

## Birds in the cold: The effects of plumage structure and environment on operative temperature, shown by spherical models

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### Abstract

What is the maximum insulating effect the available plumage of a bird can provide? To address this question I photographed free-living birds in such a way that the total volume of the bird could be estimated. It was then assumed that the bird could be represented by a sphere of the measured volume with a core (kept at 40 °C) of which the volume in cm<sup>3</sup> was equal to the bird's mass in g. The overall thermal conductance of the spherical model was calculated and compared with what could be expected for real birds based on metabolic data from the literature. The conductance calculated for the models was consistently lower than predictions from the literature. The discrepancy was as could be expected, and became smaller with decreasing size. For small

birds the fit was quite good and the relative plumage thickness approached the value where further increase would have a relatively small effect. The model suggests that the operative temperature of a small bird perching in the sun on a cold winter day can exceed the air temperature by more than 20 °C on thermally favoured sites. Alternatively expressed, the energy saved can exceed the basal metabolic rate. For a plumage penetrable for solar radiation the excess may be still higher, even when the reflectivity is rather high. It is estimated that the operative temperature may exceed the preferred range already with an air temperature of 10 °C.

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### Introduction

About a century ago it was established that also for a living animal the first law of thermodynamics holds which means that the incoming flows must match the outgoing ones. Thus, the question in bird energetics is not whether the energy loss is balanced by energy gains but rather how the birds manage to make them meet.

For a bird in the winter, the thickness of its coat, that is the degree of insulation, is not the only question, perhaps not even the most important one. To maintain its often large temperature difference with the surroundings, it must burn fuel which must be collected as food or taken from an energy reserve. Furthermore, the living tissue might quite well be limited in its capacity to produce heat even when there is plenty of fuel. The heat loss, per unit surface, of e.g. a Willow Tit *Parus montanus* can be of the same magnitude as that of a well dressed human in the winter (see Appendix), but the latter has about 25 times as much living tissue, again per unit surface, to provide the requisite heating power.

I concentrate here on the process of heat loss to the environment. The first step in the heat transport from the core of a bird to the environment is conduction, initially from the internal parts of the body to the skin and then through the plumage to the outer surface. The second step is the transfer of this heat to the surroundings. There is a direct transfer of heat from the surface to the air where it is carried off by convection currents. The convection process depends on the temperature difference between surface and air, the airflow, and the size of the bird or, as in this study, an object that mimics a bird. Parallel with the convection process there is a transfer of heat by radiation which is both emitted and received by the surface. Finally there is solar radiation that is absorbed or reflected but not emitted by the surface.

The purpose of the paper is in the first place to explore how far a simple physical model can take us to understand the thermal situation of a bird in the winter. When a little bird during a cold winter day perches with its feathers fluffed it can be seen as 'a ball of feathers' of almost spherical shape. It is

logical to assume that the spherical shape has to do with minimizing heat loss. It is, however, interesting to take a closer look at the quantitative side of the matter.

One can ask: what size is such a ball and how much living bird tissue is there inside it? I will investigate if it is possible to make an acceptable thermal model of a bird in the winter by considering its body as a sphere kept at a temperature of ca. 40 °C and surrounded by a concentric sphere of insulating feathers. The heat loss of such an object can be readily calculated in relation to environmental factors on the one hand and its dimensions and thermal properties on the other hand.

By means of photographs I estimated the volume of birds under winter conditions and then calculated the heat loss of a spherical model of the same volume, with a core kept at 40 °C, i.e. a model which imitated the thermal properties of the living bird as far as possible. Finally these data were compared with literature data on heat loss from living birds derived from metabolic measurements under laboratory and field conditions. Furthermore, I asked the question to what extent a bird can make use of the solar energy both by selecting its position in relation to sunshine, shade, or reflecting surfaces, and by structuring its plumage.

I gave special attention to small northern forest birds since they experience an especially demanding thermal and radiative environment. I could show the important result that by means of simple physical and theoretical models it is possible to understand how sunshine can mitigate the effect of a low air temperature or cause heat stress already at moderate but still fairly low air temperatures.

## Materials and methods

The volume of a range of free-living birds was estimated by photographing them in profile side by side with a sphere of known size. Alternatively, a calibration picture of the sphere was taken immediately after the bird had been photographed with an unchanged setting of the lens. The pictures were taken of active birds during short intervals of rest, in the shadow, with air temperatures of -5 to -25 °C, mainly in southern Sweden but occasionally at Abisko in northern Sweden and in the Netherlands. From the photographs I estimated the volume of the birds by considering them to be ellipsoid or egg-shaped bodies since birds are shaped like elongated round bodies rather than perfectly round balls. The volume of such bodies that "revolve" around a

central axis can be calculated by "cutting" them into series of circular discs. Focal lengths of 30 and 56 cm were used to obtain sharp pictures of sufficient size to permit good estimates of the volume.

I assumed that the volume of a bird without plumage in cm<sup>3</sup> is the same as its mass with feathers in g, a plausible approximation as the density of a 'naked' bird is somewhat below 1 (Schmidt-Nielsen 1972). From these data I calculated the dimensions of spherical, theoretical models that I used as thermal models of the birds. These models consisted of an inner spherical core surrounded by a concentric insulating layer. For example, a Great Tit *Parus major* that has a total volume of 90 cm<sup>3</sup> and a mass of 18 g was represented by a hypothetical sphere with total volume of 90 cm<sup>3</sup> and an outer radius,  $r_o$ , of 2.78 cm. The spherical core would then have a volume of 18 cm<sup>3</sup>, giving an inner radius,  $r_i$ , of 1.63 cm. The thermal conductance of the model was then calculated and compared with literature data for a real tit, based on metabolic measurements. Average mass of the birds was taken from Snow & Perrins (1998). The thermal models can be seen as links between real birds and the temperature measurements in the experimental bulbs with the only purpose of making accurate calculations possible.

The heat loss of such a spherical core of uniform temperature,  $t_b$ , depends on the thermal conductivity of the insulation, on  $r_i$  and  $r_o$  as well as on wind, air temperature  $t_a$ , and radiation (cf. Stoutjesdijk & Barkman 1992). The heat loss in Watts,  $M$ , can be expressed as

$$M = C_0 (t_b - t_a)$$

for situations where thermal or solar radiation need not be considered, as in dense forest or under laboratory conditions. Here  $C_0$  is the overall thermal conductance. The effect of radiation can be included by replacing  $t_a$  by an effective or operative temperature  $t_e$ . For living birds the term "operative temperature" is commonly used (Bakken 1976, 1992) whereas I use the term "effective temperature" for the models. These terms have a long history in medical physiology. They aim to describe a complicated thermal environment by a single temperature that easily can be measured (Evans 1945, Fanger 1972, Gonzales et al. 1974). In the following I make clear that the temperature of a simple model such as a black bulb will have a close relationship to the operative temperature of a bird.

Extensive series of measurements of the overall conductance can be found in the literature (Kendeigh et al. 1977). These were used for comparison with

the thermal models that were calculated from the photographs. The overall conductance of the models was calculated for the laboratory conditions to which most data on living birds refer. I also estimated how the models would behave under more realistic environmental conditions, in the first place how much the effective temperature in the sun could exceed air temperature.

For this purpose I measured solar radiation (Kipp Solarimeter), thermal radiation (Stoutjesdijk & Barkman 1992) and temperatures in experimental models that I constructed (Stoutjesdijk, 2002). The models were of two types: dull black bulb-shaped ones that minimize reflection and "fluffy" models that mimic the properties of real birds. These experimental models were the most important part of the instrumentation. They were made of aluminium cake forms with a wall thickness of 0.06 mm and equipped with a temperature sensor in the centre. The temperatures were measured with simple outdoor digital thermometers that were calibrated with an accurate mercury thermometer.

The black bulbs consisted of single-layered half-spheres that were glued together and painted with dull black paint. The fluffy models consisted of two concentric spheres with a layer of insulating down or fibres in between. I made two sizes of this fluffy model; a smaller one with an inner diameter of 3.0 cm and an outer diameter of 5.8 cm and a larger one with twice these dimensions. A segment that covered approximately 20% of the total surface, was removed from the outer sphere (cf. Figure 3d). Such a sphere can be considered to thermally mimic a bird with a plumage that is partially penetrable for solar radiation. The small models were made both with eider down (reflectivity ca. 20%) and with white artificial fibre (reflectivity ca. 57%) whereas the large one was made with eider down only. These models were black apart from the fluffy section resulting in a reflectivity of around 57% and 20% for approximately 20% of the surface, and a low reflectivity from the rest of the surface. In total I thus made four thermal models, one black bulb, two smaller and one larger fluffy model.

## Results

I constructed a nomogram (Figure 1) that shows the relation between mass and overall thermal conductance ( $C_o$ ) for models with a range of values of the quotient between the outer and inner radii,  $r_o/r_i$ , between 1.2 and 2.0. On a double logarithmic scale this results in a series of almost straight lines.

The calculations were made for still air and a specific conductivity of the plumage of 0.04 W/m °C. This is conservative since this is equal to the best insulators both in the animal world and among man-made materials (Scholander et al. 1950, Taylor 1986). The values of the  $r_o/r_i$ -quotient derived from the photographs were placed on their proper place in the nomogram and thus the expected overall conductance could be read.

In the nomogram the regression lines for passerines and non-passerines give the relation between mass and overall conductance,  $C_o$ , according to Kendeigh et al. (1977). Here the overall thermal conductance was derived from the metabolic heat production, i.e. oxygen consumption of birds under laboratory conditions. These measurements were made in still air with a temperature of 0 °C, which makes them comparable with those given here.

To place the data on the thermal properties of birds in an environmental context I here present calculations of the effective temperatures of spherical models. These estimates are based on measurements of air and surface temperature, solar and thermal radiation and temperatures of both the black bulbs and the fluffy models. The diameter of the bulbs was 5.8 cm when not stated otherwise. Where the physical aspects of the data per se need some explanation I give it here and for the rest I refer to the discussion.

The temperatures of the bulbs indicate how the radiation affects the operative temperature of a bird. Figure 2 shows the effective temperatures for theoretical models with the thermal properties of a "standard thermal model" corresponding to a 12 g bird. The heating power that would be required to keep such thermal models at 40 °C is expressed in units of the basal metabolic rate (BMR) of the standard model (see Figure 3 and discussion). The diameter of the standard thermal model was almost the same as the black bulb meaning that its effective temperature was equal to the black bulb temperature (see Appendix). The data in Figure 2 are based on measurements of radiation conditions and black bulb temperatures on two calm and cloudless winter days. The first set of measurements was made with a solar elevation of 10° by the end of December at noon in southern Sweden. The air was completely still, not even in the treetops there was a sign of air movement. The black bulb temperature was twelve degrees above air temperature (-5 °C) giving an effective temperature of +7 °C and the requisite heating power 1.74 B.M.R for a black standard model.

For a model (or bird) that is not black the effective

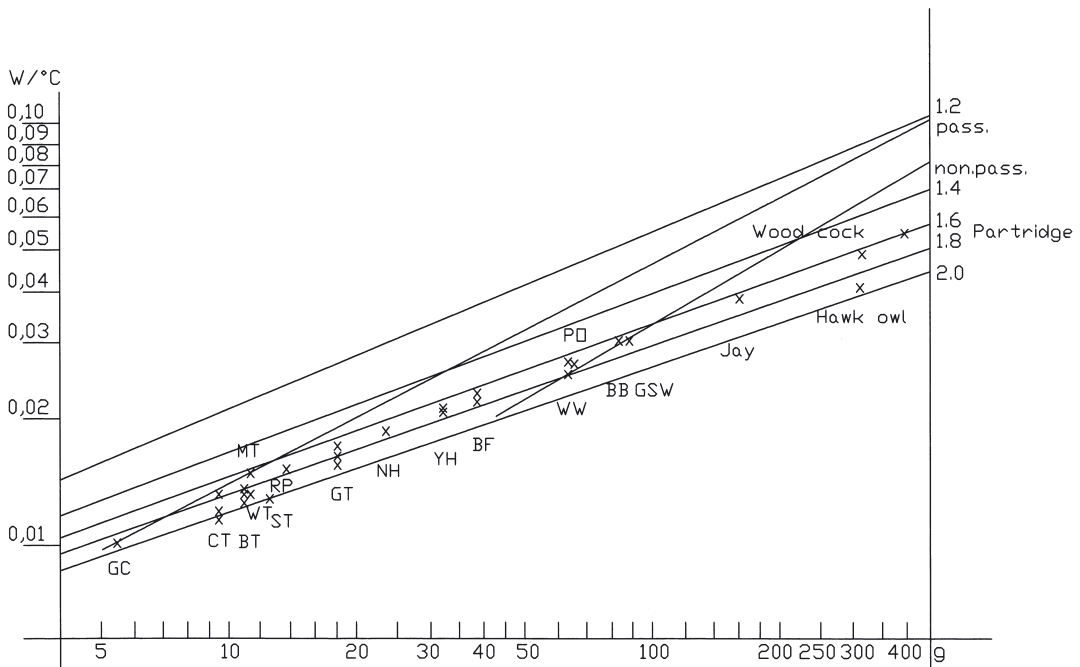


Figure 1. Nomogram showing the relation between overall thermal conductance (Y-axis, left) and mass (X-axis). It is supposed that the core volume in  $\text{cm}^3$  is equal to the mass in g. The five almost parallel lines: thermal models with plumage thickness ( $r_u/r_f$ ) between 1.2 and 2.0 (Y-axis, right). The two crossing lines: passerines and non-passerines; data from the literature. The relative coat thickness for free-living birds, derived from photographs, is shown by (x) in the diagram. The abbreviations refer to the list of species below.

De fem nästan parallella linjerna ger relationen mellan kärnvolumen ( $\text{cm}^3$ ) och total termisk konduktans ( $C_0$ ) för teoretiska sfäriska modeller med relativfjäderdräktstjocklek ( $r_u/r_f$ ) mellan 1.2 och 2.0. Värden av  $r_u/r_f$  för fåglar: x. De två korsande linjerna visar relationen mellan vikt (i gram) och  $C_0$  för tättingar och icke-tättingar från litteraturvärden.

List of the bird species *Lista över fågelarterna:*

GC, Goldcrest, *Kungsfågel*, *Regulus regulus*. CT, Coal Tit, *Svartmes*, *Parus ater*. BT, Blue Tit, *Blåmes*, *Parus caeruleus*. MT, Marsh Tit, *Entita*, *Parus palustris*. WT, Willow Tit, *Talltita*, *Parus montanus*. ST, Siberian Tit, *Lappmes*, *Parus cinctus*. RP, Redpoll, *Gräsiska*, *Carduelis flammea*. GT, Great Tit, *Tåggoxe*, *Parus major*. NH, Nuthatch, *Nötväcka*, *Sitta europaea*. YH, Yellowhammer, *Gulspary*, *Emberiza citrinella*. BF, Bullfinch, *Domherre*, *Pyrrhula pyrrhula*. WW, Waxwing, *Sidensvans*, *Bombycilla garrulus*. PO, Pygmy Owl, *Sparvuggla*, *Glauclidium passerinum*. BB, Blackbird, *Koltrast*, *Turdus merula*. GSW, Great Spotted Woodpecker, *Större hackspett*, *Dencrocopos major*. Jay, *Nötskrika*, *Garrulus glandarius*. Hawk Owl, *Hökuggla*, *Surnia ulula*. Partridge, *Rapphöna*, *Perdix perdix*.

temperature is of course lower when the surface is impenetrable for solar radiation. In Figure 2 the calculated effective temperatures are shown for theoretical spherical models of which the 20% of the surface that is penetrable to solar radiation has a reflectivity of 50% and the rest a reflectivity of 20%. A model of this kind will mimic a real bird such as a Willow Tit with fluffed breast feathers much better if the most reflective part of the insulation is assumed to be penetrable to solar radiation. In this case the radiation can be much more effective than if it is absorbed at the surface (Walsberg et al. 1978, Stoutjesdijk 2002). When the fluffy models are

directed so that their fluffed breast feathers face the sun their calculated effective temperature exceeds the black bulb temperature. The calculated effects were of medium strength when compared with the results obtained experimentally on various penetrable coats (see Figure 4, Table 1, and Stoutjesdijk 2002). The solar radiation can also be more effective, that is the operative temperature higher, when the plumage on the side facing the sun is thinner or of a higher conductance than on the "shadow" side (cf. Figure 3 and Appendix).

Up to now I have considered only freely exposed probes. Again starting from experiments with black

bulbs and radiation measurements, the calculated temperature of all the three models was found to be considerably higher close to, or almost touching, the densely needled branches of a Juniper or a spruce facing the sun (Figure 2). This happens because the diffuse solar radiation from the transparent blue northern sky is replaced by the stronger reflected radiation from the needles. Furthermore the probes receive long-wave (heat) radiation from the needles instead of the sky. The latter, when cloudless, can be considered as a dome with a temperature as low as 40 °C below air temperature, whereas the needles have a temperature up to 8 °C above air temperature (Stoutjesdijk 1977, Stoutjesdijk & Barkman 1992). A minor effect may also be the somewhat higher (1–2 °C) air temperatures close to the branches. Altogether the effective temperatures of the three models can be further enhanced several degrees (4–6 °C, see legends Figure 2, elevation 10°, right side) by choosing the right position, always considering situations within the possibilities of a small bird.

Due to the low radiation intensity on a horizontal plane (global radiation) the effect of reflected radiation was rather small here, in spite of the fact that scattered snow patches gave a surface reflectivity of 41%. Where there is much reflected radiation from a south oriented snow-covered slope, the temperature excess for a black bulb may be over 20 °C with the same solar elevation.

With a higher solar elevation (30°) the direct solar beam is stronger because of the shorter path through the atmosphere. Also the reflected radiation is more important, even though the reflectivity (albedo) was less (20%), as the radiation intensity on a horizontal plane increases strongly with elevation.

The black bulb temperature was 18 °C above air temperature. The measured radiation conditions and black bulb temperature were also used to construct Figure 3. The radiation fluxes were averaged over a sphere, and together with the black bulb temperature they were used to calculate, for the three thermal models in two positions, the temperature when passive and the heating power needed to keep the core temperature at 40 °C with an air temperature of 0 °C.

Figure 4 shows a synoptic picture of radiative conditions and the temperatures of various types of physical models on a clear still winter day with a solar elevation of 20 degrees and a closed snow cover. The black bulb attained a temperature of 21 °C over air temperature. The partially penetrable ('fluffy') model of the same size showed a temperature excess ( $\Delta t$ ) of 31 °C, and the larger fluffy model showed a  $\Delta t$  of 42 °C. On the sunny side of a large

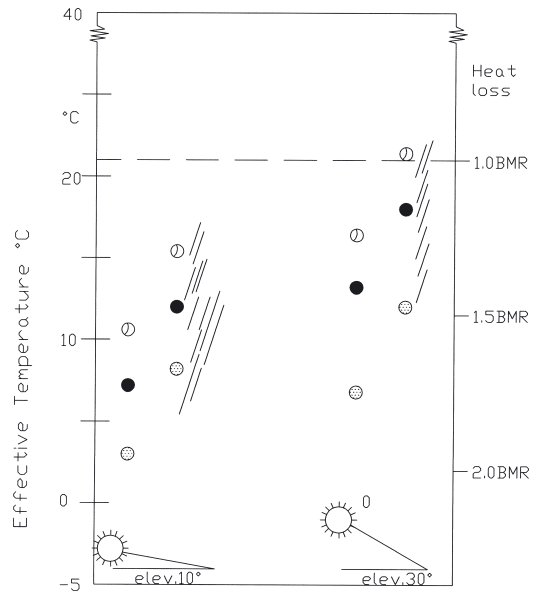


Figure 2. Operative (= effective) temperatures and heat loss for Standard Models with a relative coat thickness ( $r_u/r_l$ ) of 1.88 that represents a small Passerine of 12 g. The basal metabolic rate (BMR) is used as the unit of heat loss (see text). Air temperature: -5 °C. The calculations are based on measurements of radiation and black bulb temperatures in still air, a cloudless sky and solar elevations of 10° and 30°. The symbols ● and ○ denote the black and fluffy bulbs respectively. For the fluffy model the segment with 50% reflectivity is facing the sun and the solar radiation penetrates the coat to an average depth of 25% of the coat thickness. The symbol ⊙ gives the average effective temperature when the latter model is impenetrable and in a random position. For both solar elevations the data refer to a freely exposed model (left) and one close to dense south-exposed, spruce or Juniper branches.

Operativa (= effektiva) temperaturer (till vänster) och värmeförlust (till höger) för standardmodeller som representerar en tätting på 12 g, vars basalmetabolism har använts som enhet för värmeförlust. Lufttemperaturen är -5 °C. Beräkningarna baseras på mätningar av sol- och värmestrålning och temperaturen av en svart kula i stilla luft med en molnfri himmel. Solhöjd: 10° och 30°. Symbolerna ● och ○ står för en svart modell och en modell med 50% reflektion över 20% av ytan och 20% över resten. Segmenten med 50% reflektion är riktade mot solen och är genomträngliga för solinstrålningen till 25% av pälsens tjocklek i genomsnitt. ⊙ står för samma modell men ogenomträngligt, medelvärden för slumpartig orientering. Temperaturerna är för fristående modeller (vänster) och för modeller i närheten av tätt grenverk av gran eller en, orienterad mot syd (/).

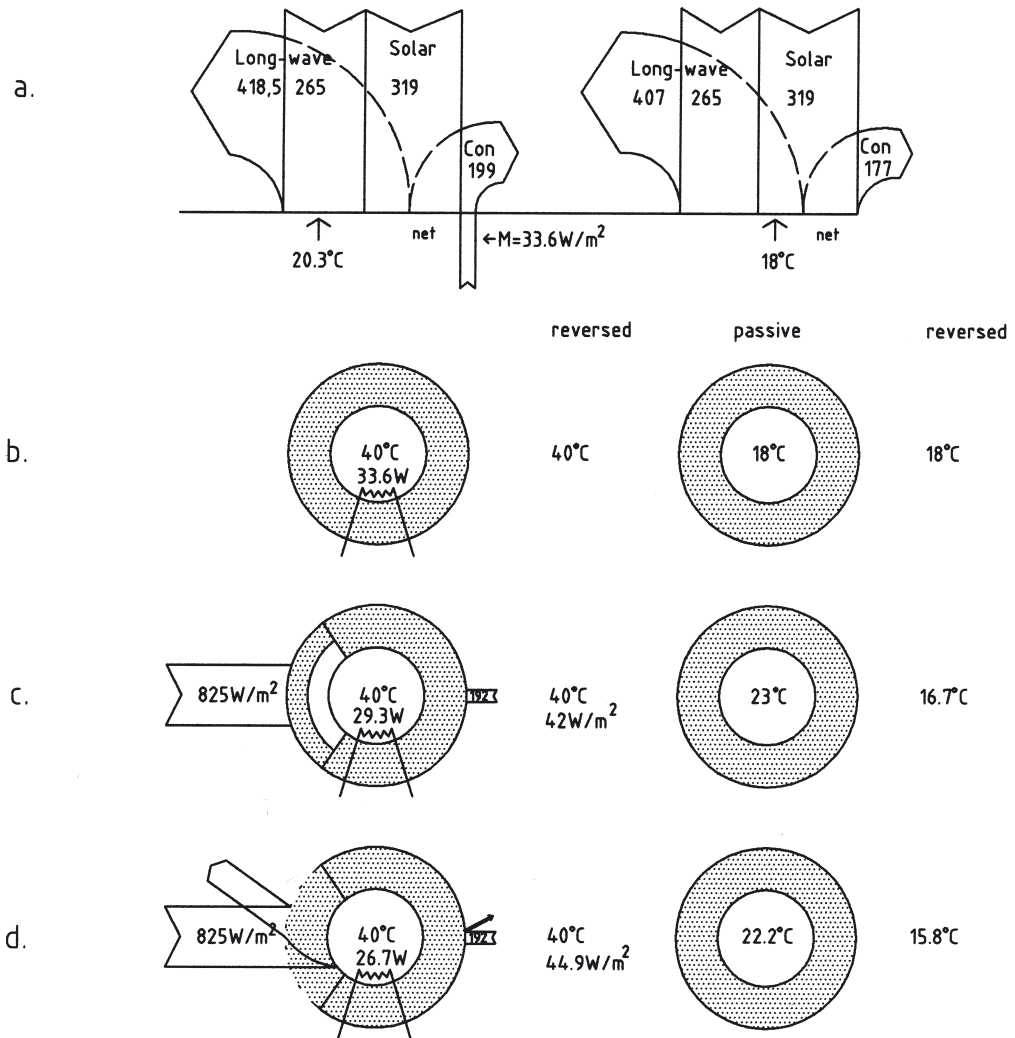


Figure 3. a. Energy fluxes [ $W/m^2$ ] averaged over the surface of a black standard model (see text) which is kept at a core temperature of  $40^\circ C$  at an air temperature of  $0^\circ C$ . The net radiation absorbed plus the heating power applied is given to the air by convection. Right side: the same for a passive (unheated) model in the same situation. The radiation conditions are the same as in Figure 2 with a solar elevation of  $30^\circ$ . b. The heating power needed to keep the core of the model at  $40^\circ C$  together with the temperature of the unheated model. c. The same as 3b when the overall thermal conductance of a segment that constitutes 20% of the total surface is doubled. Data are shown both when this segment is facing the sun and when it is reversed. Temperatures of the unheated model are also shown. d. As 3c, but with a segment that is partially penetrable to radiation. See also legends Figure 2. The heating power is given here in  $W/m^2$  of the outer surface of the Standard Model of which the surface is:  $0.00896 m^2$ .

a. Energiflöden mot och från ytan av en svart standardiserad modell (se text) med en kärntemperatur av  $40^\circ C$ . Flödena är medelvärden [ $W/m^2$ ] över den sfäriska ytan vid en lufttemperatur på  $0^\circ C$ . Den absorberade nettostrålningen plus energin producerad i kärnan överförs till luften genom konvektion. Till höger: detsamma för en passiv, uppvärmd modell i samma situation. Strålningsförhållandena som i Figure 2, solhöjd  $30^\circ$ . b. Värmeproduktionen [ $W/m^2$ ] som behövs för att hålla kärnan på en konstant temperatur av  $40^\circ C$  tillsammans med uppmätta temperaturer i den passiva modellen (jfr: 3a). c. Som 3a och 3b när konduktansen,  $C_o$ , i ett segment som utgör 20% av den totala ytan, är fördubblad. Värderna visas både när detta segment är riktat mot solen och vänt från denna. Solinstrålningen [ $W/m^2$ ] mot segmentet och resten av sfären visas separat. d. Som 3c när ett segment är delvis genomträngligt för solinstrålningen. Se också Figure 2. OBS: Värmeproduktionen beräknad i  $W/m^2$  för ytan ( $0.00896 m^2$ ) av Standard Modellen.

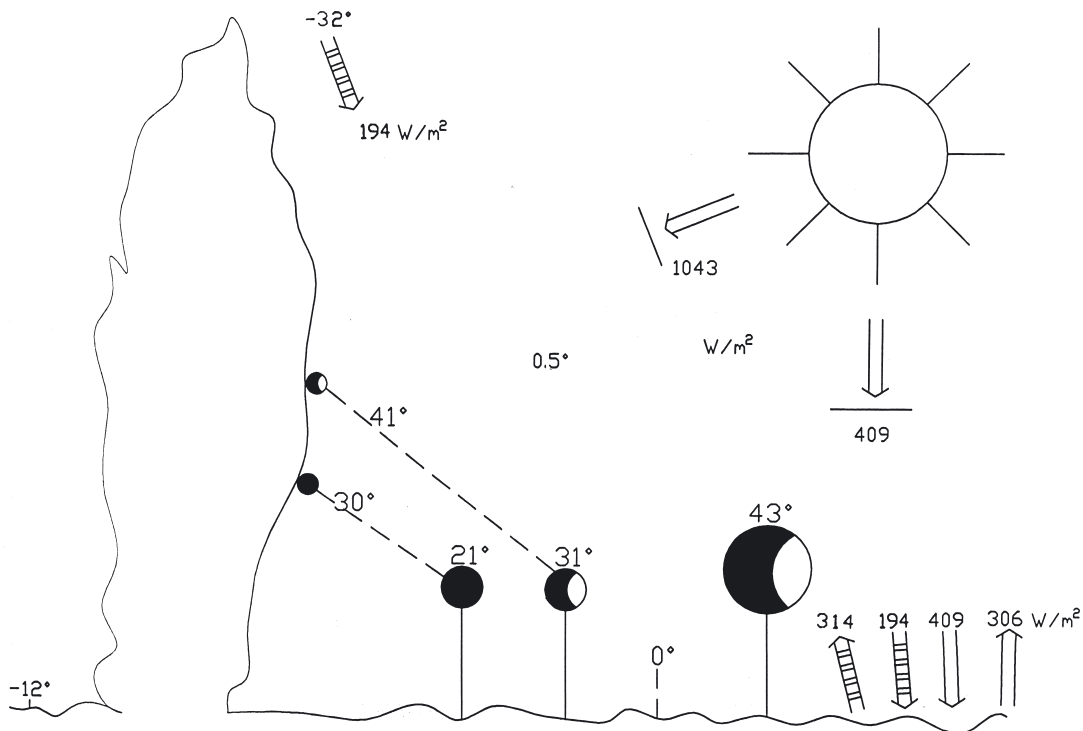


Figure 4. Radiation conditions and temperatures of black and thermally isolated bulbs on a day with closed snow cover at a solar elevation of 20°. The latter type of bulbs was partially penetrable to radiation. The upper right corner shows the solar energy received on a plane that is perpendicular to the direct rays of the sun and on horizontal planes pointing upwards (for global radiation) and downwards (for reflected radiation), respectively. The long-wave radiation emitted by the snow and received from the sky is shown by cross-hatched arrows.

Temperaturerna i svarta kulor och kulor med en isolerande skikt som var delvis genomträngliga för solinstrålningen på en sida. Mätningarna är gjorda under klar och vindstill vinterdag när marken var helt snötäckt. I övre hörnet till höger: infallande solenergi mot en yta vinkelrätt mot den direkta strålningen och mot en horisontal yta riktad uppåt (för global strålning) och nedåt (för reflekterad strålning). Den långvågiga (värme-) strålningen visas som korsstreckade pilar.

Table 1. Excess temperatures ( $\Delta t$ ) compared to air temperature of various models in relation to those of a freely exposed black bulb.

Skillnaden ( $\Delta t$ ) mellan lufttemperatur och temperaturen i sfäriska och delvis genomträngliga modeller, i förhållande till samma skillnad i en fritt exponerad svart kula.

Model	$\Delta t$ Relative range	average	$\Delta t$ Maximum °C
Black in Juniper	1.25-1.86	1.40	29.3
Fluffy grey small			
5.8 cm Ø	1.29-1.96	1.55	30.9
Fluffy white small			
5.8 cm Ø	1.34-1.87	1.54	29.3
Fluffy grey large			
12 cm Ø	1.60-2.20	1.93	43.5

Juniper (*Juniperus communis*) both the black bulb and the small fluffy model reached temperatures roughly 10 °C higher than when freely exposed. The dense (elk-browsed) surface of the Juniper had a radiative temperature of 8 °C, i.e. 40 °C higher than that of the sky. (This means that the Juniper radiates heat like a black surface of 8 °C and the thermal radiation received from above is the same as when the sky was a dome with a temperature of -32 °C).

Though the measurements were all made in southern Sweden (57° N) the situation shown in Figure 4 is probably more typical for the late winter further north. I estimate from incidental measurements that the strong effects shown in Figure 4 can be approached already with a solar elevation of 12–15 degrees when a still more stable air compensates for the lower amount of solar energy received (cf. Appendix).

Table 1 shows the excess temperatures of the fluffy models in relation to the black bulb temperature over a more extensive series of measurements. Note that the temperature excess of the white fluffy model does not differ essentially from that of the grey one. The black bulb temperature varied between 10° and 21° above air temperature, which means in non-instrumental terms: an unobscured sun, an atmosphere between very clear and somewhat turbid, and air movement indiscernible or just visible on dry grass leaves at the site of the measurements.

## Discussion

As mentioned, both the axes in Figure 1 are logarithmic. For a fixed value of the quotient  $r_u/r_i$  the relation between mass,  $W$ , and overall thermal conductance,  $C_o$ , is given by a (virtually) straight line, which means that it can be expressed by the relation:  $C_o = PW^s$ , where  $P$  is a proportionality factor and  $s$  is the slope of the line. For  $r_u/r_i = 2$  for instance,  $s = 0.35$ . Doubling the linear dimensions would increase the mass with a factor 8, the surface with a factor 4 and thickness of the plumage with a factor 2. That  $s$  is 0.35 and not 0.33 here is due to the fact that not only conduction but also surface related processes, heat transfer to the air and heat loss by radiation play a (minor) role here. When  $r_u/r_i$  decreases,  $s$  increases gradually as the surface related heat transfer processes become relatively more important. For an uninsulated core kept at a constant temperature  $s$  would be 0.66.

The proportionality with  $W^{0.66}$  also applies approximately to the basal metabolic rate. The values given for  $s$  are here between 0.66 and 0.75 (Kendeigh

et al. 1977). The basal metabolic rate (BMR) is the lowest metabolic rate that a healthy bird can maintain regardless of the circumstances. The relation between BMR and surface would be obvious if  $C_o$  increased at the same rate, but this is definitely not the case. According to Kendeigh et al. (l.c.),  $s = 0.52$  for passerines, 0.58 for non-passerines, and 0.49 for all birds, calculated from another set of data. Through my own data a line can be drawn with a slope of ~0.4. Anyway the temperature at which the BMR can fully compensate the heat loss becomes lower with increasing mass. This compensation point is called the lower critical temperature (LCT).

From Figure 1 it is clear that the overall conductance,  $C_o$ , derived from photographs is always below the trend lines derived from metabolic measurements. The difference increases with increasing mass. This could be due to the fact that smaller birds approach a spherical shape more closely than larger ones, and/or that the specific conductivity of plumage could increase with size. Another possibility is that for the larger birds the plumage was not as fully expanded in the experimental situation (at 0 °C) as it was in the field at temperatures below -5 °C and that this difference was much less for the smaller birds. Note that the metabolic measurements I refer to have been done with fasting birds. In this connection it is interesting that it is generally assumed that below the LCT the overall conductance does not increase, but, according to Dawson & Whittow (2000), 'not all birds conform to this model'. A similar remark is made by Kendeigh et al. (1977) and the common observation (e.g. Wijnandts 1984) that the relation between metabolic rate and ambient temperature is not as expected from this model can be understood by assuming that in the temperature trajectory below the LCT, there is both a decrease in overall conductance and an increase of metabolic heat production. A combination of photographic and metabolic measurements would be the best approach to test this.

For the Hawk Owl *Surnia ulula*, an  $r_u/r_i$  of 1.95 was found, quite high for a bird of this size. This is in good accordance with the low BMR and metabolic rates in general for the owls. Wijnandts (1984) found by metabolic measurements that for a Long-eared Owl *Asio otus* of 240 g, the overall conductance could be as low as 0.040 W/°C which is compatible with a thermal model with  $r_u/r_i = 1.8$ .

For small passerines with a body size between Goldcrest *Regulus regulus* and Great Tit, the photographic data lie only slightly below the trend line. For the species where I could retrieve specific



metabolic data from the literature (Kendeigh et al, 1977, Dawson & O'Connor, 1996), the Goldcrest, the Coal Tit *Parus ater*, the Willow Tit, the Redpoll *Carduelis flammea* and the Great Tit, the fit was practically perfect. This would mean that:

1. The specific conductivity of the plumage is estimated correctly.
2. The spherical model is close to reality.
3. The estimate of metabolic heat produced from oxygen consumption is right.
4. Heat loss via other pathways than conduction via the plumage is negligible.

The pessimistic viewpoint that all errors have compensated each other seems to be less probable, the more so as the calculated overall conductance is near the lower limit of what is possible with the given volume. Furthermore, the metabolic heat production includes the latent heat loss by evaporation, though this may be only a few percent of the total heat loss under winter conditions.

The overall conductance derived from both photographs and laboratory measurements can also be compared with measurements of the metabolic rate of free living Willow Tits and Siberian Tits *Parus cinctus* by means of the doubly labelled water method (Carlson et al. 1993; see also Dawson & O'Connor 1996). The energy produced by these birds in January near the polar circle was about 10% less than what was required to keep our thermal models warm under the same conditions. These differences could be explained by the difference between the measured air temperature at a nearby airport and the operative temperature experienced by the birds. Also, these species regularly save energy by entering a state of nocturnal hypothermia (Reinertsen and Haftorn 1986). It seems, however, most realistic to say that the results obtained by both methods support each other and also that the energy produced is used to maintain body temperature and that the energy that is lost to the environment through work performed 'outside the body' cannot be a large item on the energy balance.

The quotient  $r_u/r_i$  approaches 2.0 for the smaller birds, i.e. the linear dimensions of the naked bird are doubled by the plumage and the volume increases eightfold. Heat transfer considerations (e.g. MacAdams 1951, Monteith & Unsworth 1990) show that a further increase of the plumage thickness will not result in a corresponding lowering of the overall thermal conductance. For example a doubling of the plumage thickness (from  $r_u/r_i = 2$  to  $r_u/r_i = 3$ ) would

mean a decrease of the heat loss by of 22%. Note that the heat transported through the plumage by conduction will eventually be given off by the surface, which in the example increases by a factor  $1.5^2 = 2.25$  (cf. Appendix). With increasing coat thickness the effect of better insulation is more and more counteracted by the increased outer surface, though apparently still worthwhile as the photographs of Petterson (2002) show.

The thermal model produced good quantitative results when compared to measurements on birds in a metabolic chamber. This means that it seems justified to use such models to understand the energetics of a bird in natural surroundings. To define the environmental conditions simple black bulbs, in combination with the appropriate theoretical and physical models, worked well.

#### *Further details about the models*

I start with some general remarks on the use of both the physical and the calculated thermal models that I have used in this study. For an insulated spherical model, the energy needed to keep it at a constant temperature, say 40 °C, can be readily calculated in relation to air temperature, radiation and wind (cf. Appendix). And as mentioned these factors can be combined into an effective or operative temperature (cf Figure 2). Operative temperature is used here only for real birds.

When a spherical model with a symmetrical insulating layer that is impenetrable both for wind and radiation is placed in the sun, its core temperature is equal to its effective temperature and independent of the conductance (or even the presence) of the insulating layer. This means that the temperature in the centre of an uninsulated bulb of thin metal of the same size and reflectivity will be the effective temperature.

The resemblance can be very rough if only the model absorbs as much radiation per unit surface as the bird. Thus the temperature in a blackened beer can gives a reasonable approximation of the operative temperature for a Jackdaw *Corvus monedula*, provided that the can has approximately the same size and form. When there are strong asymmetries in the properties of the plumage it is much more difficult to interpret the black bulb readings as both the orientation of the bird and the conductance of the plumage are of importance. This is demonstrated by Figure 3c where for a segment of the thermal model the overall conductance is halved. The penetrability of the plumage for solar radiation also strongly

affects the operative temperature. The absorbed radiation is more effective when the insulation on the side of the bird facing the sun is thinner or better penetrable for radiation. A more detailed analysis of these effects and relevant literature is given by Stoutjesdijk (2002). Theoretical estimates are shown in Figure 2 and 3. Measurements on physical models that are penetrable on one side (fluffy) are shown in Figure 4 and collected in Table 1. Note that the measured effects are stronger than calculated (Figure 2 and 3).

A physical model that approaches the operative temperature of a real bird can be made also in more complicated cases but such models have no longer the attractiveness of the simple black bulb. The logical step is to make an as accurate as possible imitation of the real bird. This is a copper cast of the bird's body covered by the original skin and plumage. When the core is kept at 40 °C the resemblance with the real bird is as good as possible. This 'taxidermic mount' can also be used unheated to measure the operative temperature (Bakken 1992, Wiersma & Piersma 1994).

In the following section I concentrate on smaller birds for which the agreement between the thermal properties of the real bird and the thermal model were found to be best.

In the following I refer to a 'standard model' that may be seen as representative for the rather numerous group of small passerines which survive severe winter conditions in the northern forest. The model has a  $r_i$  of 1.42 cm and a  $r_u$  of 2.67 cm ( $r_u/r_i = 1.88$ ). Its effective temperature is with sufficient accuracy measured by a black bulb of 58 mm  $\phi$ .

The energy needed to keep this model at 40 °C was calculated in relation to the basal metabolic rate (B.M.R.) of a bird of 12 g. Here the relation between mass ( $M$ ) and B.M.R. is taken to be  $B.M.R. = 0.054 M^{0.66}$  Watt after Kendeigh et al. (1977).

For the standard small 'bird' an energy production equal to the B.M.R. (0.278 W) can keep it warm (40 °C) at an air temperature of 21 °C (which then is the L.C.T.) in surroundings where solar radiation is unimportant, e.g. in dense forest. With an air temperature of about -20 °C, the required heating power will be over three times the B.M.R. which is already close to the maximum sustainable energy production (Ricklefs 1996, Drent & Daan 1980). Root (1988) concludes that many passerines are restricted to winter ranges where the long-time average of the heating power required does not exceed 2.5 B.M.R. Similar ratios are given for a wide range of birds in Dawson & O'Connor (1996),

Wiersma & Piersma (1994) and Wijnandts (1984).

#### *The importance of solar radiation for different species*

A standard model in the sun can reduce its energy loss with an amount equal to the BMR when the difference ( $\Delta t$ ) between the effective temperature and the air temperature equals 19 °C. From the data in Figure 2, 3 and 4, it is clear that this difference is often exceeded with a clear and stable atmosphere in thermally favoured sites. For a standard model  $\Delta t$  can be 30 °C. A conservative estimate of the operative temperature of the smaller forest birds in the same situation would be considerably more than 20 °C above air temperature. When the fluffy model ( $\Delta t = 40$  °C) in the same way represents a bird in the sun, an operative temperature of more than 30 °C above air temperature would easily be achieved. In this connection it is significant that the penetrating radiation can be quite effective even with a strongly reflective plumage (cf. Table 1) as a higher penetration depth can compensate the lower absorption. The fact that solar radiation can considerably reduce the effect of low air temperature thus seems to be sufficiently documented. On the other hand it seems quite possible that already at relatively low air temperatures it can be difficult to dissipate all the metabolic heat by conduction, especially for an active bird where it is considerably higher than B.M.R. Of course, the real bird can reduce the plumage thickness, select the best of the range of possibilities between sun and shade, or move between extremes with alternately rising or falling body temperature.

In the heart of the Scandinavian winter the possibilities to make use of the sun are often absent or of short duration. Even when the sunshine hours are not a limiting factor, the sunning behaviour can of necessity extend over only a relatively small part of a bird's working day, but the idea that short periods of relief from a constantly high energetic load may be of importance, seems worth consideration. Lawrence (1958) gives a vivid description of the sunning behaviour of Black-capped Chickadees *Parus atricapillus* in the Canadian (46° N) winter especially after very cold nights (-30 °C). 'It seemed as if the acquisition of some warmth from this external source of heat was essential before the chickadees could throw all their effort into feeding'. For an actively foraging bird the effect of sunshine may not be as high as for a sunning bird, but during longer periods the overall gain by the accumulated

effect of many brief periods of sunning may be high.

Grubb (1976) observed that windy conditions were more clearly avoided by Carolina Chickadees *Parus carolinensis* under cloudy conditions than under conditions with sunny weather. Wachob (1996) studied the Mountain Chickadee *Parus gambeli* and compared its preference for sunny sites that were either sheltered or not, and found that the sheltered sites were preferred.

The importance of solar radiation for birds in the winter is most evident where low air temperatures are combined with a clear sky and rather long days (Huertas & Diaz 2001, Carrascal et al. 2001). In Spanish mountain forests the abundance of birds in the winter was strongest in those parts of the forest where the availability of sunlit patches on the tree trunks was highest (Huertas & Diaz 2001). The relationship between abundance and solar radiation was very strong for the Short-toed Treecreeper *Certhia brachydactyla* and gradually less, in that sequence, for the Coal Tit *Parus ater*, the Crested Tit *P. cristatus*, the Nuthatch *Sitta europaea*, and the Great Spotted Woodpecker *Dendrocopos major*.

Among these species the Treecreeper is the only purely insectivorous and also the smallest one. Foraging Treecreepers had a preference for sun-exposed tree trunks when air temperatures were low but with air temperatures above 9 °C there was an increasing avoidance, i.e. they visited the sunlit patches less often than would be expected with a random choice. Carrascal et al. (2001) conclude that the birds avoid these sites because the thermal benefits are counteracted by predation risks. By sampling the arthropod fauna they could conclude that a reduced availability of prey on the sunlit sites can only to a minor degree explain a decrease in the treecreeper's preference for these sites with increasing air temperature. Remarkably, the authors do not discuss the possibility that a continuous stay in the sun may be experienced as thermal stress that the birds should avoid.

Though the predation theory is plausible enough, it is hard to imagine that the thermal conditions on, or close to, the bark of the pine trees would not significantly affect both the treecreepers and the arthropods that they eat (Stoutjesdijk 1977, Nicolai 1980). Carrascal et al. (2001) measured the temperature of dummies, clad with the plumage of a Treecreeper, and of black cylinders of the same size. Both had average excess temperatures of 14.6 °C with a standard deviation of 6 °C. This makes it quite possible that locally the operative temperature was well over 30 °C when the air temperature was 9 °C.

The fact that avoidance because of heat stress may come into play here is supported by the work of Clark (1987) who found that for Starlings *Sturnus vulgaris* there was a gradually increasing avoidance with operative temperatures over 31 °C.

In conclusion it may be said that quite elementary physical constraints may govern the life of a bird in its natural environment when it lives 'Close to the edge' (Piersma 1994). At a safe distance from this (energetic) edge many other aspects come into play.

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## Sammanfattning

### *Fåglar i kyla: Effekterna av fjäderskrudens struktur och omgivningen på den effektiva temperaturen, studerad med sfäriska modeller*

När en liten fågel under en kall vinterdag burrar upp sig som en fjäderboll kan man ju fråga sig hur mycket ”levande fågel” det egentligen finns innanför? Eftersom fåglar är jämnvarma organismer kan man se dem som en kärna av levande materia som behöver hålla en konstant temperatur t.ex. 40 °C och för detta har en yttre isolering av fjädrar. En annan men närliggande fråga är då hur mycket energi detta kostar i relation till lufttemperatur, vind och strålning och vilken betydelse isoleringens (d.v.s. fjäderdräktens termiska egenskaper) då har. För en rund sfär är detta inte svårt att beräkna och frågan blir då istället i vilken utsträckning en sån modell kan representera en levande fågel från termisk synpunkt.

Jag uppskattade volymen av fri levande fåglar genom att fotografera dem i profil och sedan jämföra fotografiet med en kula av känd storlek som fotograferades med oförändrad inställning av linsen. Jag antog då att fågeln är en rund, avlång kropp, t ex oval eller äggformad. För att beräkna volymen av en sådan kropp tänker man sig att man skär den i runda skivor lodrätt genom längsaxeln. Om till exempel volymen av en talgoxe bestämdes till 90 cm<sup>3</sup> och vikten till 18 g så antog jag att den kunde representeras av en sfärisk modell med en kärna av 18 cm<sup>3</sup> och en inre radie,  $r_i$ , av 1,62 cm, omgiven av en isolerande mantel så att det hela formade en sfär med en yta av 90 cm<sup>3</sup> varvid ytterradien,  $r_u$ , blev 2,78 cm. Värmeförlusten av en sån modell kan skrivas som:  $C_0 (t_b - t_a)$  där  $t_b$  är temperaturen i kärnan,  $t_a$ , lufttemperaturen och strålningen har försumbar betydelse.  $C_0$  beräknades för stillastående luft under det försiktiga antagandet att den specifika värmeledande förmågan i fjäderdräkten är den lägste som kan förekomma i tekniska eller naturliga material.

Linjerna i nomogrammet (Figur 1) visar sambandet mellan kärnvolumen i cm<sup>3</sup> (alternativt vikt i g) och  $C_0$ , den totala konduktansen i W per °C, för modeller med en kvot  $r_u/r_i$  mellan 1,2 och 2,0. Om vikten och det fotografiska uppskattade värdet av  $r_u/r_i$  av en fågel placeras i nomogrammet, kan värdet av  $C_0$  avläsas. Nomogrammet visar också trendlinjer för sambandet mellan vikt och  $C_0$  beräknade från litteraturvärden. Dessa i sin tur kommer från metaboliska mätningar i laboratorier under förhållanden (temperatur ca. 0 °C och svag luft rörelse) som gör dem jämförbara med de data jag presenterar här. Överensstämmelsen är god och avvikelserna går i den riktning som kan

förväntas. De minsta fåglarna har den relativt sett tjockaste fjäderdräkten, ofta kan en kvot  $r_u/r_i$  på 2,0 uppnås (Figur 1). En ytterligare ökning av  $r_u/r_i$  över 2,0 är föga effektivt.

Jag har använt en enkel fysisk modell för att karakterisera de termiska förhållandena för små tättingar som övervintrar i den boreala skogen. För en modell med en kärnvolum av  $12 \text{ cm}^3$ ,  $r_i = 1,42 \text{ cm}$ ,  $r_u = 2,67 \text{ cm}$ ,  $C_0 = 0,0152 \text{ W/}^\circ\text{C}$  och en kärntemperatur  $t_b$  av  $40 \text{ }^\circ\text{C}$  beräknades värmeförlusten under realistiska strålnings- och temperaturförhållanden, naturligtvis med förhoppningen att komma i närheten av förhållandena för en riktig fågel.

I en naturlig situation där strålningen och vind är av stor betydelse kan ekvationen för  $C_0$  ovan fortfarande användas genom att byta ut lufttemperaturen ( $t_a$ ) mot den sk operativa eller effektiva temperaturen ( $t_e$ ) som kan ses som temperaturen som fågeln faktiskt upplever. Under förutsättning att den fysiska modellen är svart kan man använda temperaturer uppmätta i en lika stor svart kula av tunn metall som  $t_e$  i ekvationen. Sådana temperaturer bör vara mycket användbara för att karakterisera den termiska miljön för en levande fågel. Figur 2 visar bl a hur temperaturen av en svart kula ( $2r_u = 5,8 \text{ cm}$ ) är  $12 \text{ }^\circ\text{C}$  högre än lufttemperaturen när solen står  $10^\circ$  över horisonten. Värdet är ganska typiskt för en stilla vinterdag med en molnfri himmel och en klar atmosfär.

Under samma förhållanden men med mycket reflekterad strålning från en brant snötäckt slutning kan temperaturskillnaden,  $\Delta t$ , vara över  $20 \text{ }^\circ\text{C}$ . Om fågeln dessutom är i närheten av ett tätt grenverk kan detta ge ytterligare en temperaturhöjning. Om solen står högre på himlen kan  $\Delta t$  bli mycket högre. Effekten kan förstås också bli mindre om en del av solstrålningen reflekteras bort från modellens yta, men detta motverkas om det isolerande skiktet är delvis genomträngligt för solstrålning eller tunnare (Figur 3) på den sidan av fågeln som är vänd mot solen. Temperaturen i en fysisk modell kan sålunda överstiga lufttemperaturen med  $40 \text{ }^\circ\text{C}$  utan värmeförlust infifrån (Figur 4).

Om  $t_e$  är ca.  $20^\circ$  över  $t_a$  är minskningen i energiförbrukning lika stor som basalmetabolismen hos en tätting på  $12 \text{ g}$ , och det är rimligt att anta att  $t_e$  skulle kunna vara mer än  $30 \text{ }^\circ\text{C}$  över  $t_a$  för en solbadande fågel. Det är möjligt att effekten på den totala energibudgeten är liten under de korta midvinterdagarna i Skandinavien. Däremot kan den vara avsevärd under vårvintern när långa dagar kombineras med låga lufttemperaturer.

Det är också klart att redan med en lufttemperatur

av  $10 \text{ }^\circ\text{C}$  kan den effektiva (upplevda) temperaturen överstiga den optimala så mycket att små fåglar måste undvika längre vistelser i solen.

## Appendix

The energy fluxes to and from the outer surface of an insulated spherical model (outer radius  $r_u$ ) of which the core (radius  $r_i$ ) is kept at a constant temperature  $t_b$ , are shown in Figure 3. In a state of equilibrium with the environment, the heat flow from the core to the outer surface, with temperature  $t_s$ , can be written as:

$$M = a_{con}(t_b - t_s) \quad (A1)$$

where  $a_{con}$  is the conductance [ $\text{W/m}^2$ ]. For an insulated sphere we have:

$$a_{con} = \frac{r_i k}{r_u (r_u - r_i)} \quad (A2)$$

where  $k$  is the specific conductivity [ $\text{W/m}$ ] of the insulating material. At the surface the heat ( $H$ ,  $\text{W/m}^2$ ) given to the air by convection, can be expressed as:

$$H = a(t_s - t_a) \quad (A3)$$

where  $a$  [ $\text{W/m}^2 \text{ }^\circ\text{C}$ ] is the coefficient of convective heat transfer,  $a$  decreases with size and increases with air movement (cf. Stoutjesdijk & Barkman 1992). The surface receives radiant (short-wave) energy from the sun, it emits long-wave (heat) radiation and receives long-wave radiation from the sky and the surroundings. The sum of the incoming and outgoing radiation fluxes is called the net radiation:  $R_{net}$  [ $\text{W/m}^2$ ].

At the surface the sum of  $M$  and  $R_{net}$  is given to the air by convection:

$$H = \alpha(t_s - t_a) = M + R_{net} \quad (A4)$$

$M$  can be negative i.e. directed inward. It is convenient to write:

$$R_{net} = R_{net a} - \alpha_{rad}(t_s - t_a) \quad (A5)$$

where  $R_{net a}$  is the value  $R_{net}$  would have when the surface was at air temperature and  $\alpha_{rad}$  the increase of the emitted long-wave radiation when the surface temperature increases by one  $^\circ\text{C}$ . For a black heated model and an unheated black bulb of the same size in the same situation  $R_{net a}$  is equal. With help of the equations A1 to A5 the heat loss from the core ( $M$ , in  $\text{W/m}^2$ ) can be expressed in its dependence upon the environmental parameters:

$$M = \frac{\alpha_{con}}{\alpha_{con} + \alpha + \alpha_{rad}} \{ (\alpha + \alpha_{rad})(t_b - t_a) - R_{net a} \} \quad (A6)$$

Equation (A6) can be understood to describe the local situation or the average over the surface of a sphere, as is done in Figures 3a and b. For an unheated black bulb  $M=0$  when taken as an average over the sphere and the average  $t_s$  is equal to  $t_e$ , the temperature in the centre of the bulb. Furthermore:

$$t_e = t_a + R_{\text{net}} / \alpha \quad \text{or} \quad t_e = t_a + R_{\text{net}a} / (\alpha + \alpha_{\text{rad}}) \quad (\text{A7})$$

and equation A6 can be written as:

$$M = \frac{\alpha_{\text{con}}(\alpha + \alpha_{\text{rad}})(t_b - t_e)}{\alpha_{\text{con}} + \alpha + \alpha_{\text{rad}}} \quad (\text{A8})$$

Thus the temperature of a black bulb of the same size and in the same position as the heated model represents its effective temperature and it can be used to estimate  $t_e$  for a bird when allowances are made for size, reflectivity, etc. In the right hand side of equation A8, the expression:

$$\frac{\alpha_{\text{con}}(\alpha + \alpha_{\text{rad}})}{\alpha_{\text{con}} + \alpha + \alpha_{\text{rad}}} \quad (\text{A9})$$

is called  $C_{\text{os}}$  [ $\text{W}/\text{m}^2 \text{ } ^\circ\text{C}$ ] hereafter. The overall thermal conductance as commonly used, for the whole bird, can be written in the present notation as:  $C_o = S \cdot C_{\text{os}}$  [ $\text{W}/^\circ\text{C}$ ] where  $S$  is the surface in  $\text{m}^2$ .

From equations A2, A6, A8 and A9 it can be understood that though  $C_{\text{os}}$  can be strongly reduced, via  $\alpha_{\text{con}}$ , by increasing the insulation thickness ( $r_u - r_i$ ), this affects  $C_o$  much less, because  $S$  is proportional to  $r_u^2$ , especially when  $\alpha_{\text{con}}$  is small compared with ( $\alpha + \alpha_{\text{rad}}$ ) and  $r_u/r_i > 2$ .

$C_{\text{os}}$  is not very sensitive for wind velocity via  $\alpha$  since  $\alpha$  occurs both in the numerator and the denominator and  $\alpha_{\text{con}}$  usually is rather small in comparison with  $\alpha$  and  $\alpha_{\text{rad}}$ . Thus, with  $t_e = t_a$  and as long as the wind does not penetrate into the plumage, which increases  $\alpha_{\text{con}}$ , there is only a weak effect on  $M$ . When, however,  $t_e$  is much higher than  $t_a$ , that is with strong sunshine, the wind effect (via  $\alpha$ ) is much stronger (cf. equation A7). A penetration of the plumage seems to occur only when the wind velocity exceeds several m/sec (cf. Bakken 1990, Wolf & Wealsberg 1996).

The simplification of averaging the fluxes over the surface of the model is only permissible when the model is fully symmetrical. When the insulating properties of the coat are not evenly distributed over

the sphere its orientation to the sun is important. Intuitively, and with the help of equations A6 and A8, it can be understood that when the heat enters easily (high  $\alpha_{\text{con}}$ ) on the sunny side and has difficult (low  $\alpha_{\text{con}}$ ) to leave on the shadowside the effect of solar radiation will be strongest (see Figure 3). The same reasoning applies when the solar radiation is more effective on one side because it penetrates the plumage (Stoutjesdijk 2002). The general relations are illustrated by some numerical data derived from measurements (Figure 3).

The conductance  $\alpha_{\text{con}}$  is  $1.7 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ , calculated from (eq. A2) with  $r_u = 2.67 \text{ cm}$ ,  $r_i = 1.42$  and  $k = 0.04 \text{ W}/\text{m}$ . After Gavhed et al. (2003),  $\alpha_{\text{con}}$  of the 'Finnish winter military ensemble' is  $2.4 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ . The average short-wave radiation absorbed is  $319 \text{ W}/\text{m}^2$ . The long-wave radiation absorbed is  $265 \text{ W}/\text{m}^2$  and the emitted long-wave radiation at the black bulb temperature ( $18 \text{ } ^\circ\text{C}$ ) is  $407 \text{ W}/\text{m}^2$ . The emitted long-wave radiation at an air temperature of  $0 \text{ } ^\circ\text{C}$  would be  $315 \text{ W}/\text{m}^2$  i.e.  $92 \text{ W}/\text{m}^2$  less. Consequently  $R_{\text{net}}$  is  $177 \text{ W}/\text{m}^2$  and  $R_{\text{net}a}$  would be  $269 \text{ W}/\text{m}^2$ ,  $\alpha_{\text{rad}} = 92/18 = 5.1 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$  and from equation A7 we get an  $\alpha$  of  $9.8 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ . From these data  $M$  (eq. A8, Figure 3a) and  $C_o$  (eq. A9) can be calculated.

With a very stable atmosphere typically when the surface of the snow is colder than the air above it and the elevation of the sun low ( $10\text{--}15^\circ$ ),  $\alpha$  can be as low as  $8.0 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ . As furthermore  $\alpha_{\text{rad}}$  decreases with temperature the relatively strongest effects on  $t_e$  can be expected on clear cold winter mornings (eq. A7).

In Figure 3c a spherical model which over 20% of the surface had a doubled value of  $C_{\text{os}}$  ( $3.0 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ ) is placed with this segment directed to the sun. The total received short-wave radiation is split up in the part received by the high-conductance segment ( $825 \text{ W}/\text{m}^2$ ) and the rest of the sphere ( $192 \text{ W}/\text{m}^2$ ). The average over the whole sphere is still equal to  $319 \text{ W}/\text{m}^2$ .

In Figure 3d the segment directed to the sun has the same  $C_{\text{os}}$  ( $1.5 \text{ W}/\text{m}^2 \text{ } ^\circ\text{C}$ ) as the rest but the solar radiation penetrates the plumage to an average of 25% of its depth. In Figure 3c and Figure 3d  $M$  is calculated separately for the two parts of the sphere and thus the heating power needed to keep it at a constant temperature or the equilibrium temperature reached by the passive model.