

The effect of short-time fasting on metabolism and nocturnal hypothermia in the Willow Tit *Parus montanus*

Randi Eidsmo Reinertsen¹ and Svein Haftorn²

¹ University of Trondheim, Zoological Institute, Rosenborg, N-7000 Trondheim, Norway

² University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, Erling Skakkesgt. 47A, N-7000 Trondheim, Norway

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Summary. 1. The effect of body weight on O₂-consumption rate and nocturnal hypothermia was studied in winter acclimatized Willow Tits *Parus montanus*.

2. During the fasting experiments, the birds were kept at a constant ambient temperature of 0 °C, and a photoperiod of 8L:16D. O₂-consumption rate and deep body temperature were recorded continuously throughout the night. The O₂-consumption rate 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 the body weight.

3. The results obtained indicate that depending on season, ambient temperature and energy reserves, the Willow Tit regulates its metabolic rate so as to keep it at a level which corresponds fairly well to the maximum affordable energy expenditure.

Introduction

Some small species of birds minimize their energy expenditure when food is scarce by entering into a state of hypothermia (e.g. Black-chinned Hummingbird, *Archilochus alexandri* (Lasiewski 1963), Speckled Mousebird, *Colius striatus* (Bartholomew and Trost 1970), Blackbird, *Turdus merula* (Biebach 1977), Rivoli's Hummingbird, *Eugenes fulgens* (Hainsworth et al. 1977), Red-backed Mousebird, *Colius castanotus* (Prinzinger et al. 1981). Observations that these species exhibit daily hypothermia only when their food supply is limited, indicate that the hypothermic state is utilized only in emer-

gency situations, rather than as a means of reducing the necessity for feeding, by decreasing energy expenditure, when food is abundant.

The term hypothermia in this paper is used according to the definition given by Calder and King (1974), i.e. body temperature below normal (normothermia) for resting birds. This may be only a few degrees or profound.

Recent research has shown that the Willow Tit *Parus montanus* also utilizes hypothermia in order to minimize its nocturnal energy expenditure (Reinertsen and Haftorn 1983). However, unlike the bird species mentioned above, the Willow Tit exhibits nocturnal hypothermia even when an excess of food is available. The depth of the hypothermia exhibited by this species is correlated with the prevailing ambient temperature and, furthermore, depends on the season of year. A direct relationship between the depth of hypothermia and the ambient temperature has also been demonstrated for two other Tit species, namely the Siberian Tit *Parus cinctus* (Haftorn 1972) and the Black-capped Chickadee *Parus atricapillus* (Budd 1973; Chaplin 1974, 1976).

If natural selection were to favour maximal energy saving at night, one would expect to find the bird's body temperature to be lowered to a minimum every night, irrespective of the environmental condition, and not the linear correlation found between the body temperature and the ambient temperature. However, the existing state of affairs suggests that the main aim, from the bird's point of view, is not necessarily to save as much energy as possible. A low body temperature also implies a lower state of alertness and presumably a greater risk of being caught by predators. The energy used, therefore, may be a compromise between maintaining as high a state of alertness as possible and, at the same time, saving sufficient energy to survive

the night, including the necessary re-emergence from the state of hypothermia in the morning.

Based on these observations, we put forward the hypothesis that in the evening the Willow Tit regulates its metabolic rate at a specific level which corresponds fairly closely to the maximum affordable energy expenditure (Reinertsen and Haftorn 1983). According to this hypothesis, the metabolic rate in the evening is determined by at least the following three factors: the prevailing ambient temperature, the expected duration of darkness, and the actual state of the bird's energy reserves that evening.

The aim of the present work is to evaluate this hypothesis by testing the following predictions arising from it:

- 1) A bird which possesses only a small energy reserve should exhibit a deeper degree of hypothermia compared to a bird with a greater energy reserve – other factors being equal.
- 2) The state of hypothermia recorded during the night should change if the ambient temperature changes.

Materials and methods

Experimental birds. The Willow Tits used in the experiments (4 individuals) were captured in the middle of the day near Trondheim, Norway (63°N), during the winter season 1981–82, when the mean daily air temperature (December–February) was -5.1 °C (nightly minimum -21.5 °C). The birds were housed in individual cages in a Foster constant-temperature cabinet, exposed to controlled photoperiod and ambient temperature regimes. When not involved in the fasting experiments, they received a diet consisting of sunflower seeds, mealworms, a mixture of dried foods, and snow ad libitum (Reinertsen 1982). Body weight was depleted experimentally by quantitatively reducing the available supply of food such that their weight at roosting time fell to a value 10–15% below their customary weight of about 12 g ($\bar{x}=12.15 \pm \text{SD } 0.73$, 4 individuals, 26 measurements). The ambient temperature was varied between -20 and $+20$ °C, although the specific ambient temperature overnight did not differ by more than ± 5 °C from the value maintained during the daytime. The photoperiod was kept constant at 8L:16D; lights on at 0800 h, lights off at 1600 h.

Body weight. Body weight changes can be used to provide quantitative estimates of the energy reserves accumulated during the daytime and of the amount of energy expended during the night. The birds were initially weighed (± 0.01 g) just after their capture in the field. During subsequent experimental periods in captivity they were always weighed at the start and finish of the light period. The faeces were weighed in the morning. In the fasting experiments, body weight was also recorded at the time when the food supply was taken away from experimental birds. Whenever the body weight recorded at roosting time was less than 11.00 g, the experiment was terminated during the night at the time at which thermal homeostasis had been achieved and consequently the deep body temperature had stabilised. The birds were allowed to spend the rest of the night

at ambient temperatures within the thermoneutral zone, in order to avoid any further fall of body weight to below 9.70 g, which would have resulted in death from starvation.

Body temperature. All body temperatures were measured by means of a small (0.75 g) radiotelemetry transmitter implanted into the intraperitoneal cavity (Reinertsen 1980, 1982), i.e. continuous recordings of the deep body temperatures of undisturbed birds were obtained. The mean length of the operating time of the transmitters was about 500 h, 450 of which were expended during each experimental series.

Energy expenditure. The overnight energy expenditure was calculated from continuous records of oxygen consumption made, using a S-3A Oxygen analyser on an open-circuit system (Applied Electrochemistry, Inc.), from the time the light was switched off on one day to the time it was switched on again the following morning. The birds were placed in a 2 l plexiglass box placed in the Foster constant-temperature cabinet. Dry air was supplied at a rate of 200 ml/min, which guaranteed an oxygen extraction rate of less than 1% (for further details see Reinertsen and Haftorn 1983). All the recorded oxygen consumption values were adjusted to standard pressure and temperature conditions. We assumed a RQ of 0.7 (fat metabolism) overnight, with a caloric equivalent of 4.7 cal/ml (Kleiber 1961). The metabolic rates of the birds were calculated at ambient temperatures which ranged from -20 to $+20$ °C.

Body weight was recorded at the start and end of the oxygen consumption recordings. The mean of these two weights was used in the calculation of the weight-specific metabolic rates.

Results

Body weight

The mean mid-day body weight of the newly-captured birds and of the same birds in captivity ($11.86 \pm \text{SD } 0.62$ g, $n=4$, 15 weighings) did not differ from the mean value for free-living Willow Tits in Central Norway, recorded during the winter season (Haftorn 1982). Mean body weight of the experimental birds at roosting time was $12.15 \pm \text{SD } 0.73$ g ($n=4$, 26 weighings). When the birds were experimentally deprived of food, at different times each day, their body weight at roosting time varied between 11.50 and 10.30 g. When the birds were given a surplus of mealworms one hour before roosting time, this resulted in above-normal body weights (maximum 13.00 g). The weights of faeces collected differed very little, and this indicates that the error introduced by not correcting for food in the gut at roosting time is negligible.

Body temperature

When the Willow Tits were kept on a proper diet, they exhibited the typical diurnal temperature rhythm previously described (Reinertsen 1982; Reinertsen and Haftorn 1983). The mean daytime body temperature, when at rest, was

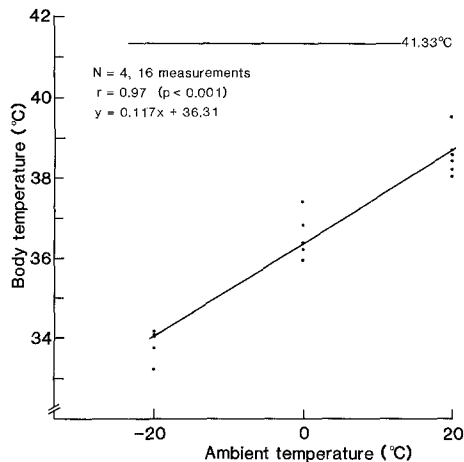


Fig. 1. The relationship of the body temperature of winter-acclimatized Willow Tits (4 birds) to differing, but stable, ambient temperatures during the night. Each of the 16 temperature measurements represents the mean value of the nocturnal body temperature during the period it remained constant (2130–0600) during one single night. The mean daytime body temperature (41.33 °C) is indicated by a horizontal line

41.33 ± SD 0.34 °C ($n=4$, 430 measurements). At roosting time body temperature gradually fell, until it stabilised at some time between 2100 and 2200 h, thereafter remaining more or less constant until two to three hours before sunrise, when it gradually rose, attaining the normal daytime level by the start of the daytime activity period. When the birds were exposed to a series of three differing, but constant, ambient temperatures (−20, 0 and +20 °C, Fig. 1), the value at which the body temperature stabilised at night was found to be significantly correlated with the ambient temperature value.

When the ambient temperature was no longer kept stable, the body temperature changed accordingly. If the ambient temperature was suddenly lowered after the bird's body temperature had reached the stable hypothermic level corresponding to the particular ambient temperature to which it was initially exposed, body temperature immediately responded by falling further, to a new stable level. In one of the experiments, for example, the body temperature of the sleeping bird fell from 38.3 to 37.4 °C after the ambient temperature had been suddenly lowered from 20 to 0 °C (Fig. 2A). If the birds were exposed to a sudden increase in the ambient temperature in the middle of the night, a corresponding rise in body temperature occurred during the deep sleep phase (Fig. 2B).

On a reduced food ration, with consequent depletion of the evening body weight, the value at which the body temperature stabilised at night was

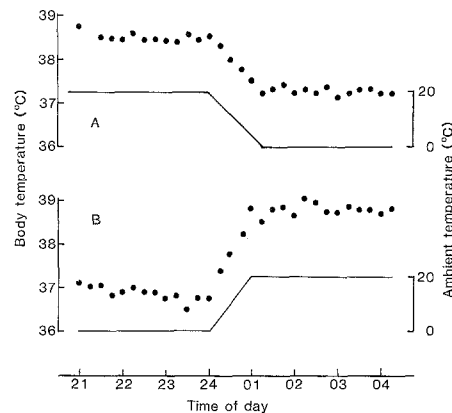


Fig. 2A, B. The change in body temperature recorded during the deep sleep phase (filled circles) after a sudden change in the ambient temperature (solid line) made in the middle of the night. On the first night the ambient temperature was suddenly lowered from 20 °C to 0 °C (A), and on the following night it was suddenly raised from 0 °C to 20 °C (B)

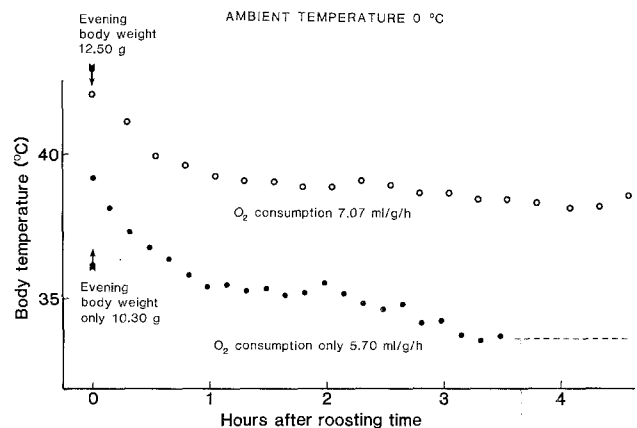


Fig. 3. The decline during the evening and final levelling-off of the body temperature of a winter-acclimatized Willow Tit, for two different body weights at roosting time

not only correlated with that of the ambient temperature, but also with the initial body weight of the bird (at roosting time). At an ambient temperature of 0 °C and an initial body weight of 12.50 g, body temperature stabilised at 38.15 °C, whereas at an initial body weight of only 10.30 g it stabilised at 33.9 °C (Fig. 3).

At ambient temperatures below −20 °C, the depth of hypothermia achieved was independent of the bird's body weight at roosting time (Fig. 4).

Metabolism

The oxygen consumption rate recorded during the night when the birds were kept at a constant ambi-

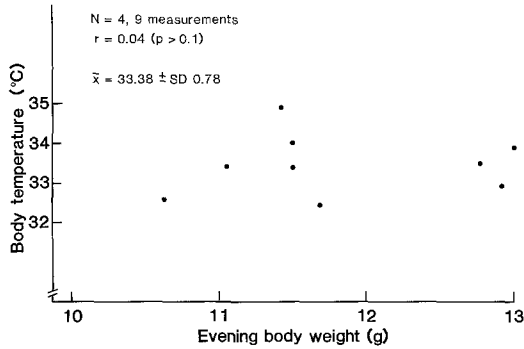


Fig. 4. The relationship between body temperature and body weight at roosting time of winter-acclimatized Willow Tits (4 birds) at a stable ambient temperature of -20°C . Each of the nine measurements represents the mean value of the body temperatures recorded during the deep sleep phase during the course of a single night

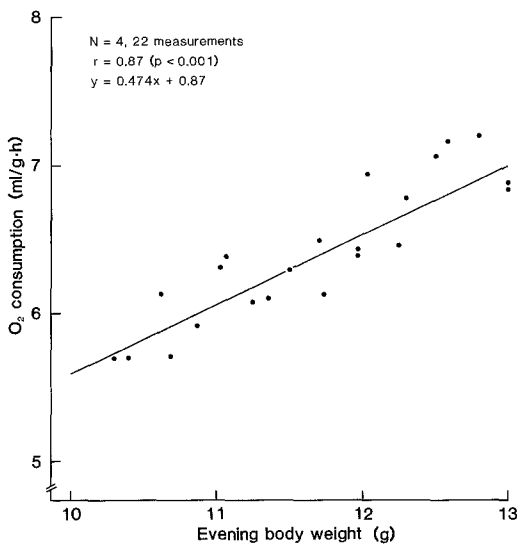


Fig. 5. The relationship between oxygen consumption during the deep sleep phase and body weight at roosting time of winter-acclimatized Willow Tits (4 birds) at a stable ambient temperature of 0°C

ent temperature of 0°C , was found to be positively correlated with the body weight at roosting time (Fig. 5). The oxygen consumption rate of adequately fed birds fell at roosting time and reached a stable level within half-an-hour (Reinertsen and Haftorn 1983). When kept on a reduced diet, the bird's metabolism still exhibited the normal diurnal pattern, but subsequently attained correspondingly lower values with decreasing body weight. A positive correlation with the depth of hypothermia achieved at thermal homeostasis was found. When body weight at roosting time was high (12.50 g) the bird maintained a relatively high metabolic rate (7.07 ml/g·h), subsequently resulting in a relatively high nocturnal body temperature (38.15 $^{\circ}\text{C}$). When body weight at roosting time was

only 10.30 g, reduced by limiting food supply, the nocturnal oxygen consumption rate recorded was only 5.70 ml/g·h and a deep degree of hypothermia (33.90 $^{\circ}\text{C}$) was recorded once thermal homeostasis had been attained. Assuming an RQ value of 0.7 (fat metabolism) and using a value of 4.8 cal/ml of oxygen as the energy equivalent, the resultant reduction in oxygen consumption of 1.37 ml/g·h would represent an overall saving of energy of 6.58 cal/g·h. At midwinter a Willow Tit of 10 g body weight, exposed to an ambient temperature of 0°C , can thus save more than 1 kcal (4.4 kJ), on an overnight basis, by being able to tolerate a deeper degree of hypothermia when food supplies are scarce.

Discussion

The results presented support the hypothesis that at roosting time in the evening the Willow Tit is able to regulate its metabolic rate at a specific level which more or less corresponds to the maximum affordable energy expenditure. When the ambient temperature was experimentally raised or lowered in the middle of the night, the birds responded by raising, or lowering their body temperature accordingly. A rise in the ambient temperature would obviously be expected to lead to a subsequent reduction in metabolic heat production, in order to maintain a steady-state body temperature. However, the Willow Tit does not seize this chance of making a further, though marginal, saving of energy. Instead, the birds increased their degree of awareness by raising the body temperature, despite the fact that this response led to a relative increase in the metabolic rate. In contrast, when the ambient temperature was lowered, the birds could apparently not afford to increase their metabolic rate to a corresponding degree, and thus a fall in body temperature resulted. To ensure that their energy reserves would last throughout the night, the birds presumably had to accept a decrease in their degree of awareness.

The significant linear relationship found to exist between the nocturnal metabolic rate and body weight at roosting time clearly demonstrates that not only the ambient temperature (and the season of year, cfr. Reinertsen and Haftorn 1983), but also the actual state of the energy reserves determined the depth of nocturnal hypothermia.

When body weight at roosting time was experimentally reduced below the normal value, the bird lowered its metabolic rate and subsequently achieved a greater degree of nocturnal hypothermia than would be expected on the basis of ambi-

ent temperature alone. By its capability of tolerating a deeper degree of hypothermia when its body weight at roosting time was abnormally low, the Willow Tit was able to save more than 1 kcal (4.4 kJ) of nocturnal energy expenditure at an ambient temperature of 0 °C. Assuming a rate of fat metabolism for which 1 g fat is equivalent to 9,500 cal (Kleiber 1961), this represents an energy saving of more than 0.1 g fat, or approximately 10% of the expected total nocturnal energy expenditure.

It seems, however, that there is a threshold value below which, in normal situations, body temperature is never allowed to fall. For the Willow Tit this value seems to be about 32–33 °C. Thus, in the experiments conducted, body temperatures lower than this could not be induced at the most extreme low temperature to which the birds were exposed (–30 °C), nor with a body weight at roosting time as low as 10.30 g.

The rate of warming by birds during active arousal from a state of hypothermia appears to be inversely related to body weight (Lasiewski and Lasiewski 1967). The relationship is such that, at an ambient temperature of 20 °C, a Black-chinned Hummingbird weighing 4 g requires approximately 10 min to raise its body temperature from the environmental level to above 35 °C, whereas a Poor-will *Phalaenoptilus nuttalli* weighing 40 g needed about 35 min to accomplish this same task (Lasiewski and Lasiewski 1967). The rate of re-warming may thus represent one of the limiting factors which determines the threshold value below which the body temperature is never allowed to fall. For Blackbirds (mean body weight 97.5 g) the body temperature did not fall below 37.2 °C, even when body weight was experimentally depleted by 30% (Biebach 1977). A 35% body weight depletion of Mousebirds (normal body weight 50–78 g) induced a fall in body temperature to 22 °C, and if the body temperature fell below 18 °C, no arousal occurred (Bartholomew and Trost 1970; Prinzinger et al. 1981). For various species of Hummingbirds (weighing between 3 and 10 g) spontaneous arousal was reported at body temperatures as low as 10–12 °C, but not below this critical limit (Lasiewski 1963; Wolf and Hainsworth 1972; Hainsworth et al. 1977).

The low body temperature threshold value recorded for the Willow Tit is still rather high compared to that reported for the Hummingbirds. Provided that body weight is not below normal, the Willow Tit utilizes its maximum permissible degree of hypothermia only when the ambient temperature is extremely low (below about –20 °C). In

the morning, a 10.5 g Willow Tit requires about 2 h to raise its body temperature from the nocturnal hypothermic value (33 °C) to its normal daytime value (41.3 °C). If the bird is disturbed in the middle of the night, however, it is able to raise its body temperature from 33 to 41.3 °C within only 15 min (see also Haftorn 1972). This is still much longer than the time required by a 4 g Hummingbird to re-warm to above 35 °C from a hypothermic value of 20 °C. Thus, the comparative slow rate of re-warming at low ambient temperatures may be one of the reasons why the Willow Tit does not let its body temperature drop below 32–33 °C.

If, by the morning, the body weight of a Willow Tit had fallen to below 9.70 g, no spontaneous arousal occurred, apparently because no further energy reserves were available to raise its body temperature to the normal daytime level. If the maximum permissible degree of hypothermia (body temperature 32–33 °C) had not been achieved during the night by birds which at roosting time weighed only 10.30 g, their body weight would have fallen below the critical value of 9.70 g by the morning. When their body weight at roosting time is critically low, Willow Tits apparently utilize nocturnal hypothermia for survival in the same way as Hummingbirds do. A state of torpor could also be induced in Mousebirds and Blackbirds if their food supply was reduced (quantitatively) and body weight depleted (Bartholomew and Trost 1970; Biebach 1977; Prinzinger et al. 1981). Mousebirds weighing 50–80 g can tolerate fasting for a couple of days, and should thus have no need to minimize their energy expenditure rate when food is abundant, whereas small-sized birds, such as Hummingbirds (3–8 g) and Willow Tits, cannot tolerate even a single day without food and, in consequence, have a greater need for an energy-saving mechanism such as hypothermia.

A critical question is why the Willow Tit does not seize the chance of saving energy by utilizing its maximum permissible degree of hypothermia every night, regardless of the ambient temperature and the state of its energy reserves. The adoption of such a strategy would enable it to start each day with a certain reserve supply of energy and the bird would perhaps thus be less at the mercy of bad weather conditions or temporary food shortages. Food shortage, however, seems to represent only a minor risk to this species, because the bird is known to store food to a great extent during the autumn and, according to the available information, these food stores, which are scattered in trees all over the bird's home range, represent a

valuable additional food resource during the wintertime (Haftorn 1956, p 73).

Some kinds of risk associated with the entry into a state of hypothermia, such as increased susceptibility to predation or the danger of physiological breakdown, are probably so important that the Willow Tit never lets its body temperature fall further than is absolutely necessary from energy expenditure standpoint, assessed in relation to night length, the prevailing ambient temperature, and the immediate state of its energy reserves. It remains to be investigated how the Willow Tit is able to make such an accurate judgement of the state of its energy reserves at roosting time.

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