpoll, only the Wil-

low tit became hypothermic regardless of its body-weight condition. The nocturnal body temperatures of the Great tit and Common redpoll, when fed ad libitum, remained within about 1 °C of the euthermic levels, even when the birds were exposed to ambient temperatures as low as -20 °C. When their body-weights were experimentally lowered by some 10–20%, however, both species became hypothermic at ambient temperatures below the thermoneutral zone. These results seem to verify the results obtained by Steen (1958), whose Great tits and Common redpolls only became hypothermic during the first night after being captured, when, judging from their body-weights, they appeared to be in a poor condition. Our results seem to contradict those of Pauritsch (1982), who captured roosting Great tits in winter and found that their nocturnal body temperature had decreased by 3.6–6.6 °C in relation to the daytime temperature, a decrease which was inversely correlated with the ambient temperature. However, it is difficult from his data to evaluate the actual physiological condition of the birds involved.

The  $T_b$  values of the hypothermic birds in the present work never fell below 32 °C. At the air temperatures which normally prevail in Central Norway during the winter (-30 to +10 °C), a substantial difference will still exist between the hypothermic  $T_b$  and  $T_a$  values (22–62 °C). Even though the energetic significance of hypothermia is less in small-sized than in larger birds (Chaplin et al. 1983), and is also less at very low ambient temperatures compared to a  $T_a$  value falling within the TNZ, the saving in energy gained by even such a moderate degree of hypothermia may be of vital importance (see below).

In their reports on a study of hypothermia for two Manakins (*Manacus vitellinus* and *Pipra mentalis*) Bartholomew et al. (1983) present two physiological models to explain the pattern of hypothermia in these birds. The first one suggests that Manakins increase their thermal conductance at night, allowing  $T_b$  to fall, whereby the  $Q_{10}$ -effect of lowered  $T_b$  depresses the rate of energy metabolism. This model does not seem to fit the results obtained for any of the three species we have studied. In Central Norway, these bird species never experience ambient temperatures within their thermoneutral zone during winter, and can quite easily lower their rate of energy metabolism at roosting time.

The second model proposed by Bartholomew et al. (1983) implies that the birds maintain their thermal conductance at, or close to, its minimal level, whilst at the same time reducing their rate of energy metabolism and allowing  $T_b$  to fall to

a level determined by the reduced level of heat production. This model seems to be more adequate for our three northern species. However, on examining the results presented in Fig. 4, we have to accept the fact that the fall in  $T_b$  towards the nocturnal hypothermic value does not seem to be an entirely passive phenomenon; the decline in  $T_b$  follows the same pattern and time-scale regardless of both the ambient temperature and the metabolic rate. It seems somewhat paradoxical that it should take 5–6 h for  $T_b$  to fall to a level at which thermal homeostasis is achieved. However, since body-weight decreases throughout the night, the weight specific  $\dot{V}_{O_2}$  value will increase, and this small increase at least partly accounts for the regulated decline in body temperature. A gradual change of conductance may also contribute to the observed pattern.

#### *Energetic significance*

The amount of energy saved during hypothermia is the difference between the  $\dot{V}_{O_2}$  of the euthermic bird and the  $\dot{V}_{O_2}$  of the hypothermic bird, multiplied by the duration of hypothermia. Due to the diurnal pattern of thermoregulation by the Willow tit, Great tit, and Common redpoll, the duration of hypothermia, in terms of body temperature, was only about 8 h, out of a total period of darkness of 16 h (Fig. 4). However, the energetic significance of hypothermia for these birds lies in the amount of energy saved, and the depressed  $\dot{V}_{O_2}$  values of the hypothermic birds lasted for about 13 h. Furthermore, both during the entry into hypothermia and during much of the warm-up period less energy is expended than during the state of euthermia.

Because of the cold environment in which the birds live, the difference between  $T_b$  and  $T_a$  will remain large even at a hypothermic maximum of about 10 °C. The amount of energy saved is the difference between the  $\dot{V}_{O_2}$  of the euthermic bird and the  $\dot{V}_{O_2}$  of the hypothermic bird at the same  $T_a$ . This saving will never be large in these small northern birds, but its contribution is significant when taken together with the other energy saving mechanisms they utilise. For example, an 11.50 g Willow tit would expend less energy during a 16 h-night with a body temperature of 32 °C, than if it kept its body temperature at 38 °C. The energy thereby saved would represent 35% of its nocturnal euthermic energy expenditure at a  $T_a$  of 20 °C. At an ambient temperature of 0 °C, the same degree of hypothermia would result in a relative saving of energy of only 15%, and the saving would be only 10% at a  $T_a$  of -20 °C.

### *Adaptive values*

The Willow tit, in particular, possesses a number of physiological and behavioural adaptations which enable the species to inhabit inhospitable subarctic regions also during winter. These include territorial behaviour (Haftorn 1958), food storage (Haftorn 1956), sheltered roosting place and a sleeping posture that utilizes its capacity for physical thermoregulation to the full, by fluffing up into a ball and remaining motionless. Furthermore, at ambient temperatures below TNZ, this bird can also save energy by going into a state of regulated hypothermia. When its food supply is limited, such nocturnal hypothermia is utilized to an even greater degree than is normally the case.

In contrast to the Willow tit, the physiological and behavioural adaptations of the Great tit and the Common redpoll do not include nocturnal hypothermia under normal conditions, and neither of them stores food to guarantee an available energy supply in winter-time. In situations of food shortage, however, with a consequent depletion of their energy reserves, both the Great tit and the Common redpoll do utilize nocturnal hypothermia as an energy-saving mechanism, in the same way as the Willow tit does.

The normal body-weight of a Great tit is about 50% greater than that of a Willow tit. According to Calder (1974), the energy stored by a bird is proportional to  $mass^{1.003}$ , but the energy used is proportional to  $mass^{0.42}$ . In consequence, due to its larger size, the Great tit daily expends a lower proportion of its energy reserves, implying that, in relation to the Willow tit, it can tolerate a prolonged fasting period before total depletion occurs and an energy crisis arises. Since food deprivation was found necessary to induce torpor in the laboratory, there is reason to believe that with a normal, adequate energy intake in the field, the Great tit is able to maintain a state of nocturnal euthermia. However, during periods with food scarcity or during inclement weather conditions that limit the opportunities for foraging, nocturnal hypothermia may be used in order to make the energy reserves last longer.

The body size of the Common redpoll lies between those of the Willow tit and the Great tit. Compared to the former, this extra couple of grammes could possibly be just enough to tip the balance, since the Redpoll, like the Great tit, does not utilize hypothermia to the same degree as the Willow tit, provided that it is adequately fed. It may also be that the selection for a regular nocturnal hypothermia in the Redpoll has been relatively

weak, because of its special feeding strategy, which is essentially different from the tits. In contrast to the tits, the Redpoll possesses a crop, which can be filled with seeds just before roosting time. Furthermore, in this species there is evidence for a seasonal change in light sensitivity of the circadian system controlling the active time, which may be responsible for the early onset of activity (below 0.02 lux) of the Redpoll during sub-arctic winter (Brooks 1968; Pohl 1972). Even in the middle of the night the Redpoll may be active in winter-time provided sufficient light (i.e. during moonlight; Haftorn unpubl.), something that has never been observed for the tits.

In the laboratory, if the light was turned on in the middle of the night, the Redpolls always started to eat. Even when their body-weights were subnormal, neither the Willow tit nor the Great tit exhibited this kind of feeding behaviour. Instead, they relied on saving energy by entering into a profound state of hypothermia, rather than attempting to replenish their nearly-exhausted fat deposits by feeding.

Available data indicate that the Willow tit depends on its own food stores to a high degree during winter (Haftorn 1956). Because amount of stored food is limited, it seems quite reasonable that the sedentary Willow tit should utilize an energy saving mechanism as its first line of defence against cold. The non-territorial Common redpoll, on the other hand, is not dependent on such a limited food reserve, that has to last throughout the winter, but moves around from place to place, stopping wherever suitable food is abundant. This mode of life may promote a strategy of increased energy consumption, rather than of energy saving, as a first line of defence against cold. If an emergency situation should arise, however, also the Common redpoll has a second line of defence because it is also able to save energy by means of hypothermia.

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