BIOPHYSICAL ECOLOGY OF THE BARN OWL

(*Tyto alba* Scopoli)

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A thesis submitted for the degree of Doctor of Philosophy
to the University of Edinburgh

Declaration
This thesis has not been submitted in any other form and is the result of my own work and composition

ABSTRACT

Severe weather conditions have previously been reported to increase the energy requirements of the barn owl (*Tyto alba*) and contribute to high mortality rates and reduced breeding success of barn owl populations in SW Scotland. In this study, the effect of weather on the metabolic rate of the barn owl was examined using a heat transfer model in a wind tunnel. Conductance of plumage increased linearly with increasing wind speed, such that from 0 to 2 ms^{-1}, typical of barn owl habitat, conductance increased by 20 %. Boundary layer resistance decreased rapidly with wind speed and was described using relationships derived from heat transfer theory. Sensible heat loss increased linearly with wind speed, equal to a rise of 18 % from 0 to 2 ms^{-1}. Wetting the plumage reduced coat resistance by 10 % at all wind speeds and combined with evaporation, heat loss increased by 34 %. Infra red thermography of a live barn owl in captivity indicated that areas of highest surface temperature were on the head, around the eyes, overlying flight muscles, and the area corresponding to the brood patch. Similar surface temperature distributions were also found to occur on the great grey owl (*Strix nebulosa*) and the snowy owl (*Nyctea scandiaca*).

The effect of weather on prey availability was considered by examining the energetics of the field vole (*Microtus agrestis*). A heat transfer model of a vole showed heat loss to increase linearly with wind speed, owing to boundary layer effects and by evaporation following wetting of the coat. The microclimate of vole habitat suggested, however, that voles were sheltered from wind and rainfall, and insulated from low temperatures with snow cover.

The microclimate of a roost / nest site of a pair of barn owls was recorded from December 1990 to April 1992. Barn owls were estimated to make metabolic savings of 18 % by roosting in a building at night and 21 % during the day, when compared with the open. Greatest heat losses of 3 x BMR occurred on wet, windy, cold conditions and during periods of snow cover. By roosting in the building on these occasions, barn owls were predicted to reduce heat loss by as much as 37 %. From January to May, owls occupied the roost for 81 - 98 % of the daytime and 45 - 51 % of the night. Roosting behaviour was in partial response to high rates of heat loss. On windy nights, however, barn owls were absent from the roost for 18 % more of the night than on calm nights, suggesting that foraging was prolonged in high winds. Combining biophysical estimates of heat loss, roosting behaviour and flight costs, the energy requirement of barn owls was estimated to be 332 - 428 $kJday^{-1}$. This was equivalent to a daily intake of 3 to 4 field voles which was also suggested by 2.5 - 3.7 exits from the roost each day. Finally, the metabolic rate of barn owls was examined with respect to mortality, reproduction, and distribution of this species.

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SYMBOLS

ROMAN ALPHABET

A	Surface area (m^2)
a	Temperature gradient through coat (^oC)
a_l	Long wave absorptivity
a_s	Short wave absorptivity
C	Convective heat loss (Wm-2)
C_p	Specific heat capacity ($Jkg^{-1}K^{-1}$)
d	Characteristic dimension (m)
E	Rate of evaporation (g H_2O $m^{-2}s^{-1}$ or g H_2O body $mass^{-1}hour^{-1}$)
e	Partial pressure of water vapour in air
F	Flow rate ($lmin^{-1}$)
F_{12}	Shape factor for radiative exchange between surfaces 1 and 2
f	Fractional area of feather composed of solid material
G	Sensible heat loss (Wm^{-2})
$\overline{G}$	Mean heat flux density from the model (Wm^{-2})
Gr	Grashof number (dimensionless)
g	Gravitational acceleration (9.8 m^2s^{-1})
h	Heat transfer coefficient ($Wm^{-2}K^{-1}$)
k	Thermal conductivity ($Wm^{-1}K^{-1}$)
k_r	Radiative conductivity of the coat ($Wm^{-1}{}^oC^{-1}$)
L	Long wave radiative exchange (Wm^{-2})
L_{abs}	Long wave radiation absorbed (Wm^{-2})
l	Length; coat depth (m)
M	Metabolic rate (Wm^{-2})
m	Mass (kg or g)
Nu	Nusselt number (dimensionless)
n	Number of feather layers per unit depth of coat (cm^{-1})
p	Interception function of coat (cm^{-1}): probability that radiation in the direction of the coat surface will be intercepted by a coat element.
R	Electrical resistance (Ohms)
r	Thermal resistance (sm^{-1}): total resistance to sensible heat loss, r_{tot}; boundary layer resistance, r_a; environmental resistance, r_e; tissue resistance, r_s and coat resistance, r_c. The coat resistance is defined by the resistance to molecular diffusion within the coat, r_d; resistance to conduction through coat elements, r_{cc}; resistance to free convection in

	the coat, r_f and the resistance to radiative transfer within the coat, r_{cr}. The resistance to water vapour transfer r_{va}
r_1	Radius (m) of model at position 1
Re	Reynolds number (dimensionless)
R_n	Net Radiation (Wm^{-2})
R_{ni}	Net isothermal radiation (Wm^{-2})
$\overline{S}_{abs}$	Total solar radiation absorbed (Wm^{-2})
S_b	Direct solar radiation on a horizontal surface (Wm^{-2})
$\overline{S}_b$	Direct solar radiation absorbed (Wm^{-2})
S_d	Diffuse solar radiation on a horizontal surface (Wm^{-2})
$\overline{S}_d$	Diffuse solar radiation absorbed (Wm^{-2})
S_t	Total solar radiation on a horizontal surface (Wm^{-2})
T	Temperature (°C or K): air temperature, T_a ; core body temperature, T_b ; coat temperature, T_c ; equivalent blackbody temperature, T_e ; surface temperature of skin ; T_s; radiative temperature of environment, T_r ; radiative temperature of coat, T_{rc}
T_0	Temperature at time = 0 (°C)
T_t	Temperature at time t (°C)
$\overline{T}$	Mean radiative temperature of coat (°C); area weighted mean temperature of IR image (°C)
$\overline{T}_c$	Mean coat temperature (°C)
t	Penetration depth of wind in coat (cm or mm)
u	Wind speed (ms^{-1} or cms^{-1})
V	Voltage (Volts)
z	Thickness (m)

GREEK ALPHABET

β	Coefficient of volumetric expansion of air (K^{-1})
δ	Thickness of laminar boundary layer (m)
δT	Temperature difference (°C)
ε	Emissivity
κ	Thermal diffusivity of dry air (m^2s^{-1})
λ	Latent heat of vapourisation of water (Jkg^{-1})
υ	Kinematic viscosity of dry air (m^2s^{-1})
ρ	Density of dry air (kgm^{-3})
ρ_s	Reflection coefficient / albedo of surface

σ	Stefan - Boltzmann constant (5.67×10^{-8} Wm^{-2}K^{-4})
τ	Thermal time constant (s)
τ_a	Turbidity coefficient of the atmosphere
ϕ	Radiative angle of view (°) between a line drawn for an object to the centre of a surface and the normal to that surface.
φ	Solar elevation (°)
ω	Ratio of actual to potential evaporation rate

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CHAPTER 1

INTRODUCTION

The barn owl (*Tyto alba*) is one of the most widely distributed owl species in the world with a total of 35 classified subspecies. Detailed reviews on the barn owl have been made by Bunn *et al* (1982) and more recently from long term studies by Taylor (in press). The subspecies present in Britain is *Tyto alba alba* which in Scotland breeds at its most Northerly distribution in Europe. Although there are occasional records of barn owls breeding up to 450 m above mean sea level in Northern England (Coombes, 1933), the altitudinal distribution generally extends to around 300 m. Barn owls nest in disused farm buildings, cottages, and in natural cavities such as tree holes and occasionally amongst rocks or cliffs. Suitable nest sites are present in lowland farmland and young forestry plantations where there is rough grassland which supports high densities of small mammals. Barn owls are specialised predators which depend principally on the field vole (*Microtus agrestis*) and the common shrew (*Sorex araneus*) in Britain. Field voles represent 50 to 60 % of the weight of prey eaten, but the diet will include several other species of small mammals where present and not uncommonly, small birds and bats. They obtain their prey by a highly specialised hunting strategy which involves techniques of perch and flight hunting. Areas of suitable habitat along the edges of fields and watercourses are favoured foraging areas. Barn owls may use fence posts for initial selection of suitable areas, followed by silent flight hunting. Prey are located almost entirely by sound before rapid pounces are made from 1 - 3 m above the ground.

Interest in the energetics of barn owls has arisen from studies that have implicated severe weather as being an important factor affecting foraging activity, leading to high mortality rates and poor breeding success (Bunn *et al*, 1982). Although not often examined in detail, these ideas have come from a large number of recorded deaths of barn owls during periods of snow cover and low temperatures (Errington, 1931; Speirs, 1940; Stewart, 1952; Honer, 1963; Marti and Wagner, 1985 and Taylor, in press). The effects of severe weather conditions on barn owls can be seen from the higher mortality of first year birds and adults over winter compared with other times of the year (Glue, 1973 and Taylor, in press). However the year to year variation in mortality rates of Scottish barn owls was not correlated with any weather variables (Taylor, in press). There is evidence that exceptionally severe winters with a large number of snow days does reduce the subsequent breeding population. Following the extreme winter of 1978 / 79, Taylor (1992) recorded a 40 % reduction in number of breeding pairs. The reduction was correlated with altitude such that from 150 - 300 m above sea level, the decline in breeding pairs was as high as 65.5 %. Studies in North America also indicate that barn owls living in the Southern states have lower mortality rates than in North Eastern states, implicating the harshness of winter as the causal factor (Henny, 1969).

The timing of laying is also known to be dependent on vole abundance and temperature immediately before breeding (Taylor, in press). The energy reserves required by the laying female are dependent on the foraging success of the male and on the female's own metabolic rate, both of which may be affected by low temperatures and associated weather variables at this time. Energy reserves may be critical at other times of high energy demands and it has been reported that European barn owls have only small fat deposits: 5.5 % of body weight compared with 10.0 % for tawny owls (*Strix aluco*) and 13.4 % for long eared owls (*Asio otus*), (Piechocki, 1960). It has also been suggested that barn owls are poorly insulated compared with other owls (Johnson, 1974).

Biophysical ecology has developed as one approach to examine the behaviour, reproduction and distribution of animals within ecosystems and is based upon a thorough understanding of the sciences of energy and fluid flow, mass exchange, chemical kinetics and other processes. By representing these specific processes with simple mathematical formulations, biophysical ecology has become an important method of placing ecological theory, experiment and observation into a coherent framework (Gates, 1980).

Procedures developed in physics and engineering have enabled the principles of energy exchange between an animal and its natural environment to be represented by appropriate equations for the transfer of sensible and latent heat. This approach has often been used to determine the metabolic response of animals to combinations of environmental variables (e.g. Porter and Gates, 1969; Morhardt and Gates, 1974; Bakken, 1976; Campbell, 1977; McArthur, 1981 and Monteith and Unsworth, 1990) and in particular for avian species by Robinson *et al* (1976), Mahoney and King (1977) and Hayes and Gessaman (1982). Heat transfer models developed in studies such as these provide a framework to examine the environmental variables which bring about thermal responses in animals. In this respect it is important to group together such variables as temperature, wind speed, humidity, thermal and solar radiation as the microclimate of an animal. Microclimate is therefore seen as the set of environmental conditions immediately surrounding an animal which directly influence exchanges of sensible and latent heat. Combined with a knowledge of physiological processes, biophysical models extend simple laboratory measurements of metabolism to an understanding of the animal's metabolic response to the simultaneous interaction of temperature, wind, humidity and radiation within the natural environment.

The thermal environment of owls can generally be divided according to the activity pattern at night and by the daytime roosting period. For temperate species, the cold nocturnal conditions impose high metabolic demands for heat production. Periods of elevated metabolism require high rates of food consumption and depletion of energy reserves. This may have immediate consequences for the allocation of energy to activities such as foraging and reproduction and limit energy reserves needed at times of food shortage. In comparison, inactivity in sheltered roost sites has distinct thermal advantages. The energetic consequences of nocturnal activity and daytime roosting patterns in owls is as yet poorly understood and therefore requires investigation.

The aim of this study was therefore to determine the effect of environmental conditions on the metabolic cost of heat production and thereby evaluate the exchange of energy between a barn owl and the natural environment. It was hoped that this would help to examine variations in mortality, breeding success and distribution of this species, which appear to be associated with severe weather conditions.

The approach taken was to develop a biophysical model of heat loss. This was carried out by examining the thermal properties of barn owl plumage according to wind speed, temperature, and wetting by rain. This gave a detailed understanding of the mechanisms of heat transfer within avian plumage and the opportunity to compare estimates of heat loss with metabolic studies (Chapter 2). The nature of energy exchange was further examined using infra red thermography, as a method of assessing significant sites of heat loss in barn owls and the effects of activity on heat exchange. Food availability during periods of severe weather was also examined by considering the energetics of the field vole and establishing how microclimate and weather conditions may determine field vole activity and hence, prey availability (Chapter 4). Energy exchanges within the environment were then investigated by measuring the microclimate of a frequently used roost and nest site of a pair of barn owls throughout the year (Chapter 5). Parameters from wind tunnel studies and infra red thermography combined with microclimate data allowed development of a biophysical model of heat loss for barn owls in the wild. This gave an estimate of the thermal value of roost sites and roosting behaviour, according to different weather conditions. Hypotheses regarding the metabolic savings associated with roosting were tested by recording the roosting behaviour of barn owls in the field (Chapter 6). Finally, the metabolic heat production of barn owls was discussed in relation to thermal resistance, roosting behaviour and weather conditions experienced by barn owls in Scotland. The influence of maintenance energy requirements on reproduction, mortality and distribution of barn owls was then considered (Chapter 7).

The study was carried out from October 1989 to June 1993 and field studies were made during the period 1989 to 1992 in South West Scotland where a population of barn owls had been extensively studied for 14 years by Taylor (in press). Investigations were based on a winter roost and nest site of a pair of barn owls at an altitude of 300 m above sea level, which was the highest recorded breeding site for this population. The site was located in a small river valley within the area of Eskdalemuir Forest and the roost site was a disused stable made from corrugated iron (Figure 1.1). The building was positioned on the edge of a fire break within a plantation of sitka spruce (*Picea sitchensis*), with trees approximately 8 m in height. Suitable rough grassland habitat was available in the fire breaks and extensively around the river.

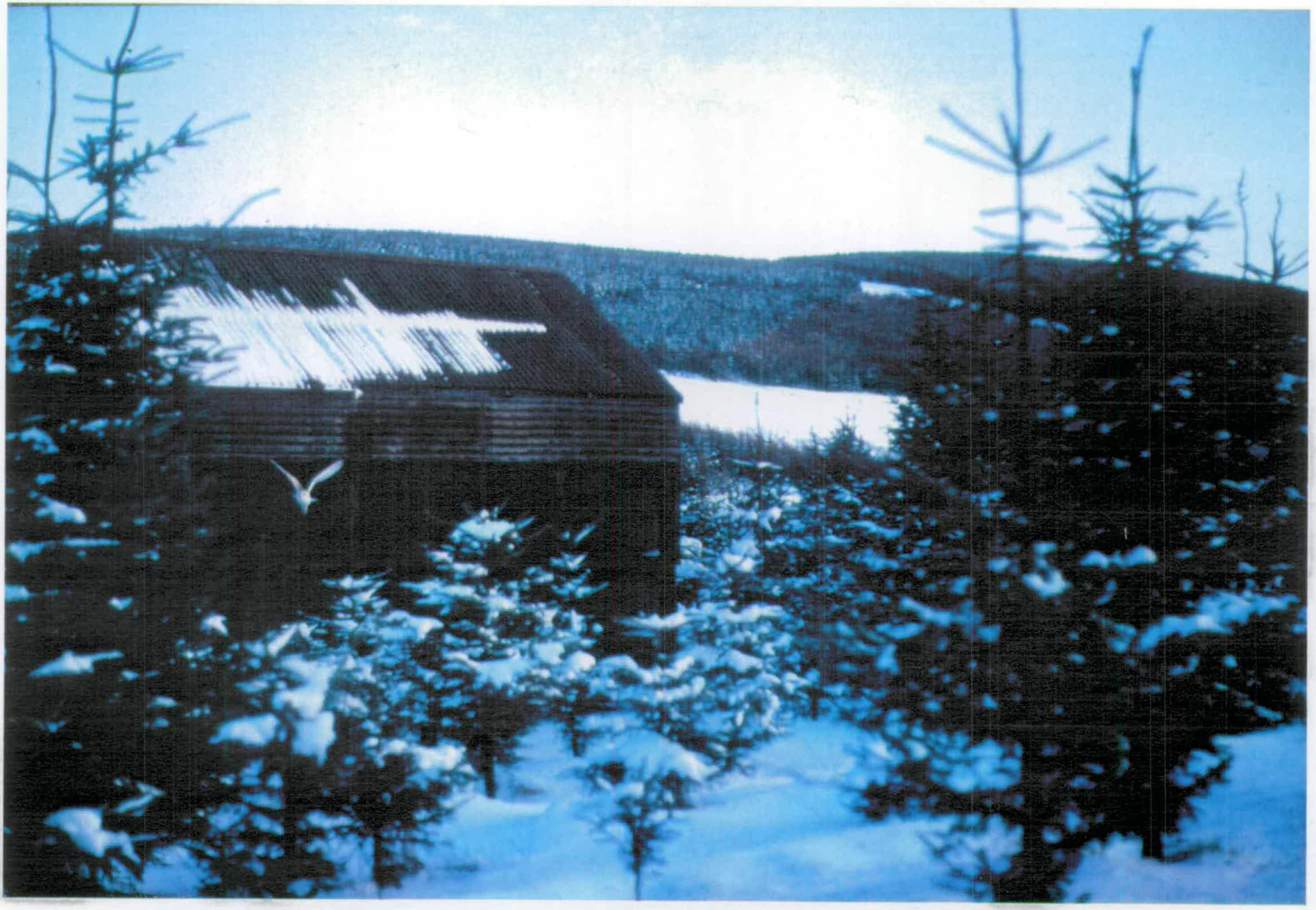


Figure 1.1 The roost and nest site of barn owls in this study. The photograph shows a male leaving the building in January 1991.

CHAPTER 2

THERMAL RESISTANCE AND HEAT LOSS FROM BARN OWLS

2.1. INTRODUCTION

2.1.1 Background

An increase in metabolic rate with decreasing temperature has been well documented for birds. The metabolic rate of barn owls as measured by oxygen consumption has been reported to increase linearly below the thermo-neutral zone by Johnson (1974), Hamilton (1983, 1985a) and Edwards (1987) and by measurement of food consumption by Marti (1973) and Hamilton (1983, 1985b). Metabolic rates have also been shown to increase significantly with increasing wind speed in the snowy owl (*Nyctea scandiaca*) by Gessaman (1972), in the long eared owl (*Asio otus*) by Wijnandts (1984), and in diurnal raptors of different body sizes (Hayes and Gessaman, 1980), but this response has not been investigated for barn owls.

The effects of wetting by rain on the metabolic rate of birds is poorly understood. For starlings (*Sturnus vulgaris*) in captivity, severe wetting resulted in increased oxygen consumption, lowered body temperatures and occasionally, in death (Lustick and Adams, 1977). More realistic studies on rooks (*Corvus frugilegus*) have, however, indicated increases in metabolism of 23 to 35 % (Swingland, 1973, 1977), while the metabolic rate of bald eagles (*Haliaeetus leucocephalus*) have shown increases of up to 26 % depending on the wetting regime (Stalmaster and Gessaman, 1984).

The metabolic response of the barn owl to changes in environmental conditions can be understood by considering the exchange of energy between an owl and its environment. Biophysical models provide a means of examining the relationship between energy exchange and environmental conditions and have been developed for raptors by Hayes and Gessaman (1982), for small birds by Robinson *et al* (1976) and Mahoney and King (1977). Sensible heat loss G ($\mathrm{Wm^{-2}}$) from a bird can be considered to occur from a homogenous bird with uniform core temperature T_b such that:

$$G = \rho C_p (T_b - T_e)/r_{tot} \tag{2.1}$$

where ρC_p is the volumetric specific heat of air ($Jm^{-3}K^{-1}$), T_e is the equivalent temperature and can be considered as an environmental temperature from the sum of air temperature T_a with radiative and convective components according to:

$$T_e = T_a + R_{ni} . \rho C_p / r_e \tag{2.2}$$

where R_{ni} is the net isothermal radiation, defined as the net radiation of a surface that is at air temperature. The total thermal resistance r_{tot} (sm^{-1}), consists of three resistances in series given by the body tissue (r_s) coat (r_c)and the environment (r_e):

$$r_{tot} = r_s + r_c + r_e \tag{2.3}$$

and where r_e consists of a boundary layer resistance (r_a) and a radiative resistance (r_r) acting in parallel (Figure 2.1), according to:

$$1/r_e = 1/r_a + 1/r_r \tag{2.4}$$

The thermal response of a bird to changes in environmental temperature, wind speed, and wetting of the plumage surface is a complex function of physiological, behavioural and physical changes. Tissue resistance is largely under physiological control of blood circulation, dilation and contraction of blood vessels and may have strong local effects on areas of the body (McArthur, 1981). The coat resistance depends on the physical properties of the feather layer and the degree to which air or water is able to penetrate the surface. The coat can however be modified by ptiloerection to increase the effective depth of insulation. Similarly the boundary layer resistance is determined by the physical shape and structure of the bird which can be altered by postural adjustments.

Using the model described above, it is possible to predict that the rate of sensible heat loss from barn owls will be driven both by changes in the temperature gradient between the body core and environment, and changes in the total resistance to sensible heat transfer. The aim of this investigation was therefore to examine the effect of air temperature, wind speed and wetting on the thermal resistance of the coat and boundary layer and thereby estimate, in the absence of physiological and behavioural modifications of total resistance, the rate of heat loss from a barn owl in response to environmental conditions.

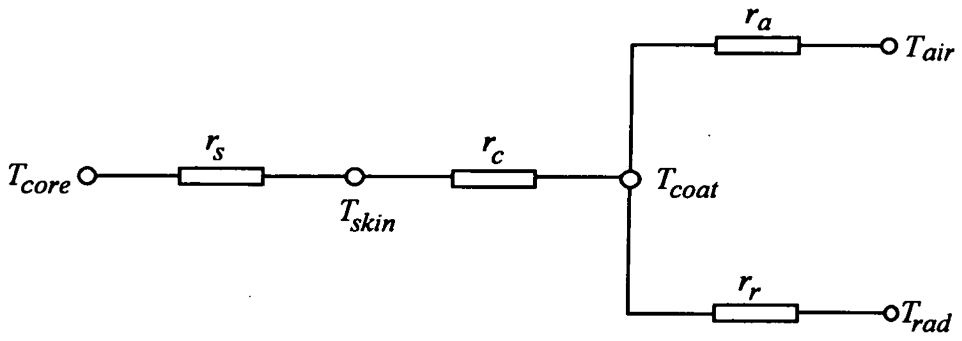


Figure 2.1. Electrical analogue of thermal resistances to sensible heat transfer from core to environment for a bird.

2.1.2 Theory

2.1.2.1 Coat Resistance

Sensible heat transfer through the coat G (Wm^{-2}), can be calculated from

$$G = \rho C_p (T_s - T_c)/r_c \qquad (2.5)$$

where T_s and T_c are the surface temperature (°C) of the skin and coat. Excluding latent heat transfer in still or slowly moving air, heat transfer through an animal's coat can occur by molecular diffusion through air contained in the coat (r_d), conduction through the coat elements (r_{cc}) by radiation (r_{cr}) and by free convection (r_f). Radiative transfer within animal coats has been shown to agree with theoretical calculations (Cena and Monteith, 1975a, 1975b) in which a radiative conductivity of the coat, k_r (Wm^{-1}°C^{-1}) was defined as:

$$k_r = 4b/3p \qquad (2.6)$$

where p is the probability per unit coat depth that a ray propagating in the direction of the upper coat surface will be intercepted by a coat element (solid portion of feather) and the variable b is calculated as:

$$b = 4\sigma\overline{T}_c^3 \qquad (2.7)$$

where σ is the Stefan-Boltzmann constant and $\overline{T}_c$ is the mean coat temperature (K).

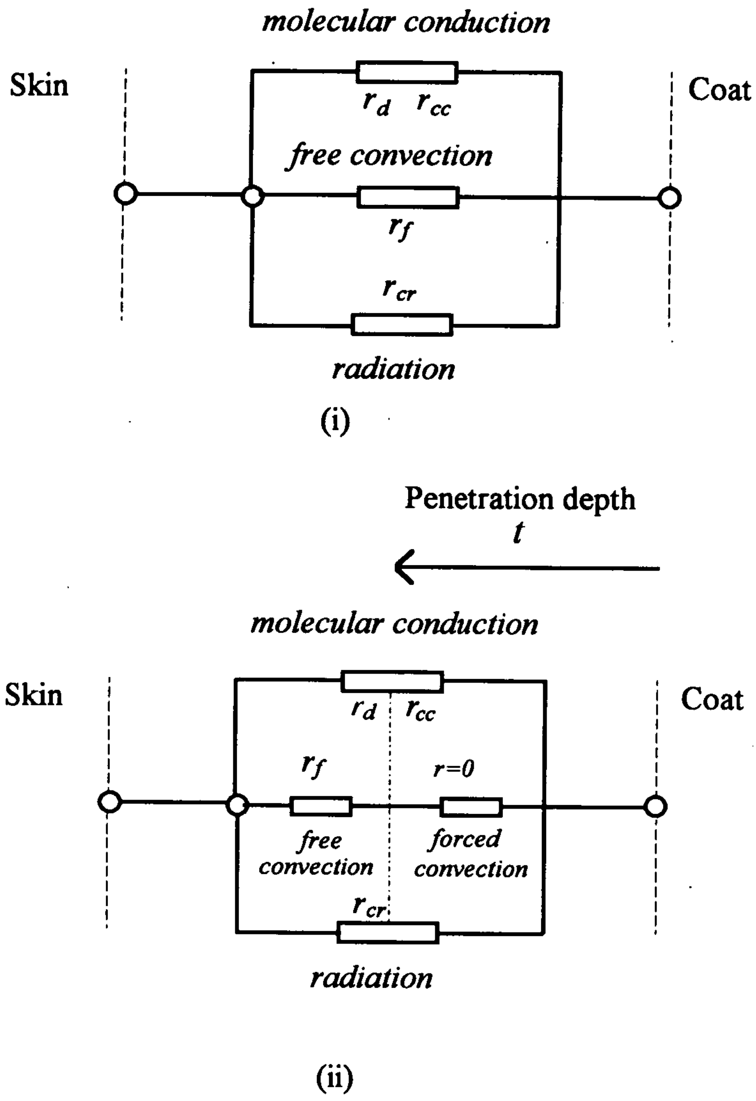


Figure 2.2. (i) Electrical analogue for sensible heat transfer through plumage in still air with resistance to conduction, radiation and free convection arranged in parallel and (ii) electrical analogue for sensible heat transfer through plumage in wind which penetrates to a depth t below the outer coat surface. Based on that of McArthur and Monteith (1980b).

The coat resistances can be regarded as acting in parallel throughout the coat in still air, but in wind, the resistance of the coat is dominated by the penetration of wind to a depth t below the outer surface (Figure 2.2). In this case, heat transfer occurs by molecular conduction in air, conduction through feather elements, radiation and free convection in a layer between the skin surface and the penetration depth; however, between this depth and the outer coat surface, heat transfer is dominated by forced convection and in this zone the resistance is effectively zero (McArthur and Monteith, 1980b).

The relationship between coat resistance and wind speed is often expressed in terms of coat conductance, $1/r_c$ (ms^{-1}) which has been found to increase linearly with wind speed, u (ms^{-1}) (Campbell *et al*, 1980) such that:

$$1/r_c(u) = 1/r_c(0) + au \tag{2.8}$$

where $1/r_c(0)$ is the conductance (ms^{-1}) in still air and a is a constant of proportionality dependent on coat type. Following this it can be shown that the wind penetrates the mean coat depth l to a depth t defined by:

$$t = lau/\{au + 1/r_c(0)\} \tag{2.9}$$

2.1.2.2 Environmental Resistance

Sensible heat transfer from the surface of the coat occurs by convection and radiation. Convective heat transfer C (Wm^{-2}) is calculated by:

$$C = \rho C_p(T_c - T_a)/r_a \tag{2.10}$$

where T_c and T_a are the outer coat surface and air temperatures respectively and r_a is the boundary layer resistance (sm^{-1}) which is provided by a layer of air which adheres to the surface by viscous forces. In still air, convection occurs by a process known as free convection, the movement of air by buoyancy forces which are set up by temperature gradients. In air flow, the loss of heat by convection is dominated by the movement of air in a weakened boundary layer, a process known as forced convection. The boundary layer resistance of an object is calculated from the relationship:

$$r_a = d/\kappa Nu \tag{2.11}$$

where d is the characteristic dimension (m) (usually taken to be the diameter of the object), κ is the thermal diffusivity of air (m^2s^{-1}) and Nu is the dimensionless Nusselt number. The Nusselt number provides a basis for comparing rates of convective heat loss and is defined as the ratio of characteristic dimension to thickness of the laminar boundary layer, d/δ. In still air where free convection is dominant the Nu number is related empirically to the Grashof number (Gr) which is the ratio of buoyant to viscous forces in natural convection and is calculated as:

$$Gr = \beta g d^3 (T_c - T_a)/v^2 \qquad (2.12)$$

where β is the coefficient of volumetric expansion of air (K^{-1}), g is gravitational acceleration (ms^{-2}), d is the characteristic dimension (m), $T_c - T_a$ is the temperature gradient between coat surface and air (°C) and v is the kinematic viscosity of air (m^2s^{-1}). Where forced convection dominates, the Nusselt number is related to the Reynolds Number which itself is a measure of the ratio of momentum and viscous forces ud/v. Relationships between Nu and Re numbers in air have been experimentally determined for many geometrical shapes and for birds can be approximated as cylinders with the form $Nu = ARe^n$ where A and n are constants of proportionality for geometry.

The boundary layer resistance acts in parallel with the radiative resistance, r_r (sm^{-1}) and therefore the radiative loss L (Wm^{-2}) is calculated from:

$$L = \rho C_p (T_{rc} - T_r)/r_r \qquad (2.13)$$

where T_{rc} is the radiative temperature of the surface and T_r is the radiative temperature of the environment (°C). The radiation flux density from a surface behaving as a black body emitter is proportional to the fourth power of its absolute temperature. The rate of heat transfer by thermal radiation is therefore given by:

$$L = \sigma\left(T_{rc}{}^4 - T_r{}^4\right) \qquad (2.14)$$

where σ is the Stefan-Boltzmann constant and T is in Kelvin. For small temperature differences the resistance to radiative transfer is approximately equal to $\rho C_p \big/ \left(4\sigma \bar{T}^3\right)$ where $\bar{T}$ is the mean of T_{rc} and T_r.

2.2. MATERIALS AND METHODS

2.2.1 Heat Transfer Model

The thermal properties of plumage and the nature of heat transfer for a barn owl was examined using a heated model which was maintained at a constant temperature by circulation of hot water through the centre and allowed samples of plumage to be fixed to the model surface (Figure 2.3). The heated section of the model was constructed from 0.5 mm copper sheet which was shaped in a pre-formed mould. Inlet and outlet pipes were soldered to the base and a platinum resistance thermometer was fitted at the back. Expanded polyurethane foam (J. Manger and Son Ltd) was fixed to the copper form to insulate around the heated section. Six Peltier heat flux transducers (see below) were fitted to the surface of the copper with epoxy adhesive and following this, the surface was covered with epoxy up to the depth of the transducers (4 mm). The model was connected via insulated plastic tubing to a thermostatically controlled water bath and a water pump allowed water at 40.4 ^{o}C (SE = 0.02) to be circulated at a flow rate of 0.36 lmin^{-1}. Water passed through a coiled copper pipe inside the water bath and then through the model before being returned to the bath.

The model was placed inside a wind tunnel with a working section of 1.6 x 0.9 x 0.7 m and with semi-automated computer control of temperature and humidity. Wind speed in the tunnel was controlled manually and measurements of wind speed were made using a pitot tube and atmospheric pressure readings. The flow regime was shown to be laminar, with a turbulent intensity of 1 % in the empty tunnel at 4 ms^{-1} (Grace , 1978).

2.2.2 Construction and Calibration of Heat Flux Transducers

Commercially available 0.32 W Peltier effect heat pumps (RS Ltd) were modified for use as heat flux transducers according to Weaver and Campbell (1985). The Peltier devices (4.2 x 4.2 x 2.7 mm) were fitted with extension wires (10 / 0.1 mm core) and were filled with epoxy resin to increase the thermal conductivity of the device.

Transducers were calibrated according to a method used for soil heat flux sensors, described by Biscoe *et al* (1977). The calibration apparatus consisted of an insulated wooden box fitted with a guard heater and filled to a depth of 20 cm with dry sand. The power dissipated by the heater provided a uniform heat flux over a total surface area of 0.07 m^2 and was controlled by a stabilised power supply such that the flux density was calculated as $current \times voltage / area$. The vertical temperature gradient through the sand was measured with thermocouples placed 2 cm apart on a 0.5 cm diameter wooden dowel and the calibration box was placed in a temperature controlled room.

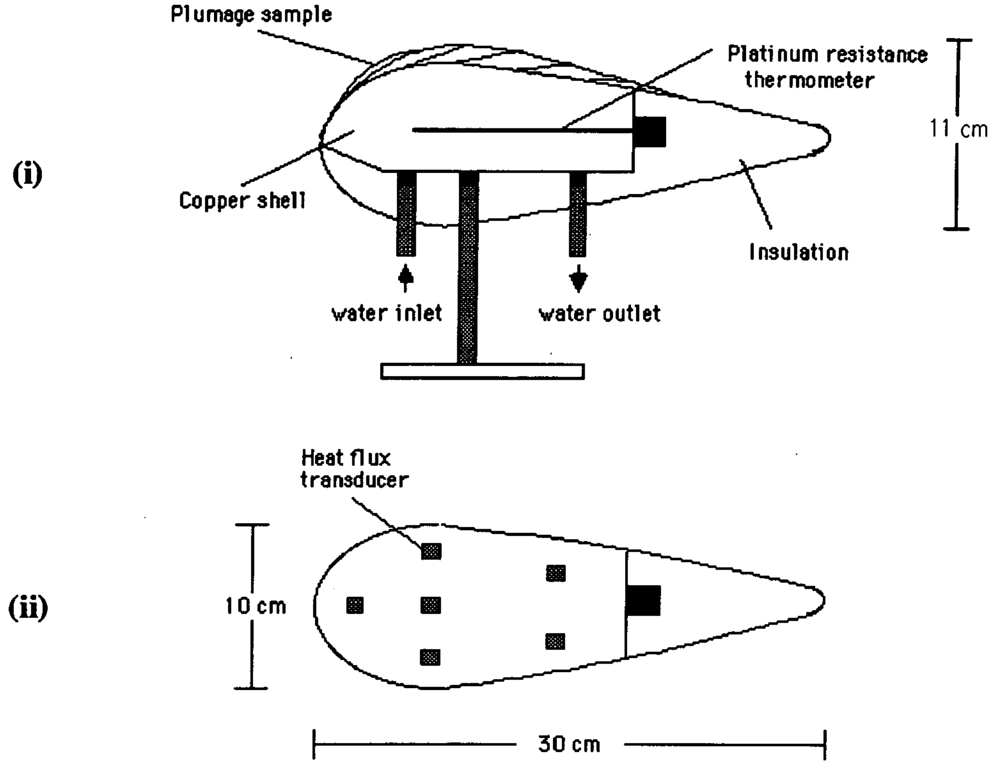


Figure 2.3. Design of heat transfer model used in wind tunnel studies to investigate the thermal properties of owl plumage: (i) side elevation and (ii) plan from above.

Peltier heat flux transducers were evenly spaced at a depth of 5 cm from the surface of the heater and were calibrated over the range 0 to 30 Wm^{-2} by recording five minute averages of voltage output from the transducers using a Campbell Scientific CR10 logger when the calibration device had reached steady state (typically 24 - 48 hours). Heater voltage and current were recorded by a portable multi-meter (Philips PM 2157X). The output from the six Peltier heat flux transducers was found to be linear giving a mean calibration coefficient at 20 °C of 509 $Wm^{-2}mV^{-1}$ (R=0.99, SE = 41.4).

The effect of temperature (11 - 32 °C) on the output from the transducers was investigated using the calibration box as above. The heat flux density was held constant at approximately 20 Wm^{-2} at a fixed air temperature and allowed to reach steady state over 48 hours. Measurements were made as before and temperature was then reset by adjusting the control temperature of the room. In this way the transducer was found to have a temperature coefficient of 0.957 $Wm^{-2}mV^{-1}{}^{o}C^{-1}$ (R = 0.98) over the temperature range.

Heat flux disturbance due to differences between the thermal conductivity of transducer and calibration medium (sand) was corrected for, according to Weaver and Campbell (1985), such that the ratio between heat flux density through sand and transducer (G_s/G_t) was calculated from:

$$G_s/G_t = 1 - 1.7(z/l)(1 - 1/R) \qquad (2.15)$$

where z and l are the thickness and length (m) of a square transducer and R is the ratio of transducer thermal conductivity to sand conductivity (0.675 $Wm^{-1}{}^{o}C^{-1}$). The thermal conductivity of the Peltier transducer was determined by measuring the temperature difference across a transducer at a steady state flux density of 20 Wm^{-2}. The temperature difference was measured by attaching a 42 s.w.g thermocouple to the upper and lower surface of the transducer using super-glue (Bostik Super Glue 4). and the thermal conductivity was found to be 1.089 $Wm^{-1}{}^{o}C^{-1}$ giving a heat flux ratio of 0.6. Including corrections for temperature and disturbance, the mean temperature adjusted calibration coefficient C_T ($Wm^{-2}mV^{-1}$) for the Peltier transducer was evaluated as:

$$C_T = c + m(T - 20) \qquad (2.16)$$

where c ($Wm^{-2}mV^{-1}$) is the calibration coefficient at 20 °C and m is the correction for transducer temperature ($Wm^{-2}mV^{-1}{}^{o}C^{-1}$). Peltier transducers had values of c between 228 and 368 with a mean of 305 $Wm^{-2}mV^{-1}$ (SE = 24.8) and m corrected as 0.574 $Wm^{-2}mV^{-1}{}^{o}C^{-1}$. In wind tunnel experiments individual calibrations were used.

2.2.3 Calibration of Heat Transfer Model

To take into account heat flux differences due to positioning of transducers and changes in calibration of transducers *in situ*, the mean heat flux from the model was determined by calibrating the model (with no coat covering). This was achieved by measuring the change in temperature δT (°C) of water entering and leaving the model with a 38 s.w.g thermocouple junction fitted to the inside of the inlet and outlet pipes. The mean heat flux density $\overline{G}$ (Wm^{-2}) from the model was then calculated from:

$$\overline{G} = FC_p\delta T/A \qquad (2.17)$$

where F is the flow rate (kgs^{-1}), C_p is the specific heat capacity of water ($Jkg^{-1}{}^oC^{-1}$) and A is the surface area of the heated section, (0.028 m^2). The surface area of the heated section was determined by approximating the non-insulated surface as a front section of a quarter of a sphere (radius r_1) and a back section of half a hollow cylinder (radius r_2, length l). The total surface area A (m^2)was then calculated from:

$$A = \pi r_1^2 + \pi r_2 l \qquad (2.18)$$

This agreed with the measured surface area which was obtained by placing aluminium foil over the surface of the model and determining the area by tracing onto 1 cm^2 graph paper.

Heat flux density calculated from the mean of the Peltier transducers overestimated the heat flux density from the model as measured by the change in temperature of water, such that the mean adjusted heat flux density from the model $\overline{G}$ (Wm^{-2}) had a calibration defined by

$$\overline{G} = 0.68G - 8.44 \qquad (2.19)$$

where G (Wm^{-2}) is the mean heat flux density calculated from the six Peltier transducers. Heat flux density through the plumage was expressed as the heat flux per unit of external plumage surface area by multiplication of the calibrated flux density with the ratio of model area to external plumage surface area. Substitution with the appropriate dimensions based on mean plumage depths gave ratios of 0.52, 0.79 and 0.65 for the front, back and total area of the model.

2.2.4 Determination of Thermal Properties of Plumage

2.2.4.1 Preparation of Plumage

Before measurements were made on plumage samples, the depth of feathers was measured on owls which had been killed on the road or had been found dead in the field. A total of nine barn owls (4 male and 5 female), one short eared owl (female) and one tawny owl (sex unknown) were examined. These specimens had been stored in a freezer at -20 °C and were selected according to undamaged plumage and minimum skeletal damage. When defrosted, the body of each owl was shaken gently and feathers fluffed and flattened gently by running a 1 mm diameter dissection needle through the plumage, to reduce the effect of compression during freezing. The plumage depth was estimated by placing the needle through the plumage and perpendicular to the feather surface. The depth was measured from the needle with callipers to the nearest 0.1 mm. Plumage depth was measured at eighteen different positions on the body where plumage was intact and in good condition. These were divided as follows:

(i) *head* : top, sides and back of head, facial ruff, front and back at base of neck
(ii) *ventral* : under wings, mid breast
(iii) *dorsal* : mid back, above tail
(iv) *legs* : tarsi, tibiae

Measurements were made on plumage lying normally and when fluffed. This was achieved by running a needle through the feathers several times and then once over the outer surface to contour the outer feathers.

Plumage samples were prepared for wind tunnel studies following standard taxidermic techniques (Metcalf, 1987). The skeleton was removed leaving only radius and ulna in the wing and tarsus and talons within the skin. All traces of blood or dirt were removed from the plumage and any conspicuous deposits of fat or remaining tissue were removed from the skin. Samples were then wrapped in damp paper before being placed in plastic bags and stored uncured in the freezer at -20 °C.

2.2.4.2 Effect of Wind Speed on Heat Transfer

The thermal properties of plumage from two male and two female barn owls, a short eared owl and a tawny owl were determined in a series of experiments using the heat transfer model. The temperature difference across the plumage was measured using differential thermocouples on the model and plumage surfaces at each of the transducer positions. At the model surface, thermocouple junctions were secured with small sections of Selotape. A thin covering of paraffin jelly was applied to the surface of the model to reduce contact resistance and the body pelage was stretched over the surface of the model and held in position with adhesive tape to the insulated section of the model. Three of the barn owl samples had wings folded over the insulated sides of the model but with the remaining sample the wings were held outstretched. No significant difference was observed between rates of heat loss because of this and therefore for analysis, these were grouped together. The depth of plumage above each of the transducers was measured as described above and the corresponding thermocouple junction was held in position on the outer feather surface. The temperature profile through the plumage in the centre of the model was measured by thermocouples mounted on a 3 mm diameter perspex rod and spaced at 2 mm intervals.

At steady state, measurements were made over a period of 10 - 20 minutes at wind speeds from 0 to 7 ms^{-1}, at air temperature of 20.4 ^{o}C (SE = 0.1) and 43 % (SE = 1.6) relative humidity. A Campbell Scientific 21X logger with a 32 differential channel multi-plexer recorded two minute averages of temperature and voltage.

Following measurements on dry plumage, the plumage was wet by spraying water (at room temperature) onto the plumage with a fine hand spray until the water began to run off the surface. Measurements were made following steady state at 20.2 ^{o}C (SE = 0.1) and 43 % (SE = 1.5) relative humidity for 10 - 20 minutes before evaporation of water caused significant changes in readings.

The effect of air temperature on heat transfer from the model was also examined with a single barn owl sample at air temperatures of -1, 4 and 10 ^{o}C with relative humidities of 83 %, 66 %, and 46 % and on a short eared owl sample at 20 ^{o}C and 10 ^{o}C (36 % RH). A repeat wetting experiment at 10 ^{o}C, 72 % RH was also carried out on this barn owl sample and the thermal properties of tawny owl plumage in still air at 20 ^{o}C, 30 % RH were also examined. The radiative temperature of plumage was examined in experiments at 10 ^{o}C using a mini net radiometer Type ME-1 (Swissteco Ltd) which was held less than 10 mm above the surface of the coat. In this way the radiative temperature of the plumage, T_r (^{o}C) was calculated by rearrangement of the equation which describes the net radiation, R_n (Wm^{-2}) at the plumage surface in the absence of short wave radiation:

$$R_n = \varepsilon_s \sigma T_{rc}^{\ 4} - \varepsilon_w \sigma T_w^{\ 4} \qquad (2.20)$$

where T_w is the radiative temperature of the wind tunnel wall surface, ε_s and ε_w are the emissivity of plumage and wall surfaces (assumed to equal 0.98) and σ is the Stefan-Boltzmann constant.

2.2.4.3 Physical Characteristics of Owl Plumage

The physical characteristics of each feather coat were determined following the methods of Walsberg *et al* (1978). The mass of feather material per unit area of coat was determined by punching out, two 1.6 cm diameter holes from dorsal (head and mid dorsal) and ventral regions of the coat. These were dried at 40 °C for 12 hours and weighed to the nearest 0.1 mg. The mass of intact down and contour feather layers were measured individually and allowed calculation of the number of feather layers per unit depth of plumage (n). The fractional area of an individual feather which was composed of solid material (f) was estimated by examining contour and down sections of head, back and ventral feathers, mounted on a glass slide and viewed at 600x magnification. An ocular micrometer in the microscope projected a linear scale of 100 onto the field of view and the fraction of feather surface area which was solid was estimated by counting the number of dividing marks which were projected onto solid structure. This was repeated 5 times at random on both down and contour regions of the feather. The product $f \times n$ was then calculated which gave the probability, p per unit coat depth that a ray propagating in a direction perpendicular to the skin will be intercepted by the feather element.

2.2.5 Determination of Nusselt Numbers

The relationship between the Nusselt and Reynolds numbers for the model was compared with that of smooth cylinders from cooling curve experiments. Newton's Law of cooling states that the rate of cooling of an object can be described by the relationship :

$$T_t - T_a = (T_0 - T_a)e^{-t/\tau} \tag{2.21}$$

where T_t T_0 and T_a are the temperature (°C) of the object at time t (s), starting temperature and air temperature respectively.

A graph of $\ln(T_t - T_a)$ against $\ln(T_o - T_a)$ has a line of gradient $-1/\tau$, where τ is known as the thermal time constant (s). The time constant depends on the thermal capacity of the object, the surface to volume ratio and the efficiency with which heat is transferred to the surroundings and is defined by:

$$\tau = mC_p/hA \tag{2.22}$$

where m, C_p, h and A are the mass (kg), heat capacity (Jkg^{o}C^{-1}), heat transfer coefficient (Wm^{-2} ^{o}C^{-1}) and surface area (m^2) respectively.

The rate of sensible heat loss from the object, G is calculated according to:

$$G = \frac{Nuk\,\delta T}{d} = h\delta T \tag{2.23}$$

where Nu *is* the Nusselt number, k is the thermal conductivity of air (Wm^{-1}^{o}C^{-1}), δT is the temperature difference between object and air (^{o}C) and d is the characteristic dimension of the object.

Cooling curves were determined for horizontally and vertically orientated aluminium cylinders in the wind tunnel. Cylinders of length 15 cm and 8 cm diameter were placed in a thermostatically controlled water bath at 40 ^{o}C. When the cylinders had equilibrated with the water, two were removed from the bath, dried and then mounted in the wind tunnel on insulated arms of retort stands. The mean surface temperature of the cylinders was measured with 42 s.w.g thermocouples secured to the surface of each cylinder (top, windward and leeward sides) with plastic tape and the cylinders were allowed to cool to air temperature. Surface temperatures, air and wind tunnel surface temperatures were recorded as one minute averages on a Campbell Scientific 21X logger and this procedure was repeated at wind speeds between 0 and 7 ms^{-1}.

Unless otherwise stated, thermocouple junctions in wind tunnel studies were made from type T copper constantan 42 s.w.g thermocouple wire (Dural Plastics and Engineering) with type T extension wires (TC Ltd). These were calibrated in a thermostatically controlled water bath against a standard platinum resistance thermometer (Guild Line).

2.3. RESULTS

2.3.1 Characteristics of Owl Plumage

For the three species examined, the plumage was thinnest overlying the legs and the plumage was thickest around the head of the barn owl and tawny owl but thickest in ventral areas on the short eared owl (Table 2.1). The mean plumage depths in these regions ranged from 9.5 - 25.1 mm on the barn owl, 9 - 22.9 mm on the short eared owl and 8.2 - 25.0 mm on the tawny owl. Comparison with the depth of fluffed plumage indicated that barn owls were estimated to increase plumage depth by 22 - 86 % on different areas of the body by ptiloerection and by 26 - 59 % for the short eared owl and 17 - 55 % for the tawny owl.

		Plumage Depths (mm)			
Species	**State**	**Legs**	**Ventral**	**Dorsal**	**Head**
Barn owl	Normal	9.5 (0.7)	15.0 (0.7)	15.9 (1.6)	25.1 (0.5)
Barn owl	Fluffed	17.7 (0.7)	27.2 (1.9)	23.0 (2.1)	30.6 (0.6)
SE owl	Normal	9.0	22.9	13.7	19.5
SE owl	Fluffed	14.3	32.2	17.6	24.5
Tawny	Normal	8.2	21.3	20.8	25.0
Tawny	Fluffed	12.7	30.4	24.4	38.1

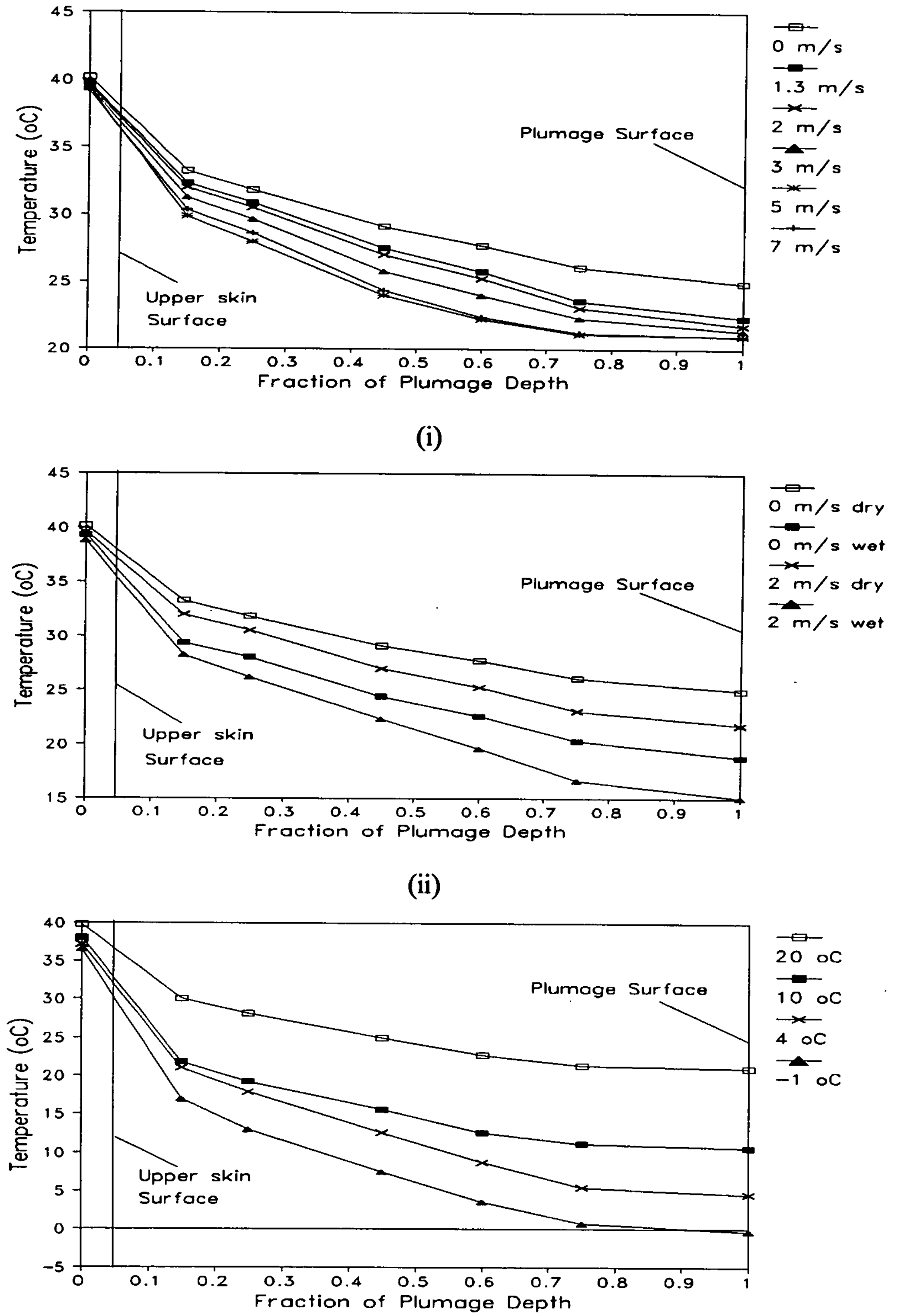
Table 2.1. Plumage depths of the barn owl (n = 9), short eared owl (n = 1) and tawny owl (n = 1) in normal and fluffed coat states. Standard errors are given in brackets.

Barn owl coats in wind tunnel studies consisted of 34.9 mg cm^{-2} (SE = 1.9) of feathers overlying the skin surface in 23 (SE = 1.65) feather layers per cm of coat depth. Each layer consisted of 0.61 (SE = 0.03) of solid material which gave an estimated probability (p) of 14.2 (SE = 0.9) per cm of coat depth, that a ray propagating in a direction perpendicular to the skin will be intercepted by a feather element. Plumage sampled from head, ventral and mid-dorsal areas indicated that despite the greater thickness of plumage around the head, this area had a smaller number of feather layers, (21) with p equal to 12.2 cm^{-1} than plumage from the mid-dorsal area which was thinnest but had the greatest number of layers, (31) and with p equal to 20 cm^{-1} (Table 2.2).

Short eared owl and tawny owl coats were found to have a similar mass and number of layers of feathers per cm of coat depth as barn owl coats. The fraction of each layer which was solid was found to be higher in these coats, 0.81 and 0.74 in short eared and tawny owl resulting in higher interception probabilities of 20.2 and 22.2 $\mathrm{cm^{-1}}$ respectively. The variation in coat characteristics of the tawny owl was also similar to that found in barn owls with the highest number of feather layers and highest interception function on the mid-dorsal region and the lowest at the head. The short eared owl coat did not show this pattern and had 63 layers of feathers per cm of coat, which was most probably due to measuring the mass of only one feather layer from the head plumage.

	Depth cm	**Mass/Area** $\mathrm{mg\ cm^{-2}}$	**Mass/Layer** $\mathrm{mg\ cm^{-2}}$	n $\mathrm{cm^{-1}}$	f	p $\mathrm{cm^{-1}}$
Mean Plumage Characteristics						
B owl (4)	2.0 (0.13)	34.9 (1.9)	0.74 (0.05)	23	0.61 (0.03)	14.2 (0.9)
SE owl (1)	1.9 (0.25)	30.5 (3.2)	0.63 (0.09)	25	0.81 (0.02)	20.2
T owl (1)	2.1 (0.25)	35.0 (4.4)	0.56 (0.07)	30	0.74 (0.03)	22.2
Barn Owl Plumage						
Head	2.4 (0.2)	32.8 (3.2)	0.64 (0.03)	21	0.58 (0.05)	12.2
Ventral	*1.5	40.2 (5.9)	0.96 (0.12)	28	0.61 (0.04)	17.1
Mid dorsal	1.3 (0.1)	34.5 (2.3)	0.84 (0.04)	31	0.66 (0.08)	20.0
Short Eared Owl						
Head	2.1 (0.3)	39.9 (0.0)	0.30 (0.0)	63	0.84 (0.04)	52.9
Ventral	*2.3	28.4 (0.4)	0.65 (0.16)	19	0.80 (0.03)	15.2
Mid - dorsal	1.4 (0.4)	27.9 (7.1)	0.72 (0.07)	24	0.78 (0.03)	18.7
Tawny Owl						
Head	2.4(0.14)	28.0 (0.0)	0.58 (0.08)	20	0.80 (0.05)	16.0
Ventral	*2.1	38.9 (12.2)	0.55 (0.14)	34	0.67 (0.06)	22.8
Mid - dorsal	1.5 (0.5)	34.4 (2.6)	0.62 (0.11)	37	0.74 (0.06)	27.4

Table 2.2. Mean plumage characteristics and differences between head, ventral and mid - dorsal plumage of barn owl, short eared owl and tawny owl coats used in wind tunnel studies. The number of feather layers (n) and the fractional area of solid material (f) were used to calculate the radiation interception function (p). (*) Ventral thickness estimated from measurements on dead specimens. Standard errors of measurements are given in brackets.



(i)

(ii)

(iii)

Figure 2.4. (i) The effect of wind speed on the temperature gradient through a barn owl coat at an air temperature of 20 °C, (ii) the effect of wetting barn owl plumage at 0 and 2 ms^{-1} and (iii) the effect of air temperature on temperature gradients at 3 ms^{-1}.

2.3.2 Temperature Gradients Across the Coat

Temperature gradients measured through barn owl coats on the model were non-linear and were characterised by an initial steep gradient across the skin surface followed by a reduction in gradient which remained constant to 0.75 of the total depth. Following this, there was little change in temperature through the outer feather layers to the surface (Figure 2.4 (i)). The effect of wind was to bring about closer coupling of the surface with air temperature and resulted in larger temperature gradients at higher wind speeds. At a wind speed of 7 ms^{-1} the temperature at the inner plumage depths was found to be greater than the temperature recorded at wind speeds of 5 ms^{-1} and may have been due to changes in the structure of the plumage at this wind speed. Temperature gradients were similar in short eared owl and tawny owl coats.

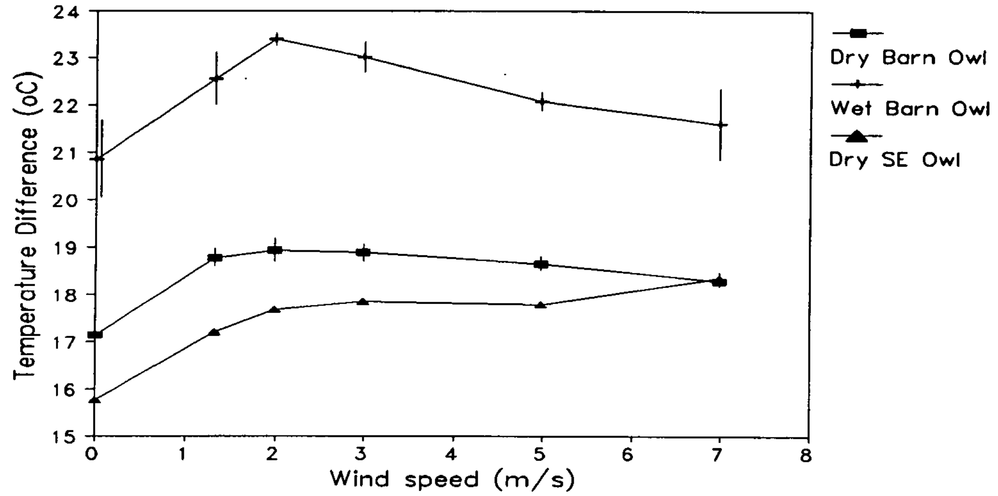


Figure 2.5. The temperature difference across dry and wet barn owl coats and a dry short eared owl coat at an air temperature of 20 °C. Bars indicate +/- standard errors of 4 coats.

Wetting the surface of barn owl coats resulted in evaporative cooling of the surface to below air temperature and decreased the temperature at each point within the coat (Figure 2.4 (ii)). The combination of wind and wetting increased the coupling of the coat surface to air temperature. This was examined by plotting the temperature difference across the coat against the mean wind speed for dry and wet coats (Figure 2.5). The temperature difference increased rapidly on dry coats at 1.3 ms^{-1} but remained constant thereafter and indicated that the model became closely coupled to air temperature at low wind speeds. The temperature difference across wet coats was greater than on dry coats but also reached a constant value at low wind speeds. Rapid drying accounted for a small fall in the temperature gradient at high wind speeds.

The temperature gradient measured on a single barn owl coat increased with decreasing air temperature, at all wind speeds (Figure 2.4 (iii)). The surface temperature of barn owl plumage was best described by multiple linear regression of air temperature and the square root of wind speed for dry and wet plumage conditions (Table 2.3).

Dry barn owl	$T_c = 2.43 - 0.78\sqrt{u} + 0.98T_a$	R = 0.99	-1 to 20 °C
Wet barn owl	$T_c = 0.61 - 0.19\sqrt{u} + 0.73T_a$	R = 0.94	10 to 20 °C
Dry SE owl	$T_c = 6.09 - 1.9\sqrt{u} + 0.92T_a$	R = 0.99	10 to 20 °C

Table 2.3. Multiple linear regression of coat surface temperature, T_c (°C) with wind speed, u (ms^{-1}) and air temperature, T_a (°C) for barn owl and short eared owl coats.

Radiative temperatures of barn owl and short eared owl plumages were greater than the temperature at the physical surface of the plumage for all wind speeds (Figure 2.6). In still air, the radiative temperature corresponded to the temperature of the plumage at a depth of 15 mm in a 20 mm barn owl coat and to 16.8 mm in a 19 mm short eared owl coat (Figure 2.7). Thermal depth declined to 8.5 mm at 7 ms^{-1}, as wind penetrated barn owl plumage but in short eared owl plumage the thermal depth remained constant with wind speed. The radiative temperature of wet barn owl plumage was less than dry plumage at all wind speeds and was approximately equal to the temperature at the wet plumage surface. With increasing wind speed the thermal depth declined to a minimum of 12 mm but remained greater than the thermal depth of dry plumage.

2.3.3 Coat Resistance

2.3.3.1 Nature of Heat Transfer Within the Coat

The nature of heat transfer within the coat of dry barn owl plumage was examined by plotting the mean heat flux density at steady state against the temperature difference across the coat for one sample examined at air temperatures of 2 - 20 °C (Figure 2.8).

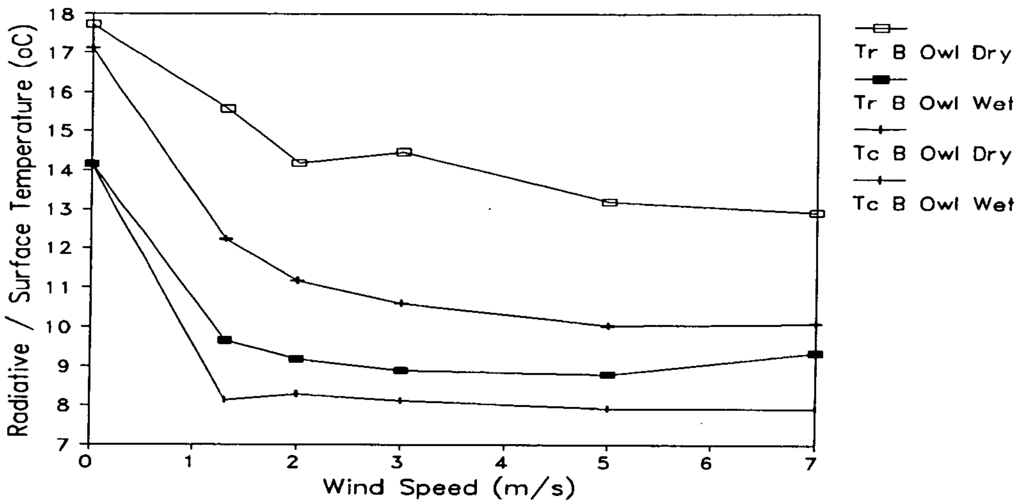


Figure 2.6. The radiative temperature (Tr) and surface temperature (Tc) of a dry and wet barn owl coat at an air temperature of 10 °C.

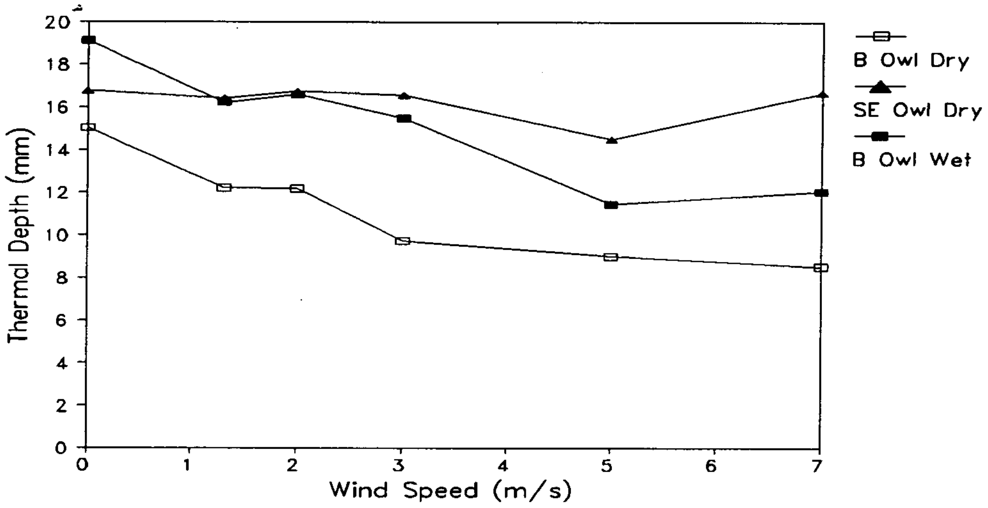


Figure 2.7. The thermal depth (measured from the skin surface) of a dry and wet barn owl coat (total depth 20 mm) and a short eared owl coat (total depth 19 mm) at an air temperature of 10 °C.

Linearity of the relationship indicated that heat transfer within the coat was dominated mostly by true conduction rather than temperature dependent free convection. Conductivity of still air within the coat is approximately equal to 26 mWm^{-1} ^{o}C^{-1} at mean coat temperatures of 22 - 32 ^{o}C. At these coat temperatures, the radiative conductivity was calculated to be between 6 and 5.5 mWm^{-1} ^{o}C^{-1} using a mean interception probability of 14.2 cm^{-1} (Table 2.2) and the conductivity of coat elements was assumed to be equal to 34 mWm^{-1} ^{o}C^{-1} (Walsberg, 1988a). With small temperature differences these calculations overestimated the heat flux density by less than 1 Wm^{-2}. Assuming therefore, that free convection was negligible with small temperature differences, the actual thermal conductivity of the coat elements was calculated to be 33 $mWm^{-1}{}^{o}C^{-1}$. From these calculations it was estimated that radiation, conduction through air within the coat and conduction by coat elements accounted for 7 - 9 %, 35 - 40 % and 45 - 51 % respectively of the total heat flux density through the coat. At the highest temperature difference, however, free convection accounted for around 11 % of total heat transfer.

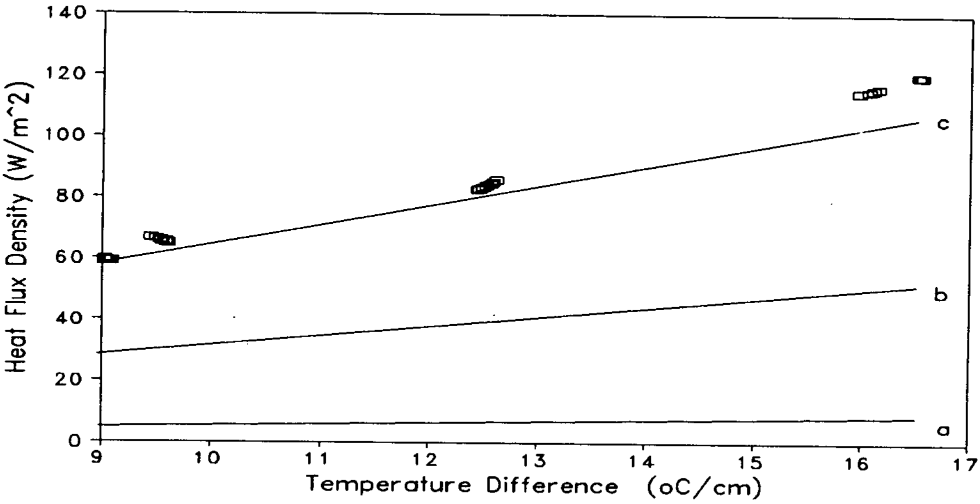


Figure 2.8. The relationship between the heat flux density and the temperature difference per unit depth for a barn owl coat (symbols). The contribution of (a) radiation, (b) radiation and molecular diffusion through air within the coat and (c) the sum of radiation, diffusion and conduction through feather elements of the coat were included for comparison (lines).

Free convection was also negligible in short eared owl and tawny owl coats at an air temperature of 20 °C. Radiative conductivities of short eared owl and tawny owl coats were 4.1 and 3.9 $mWm^{-1}\ {}^{o}C^{-1}$ and the thermal conductivity of coat elements was calculated to be 33 and 35 $mWm^{-1}\ {}^{o}C^{-1}$. For the short eared owl coat, radiation, conduction through air within the coat and conduction by coat elements contributed 6, 41 and 53 % to total heat transfer and for the tawny owl coat accounted for 6, 40 and 54 % of the total heat flux density through the coat.

2.3.3.2 Effect of Wind and Wetting on Coat Resistance

The resistance to heat transfer provided by the coats of 4 dry barn owls ranged from 356 to 435 sm^{-1} with a mean of 398 sm^{-1} (SE = 16.2) in still air. Resistance of wet coats ranged from 330 to 430 sm^{-1} with a mean of 374 sm^{-1} (SE = 20.9) and in all cases wetting resulted in a reduction of 5 to 48 sm^{-1}. Some of the variation in resistance may have been due to differences in coat depth. The thinnest coat had the lowest resistance but the second thickest coat had the highest resistance. Resistance was not related to the mass of feather per unit area of skin surface or number of layers per cm depth. The resistance per unit coat depth of dry coats was significantly greater than that of wet coats (paired t test, $p = 0.05$) and was relatively constant, with means of 1.95 scm^{-2} (SE = 0.07) and 1.83 scm^{-2} (SE = 0.09) for dry and wet coats, respectively. This compared with resistances of 400 and 418 sm^{-1} for single samples of short eared owl and tawny owl coats which represented resistances per unit coat depth of 2.1 and 2.0 scm^{-2}, respectively.

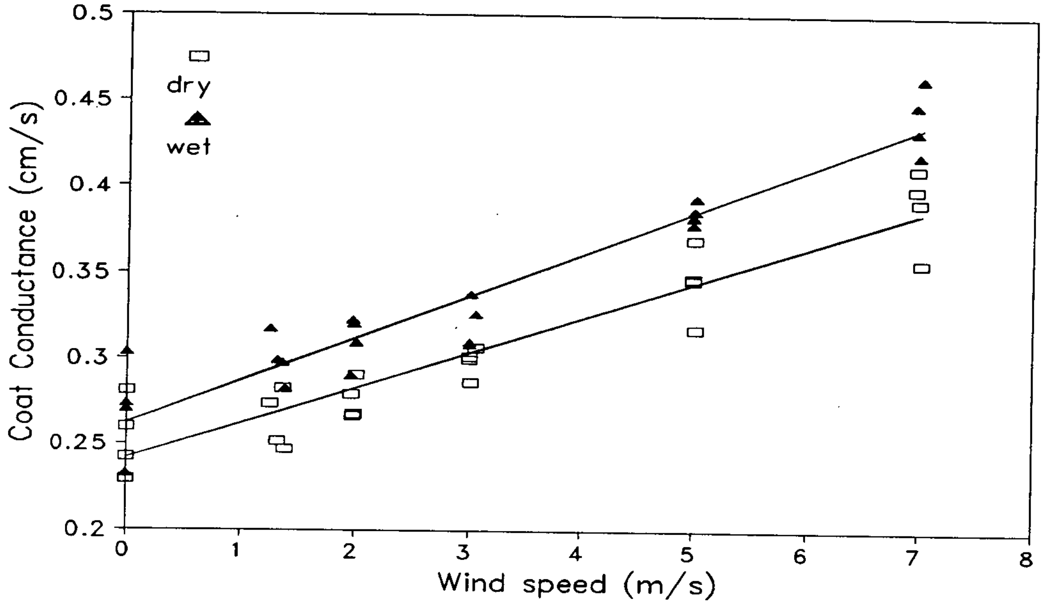


Figure 2.9. The effect of wind speed on the coat conductance of barn owl plumage at an air temperature of 20 °C when dry and following wetting.

Coat resistance decreased with increasing wind speed. The reduction in resistance was more closely correlated with wind speed when expressed as a conductance (Figure 2.9). The mean conductances of barn owl coats in still air were underestimated with regression equations which included data from all wind speeds and indicated that the relationship which holds for forced convection did not describe conditions where heat transfer by free convection dominated (Table 2.4). The variation in conductances of the 4 coats obscured the finding that for individual coats the increase in conductance between still air and 1.3 ms^{-1} was considerably less than that predicted by extrapolating the relationship from higher wind speeds (Figure 2.10).

Dry barn owl	All data	$1/r_c = 0.0205u + 0.242$	R= 0.94
	Wind only	$1/r_c = 0.0224u + 0.232$	R= 0.95
Wet barn owl	All data	$1/r_c = 0.0246u + 0.262$	R= 0.96
	Wind only	$1/r_c = 0.0258u + 0.256$	R= 0.96
S.Eared Owl	All data	$1/r_c = 0.0168u + 0.229$	R = 0.91
	Wind only	$1/r_c = 0.0200u + 0.213$	R = 0.98

Table 2.4. Linear regression of coat conductance $1/r_c$ (cms^{-1}) with wind speed *u* (ms^{-1}) for dry and wet barn owl coats and a single dry short eared owl coat. Regressions were calculated including (all data) and excluding values in still air (wind only).

Wetting the coat increased coat conductance and mean conductances were greater at all wind speeds (paired t test p = 0.05) with the exception of data at a wind speed of 3 ms^{-1} which were not significantly different (p = 0.1). Incomplete wetting of samples may have caused this difference, but for each coat at this wind speed there was an increase in conductance of 0.009 to 0.052 cms^{-1} (Figure 2.9). The conductance of short eared owl plumage also increased with increasing wind speed (Figure 2.10) and the regression equation suggested that the increase in conductance per unit change in wind speed was smaller than that of barn owl plumage (Table 2.4).

2.3.3.3 Differences in Coat Resistance with Position on the Model

The mean coat resistance of dry barn owl plumage at the front of the model was 506 sm^{-1} (SE = 23.6) and at the back was 315 sm^{-1} (SE = 18.6) in still air. The conductance of both dry and wet coats at the front of the model increased linearly with increasing wind speed but at the back the change in conductance per unit change in wind speed was considerably smaller. The conductance of dry plumage at the front of the model was significantly smaller than back plumage between 0 and 5 ms^{-1} (two sample t test p = 0.05) but at the highest wind speed of 7 ms^{-1} there was little difference (Figure 2.11). The conductance of wet plumage at the front of the model was, however, significantly smaller than that of back plumage, at all wind speeds (p = 0.05) and again showed a much greater increase per unit change in wind speed than plumage at the back (Figure 2.12).

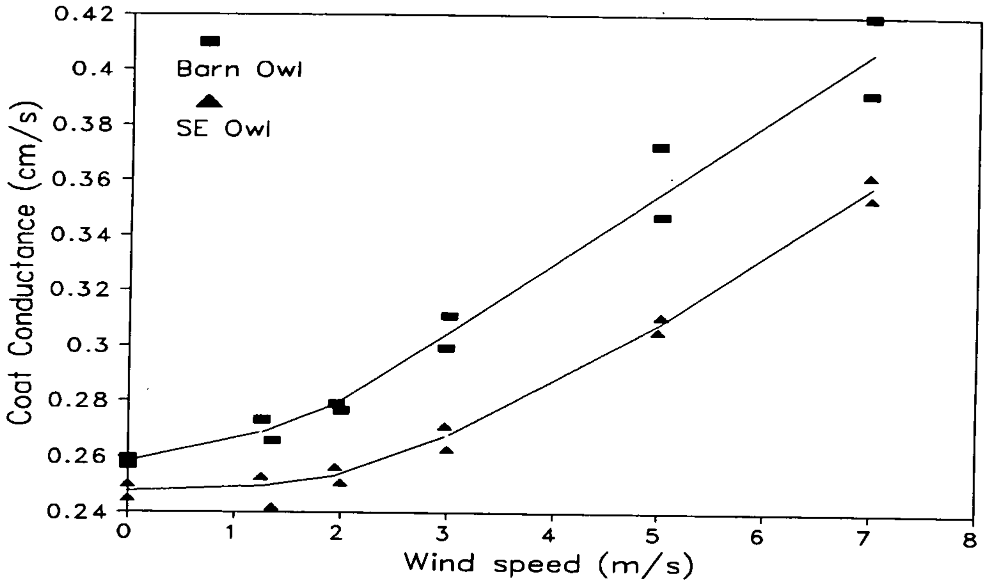


Figure 2.10. The effect of wind speed on the coat conductance of a dry barn owl and a short eared owl coat. Each point represents repeat measurements on the same coat at air temperatures of 10 and 20 °C.

Differences in resistance with position on the model may have been due to differences in depth of plumage at the front and back of the model. The mean depth of barn owl plumage at the front of the model was 2.42 cm (SE = 0.2) and at the back was 1.32 cm (SE = 0.13) which gave mean resistances per unit coat depth in still air of 2.12 (SE = 0.11) and 2.43 (SE = 0.22). There was no evidence that the resistance per unit coat depth was different between the two plumage areas at wind speeds from 0 and 3 ms^{-1} but at wind speeds greater than 5 ms^{-1}, the plumage at the front of the model was less efficient per unit coat depth in resisting heat transfer than the plumage at the back (two sample t test p = 0.05).

The plumage at the front of the model was from the area around the head (dorsal surface) of the barn owl and was visibly different in structure from the lower dorsal plumage at the back of the model. Head feathers were found to be much softer than the larger contour feathers overlying the surface at the back. The greater curvature of the model at the front (and around the head of an owl) also meant that the front feathers were held more upright than the feathers which lay along the back and as a result may have allowed greater penetration of wind (Section 3.3.4). Comparison of coat properties between front and back indicated that the thicker front plumage had a similar mass of plumage overlying the skin surface, resulting in a smaller number of feather layers per unit coat depth (Table 2.2) and therefore suggested that a combination of physical coat structure and position in relation to wind interception may account for the greater change in conductance at the front of the model.

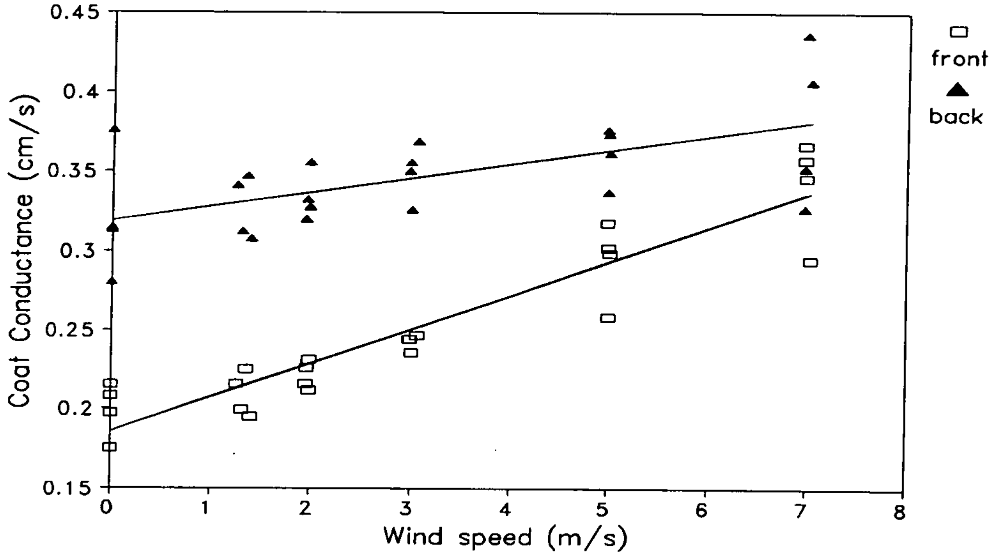


Figure 2.11. The effect of wind speed on the coat conductance at the front and back of the model with dry barn owl coats measured at an air temperature of 20 °C.

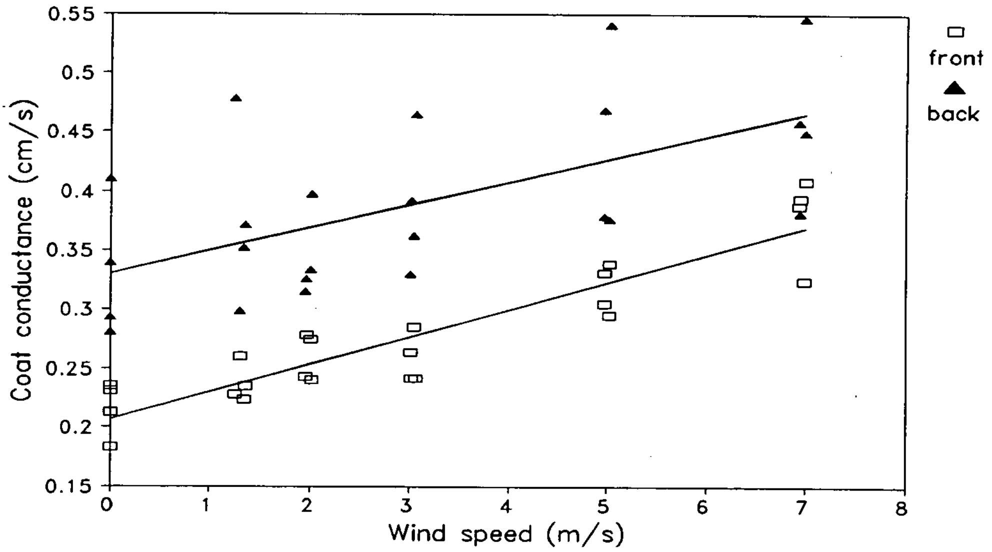


Figure 2.12. The effect of wind speed on the coat conductance at the front and back of the model with wet barn owl coats measured at an air temperature of 20 °C.

2.3.3.4 The Penetration Depth of Wind

Using regression equations derived from the change in conductance with wind speed (all data included), the mean penetration depth was found to increase from 0.20 to 0.76 cm for dry barn owl coats between 1.3 and 7 ms^{-1} (Table 2.5). This indicated that at 7 ms^{-1} the wind had penetrated 37 % of the coat. Dry short eared owl plumage was penetrated to similar depths from 0.16 to 0.64 cm which was equivalent to 34 % penetration at the highest wind speed. Wind penetrated deeper into the coat at the front of the model from 0.31 to 1.08 cm, representing a maximum of 45 % of total depth which was considerably greater than from 0.05 to 0.21 cm or to a maximum of 16 % at the back of the model.

Wetting the coat resulted in a small increase in penetration between 0.22 and 0.81 cm (40 %) over the range in wind speeds. When wetted, wind penetration at the front did not change but at the back of the model wetting resulted in penetration of 0.09 to 0.38 cm which represented 29 % penetration of the coat at the highest wind speed.

	Barn owl						**SE Owl**
Wind speed	**Mean**		**Front**		**Back**		**Mean**
u ms^{-1}	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
1.3	0.20	0.22	0.31	0.31	0.05	0.09	0.16
2	0.30	0.32	0.45	0.44	0.07	0.13	0.24
3	0.42	0.45	0.62	0.61	0.10	0.20	0.34
5	0.61	0.65	0.88	0.87	0.16	0.30	0.51
7	0.76	0.81	1.10	1.10	0.21	0.38	0.64
Depth	2.05	2.05	2.42	2.42	1.32	1.32	2.08

Table 2.5. Penetration depths (cm) of wind in dry and wet barn owl coats and a dry short eared owl coat for the mean coat depth and for the coat at the front and back of the heat transfer model.

2.3.4 Boundary Layer Resistances

Boundary layer resistances of the bare model were determined when the model was calibrated at steady state at temperatures of 20 to 43 °C in air temperature of 20 °C. At all temperatures the boundary layer resistance declined between wind speeds of 0 and 7 ms^{-1} (Figure 2.13). Dependence of free convection on the difference between temperature of the surface and air meant that in still air the mean boundary layer resistance declined with increasing temperature of the model, from 189 to 93 sm^{-1} at 20 and 43 °C, respectively. Increasing wind speed brought about convergence of resistance at all temperatures, and from 3 to 7 ms^{-1} boundary layer resistances were equal. The relationship between Nusselt (*Nu*) and Reynolds (*Re*) numbers for the model were of similar magnitude to that derived for air flow over smooth heated cylinders and for smooth aluminium cylinders determined by cooling curves (Table 2.6).

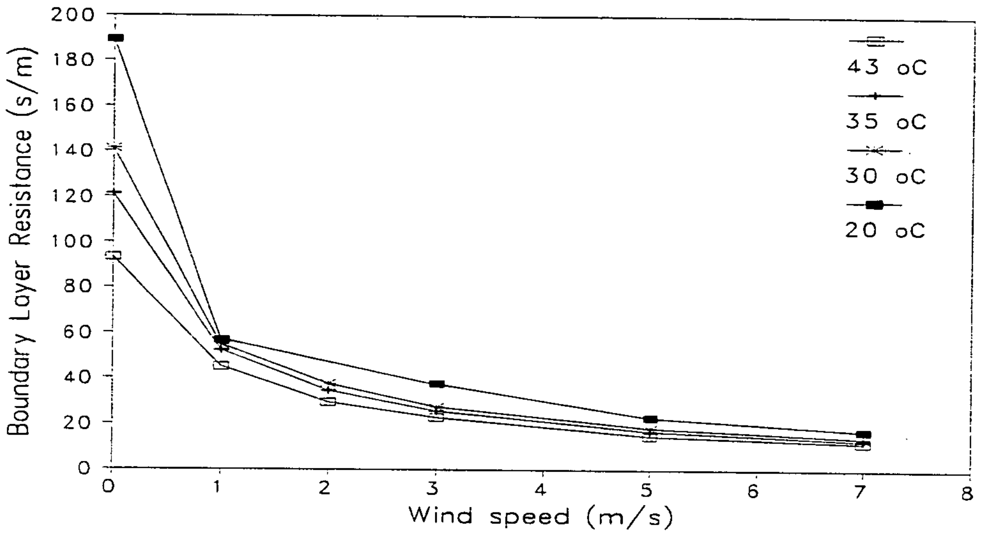


Figure 2.13. The effect of surface temperature (20 - 43 °C) on the boundary layer resistance of the heat transfer model at an air temperature of 20 °C. Anomalous data for 20 °C at 2 ms^{-1} was discarded from analysis.

Nusselt numbers for the model with plumage sample were found to be poorly correlated with Reynolds numbers (R = 0.27), (Table 2.6). The data however, could be divided into two groups: (i) three coat samples fitted by the relationship derived for a smooth horizontal cylinder and (ii) one coat sample close to the relationship for the bare model (in both cases characteristic dimension was increased to take account of plumage depth), (Figure 2.14). The latter had the thinnest coat depth and therefore, changes in shape by covering with plumage may have accounted for the differences between these samples. The model with the wings outstretched was in the group which corresponded to heat transfer from a smooth cylinder and had similar Nusselt numbers to other samples with similar coat depths.

The relationship between Nusselt number and Grashof number was determined for the bare model with no plumage sample and was typical for free convection from a horizontal cylinder:

$$Nu = 1.58Gr^{0.22} \qquad R = 0.94 \qquad (2.24)$$

The Nusselt numbers determined from the model with dry barn owl plumage had a mean of 25.8 (SE = 2.45) with mean Grashof number calculated as 9.1×10^5 (SE = 9×10^4) which was smaller than that predicted from the relationship derived for the model.

	Relationship	R	Range of *Re*
Model	$Nu = 0.22Re^{0.68}$	0.99	7000 - 46000
Model with Plumage	$Nu = 4.27Re^{0.34}$	0.27	10000 - 60000
Horizontal Cylinder	$Nu = 0.56Re^{0.53}$	0.99	10000 - 70000
Vertical Cylinder	$Nu = 0.55Re^{0.51}$	0.99	10000 - 70000

Table 2.6. The relationship between Nusselt and Reynolds number for the model and smooth aluminium cylinders. R is the correlation coefficient.

Boundary layer resistance of the model with plumage samples declined from a mean of 211 in still air to 33 sm^{-1} at a wind speed of 7 ms^{-1} (Figure 2.15). The resistance in still air was significantly greater than the resistance of the model with no plumage (paired t test p = 0.05). At low wind speeds, resistances were similar but at 5 and 7 ms^{-1} the model with plumage had greater resistances than predicted for the smooth model (p = 0.05). The boundary layer resistances of the model with short eared owl and tawny owl coats were similar to barn owl measurements with values of 228 and 230 sm^{-1} in still air, respectively.

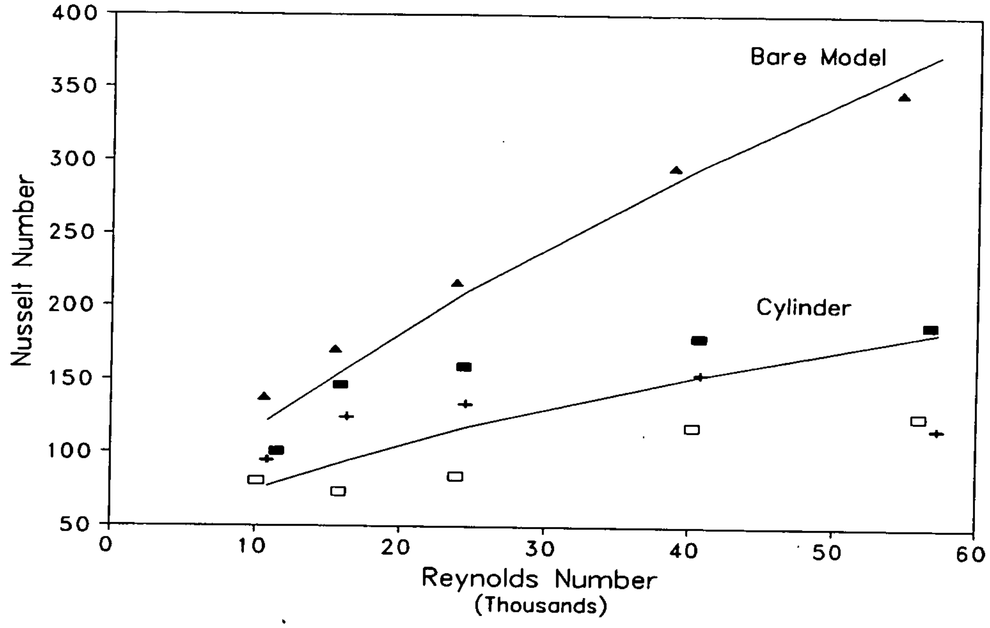


Figure 2.14. Relationship between Nusselt and Reynolds numbers for the model with barn owl coats (each symbol represents a different coat) compared with relationships derived for the bare model and for a smooth aluminium cylinder (lines) at an air temperature of 20 °C.

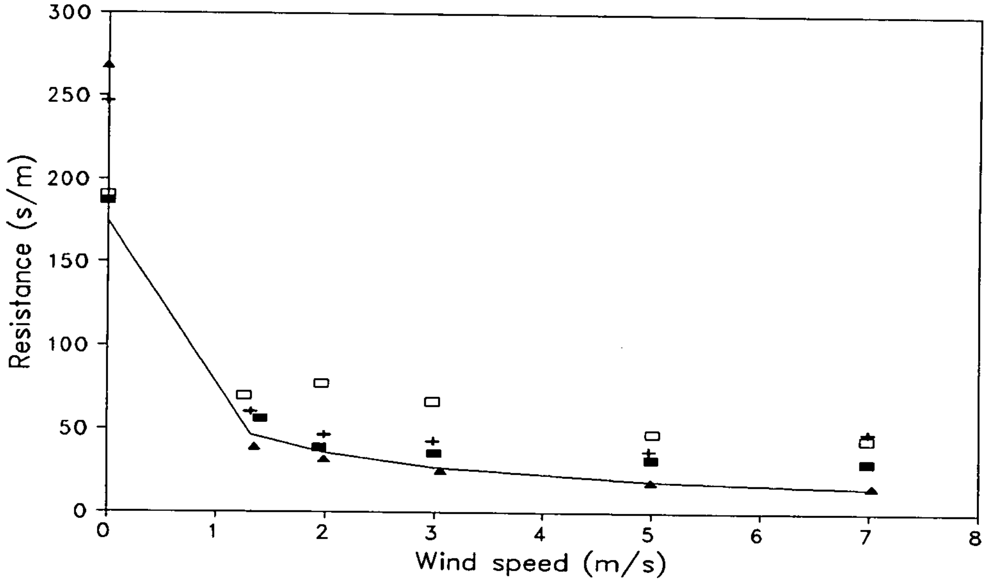


Figure 2.15. Comparison between the boundary layer resistance of the model with barn owl coats (each symbol represents a different coat) with that predicted using the relationship derived for the bare model (line) at an air temperature of 20 °C.

2.3.5 Total Thermal Resistances

The total thermal resistance (r_{tot}) of the model was calculated as the sum of coat resistance (r_c) with the radiative resistance (r_a) and boundary layer resistance (r_r) acting in parallel (Table 2.7). The total thermal resistance with dry plumage showed a linear decline with the square root of wind speed given by:

$$r_{tot} = 515 - 85u^{0.5} \qquad R= 0.96 \qquad (2.25)$$

Radiative resistance was independent of wind speed with a mean of 223 sm^{-1} (SE = 0.5). All other resistances declined with increasing wind speed but the non-linear decrease of the boundary layer resistance was seen to bring about the correlation between total resistance and the square root of wind speed. The total resistance of the model with short eared owl and tawny owl coats in still air were similar and were calculated to be 512 and 531 sm^{-1}, respectively.

Wind speed (ms^{-1})	r_c	r_a	r_r	r_{tot}
Dry Barn Owl Plumage				
0	398 (17.2)	223 (20.4)	221 (0.7)	508 (14.9)
1.3	380 (12.3)	56 (6.4)	223 (0.5)	425 (14.4)
2	363 (7.2)	48 (10.0)	224 (0.6)	402 (10.0)
3	336 (5.0)	43 (8.8)	224 (0.5)	371 (8.1)
5	291 (9.1)	34 (6.0)	223 (0.5)	320 (6.5)
7	257 (8.0)	35 (7.5)	223 (0.5)	287 (4.1)
Wet Barn Owl Plumage	r_c	r_{va}	r_r	r_{tot}
0	374 (20.9)	206 (20.3)	228 (1.5)	486 (16.4)
1.3	335 (7.8)	52 (5.6)	231 (0.3)	380 (6.8)
2	323 (7.9)	45 (9.1)	231 (0.8)	362 (13.6)
3	313 (6.8)	39 (8.1)	231 (0.5)	348 (11.8)
5	260 (2.2)	31 (5.4)	230 (0.4)	288 (6.1)
7	227 (5.0)	32 (6.7)	229 (0.4)	256 (10.3)

Table 2.7. Thermal resistances of the model with dry and wet barn owl coats, between wind speeds of 0 and 7 ms^{-1}. Values in brackets are standard errors (n = 4).

The thermal resistance of wet plumage has an additional resistance to latent heat transfer. Wetting the plumage resulted in the wetting of the top layers of feathers only and therefore the resistance to latent heat transfer is essentially the boundary layer vapour resistance (r_{va}). This resistance was calculated according to Monteith and Unsworth (1991) where the ratio between the boundary vapour resistance and the boundary resistance to heat transfer (r_{va}/r_a) is equal to the ratio of thermal diffusivity of air to the diffusion coefficient of water vapour in air $(\kappa/D_v)^{0.33}$ equal to 0.93. The vapour resistance was calculated by assuming that the boundary layer resistance of the wet model was similar to the dry model and the total resistance to heat transfer with wet plumage was calculated using the measured values of r_c and r_r. This indicated that the total resistance to heat transfer of the wet model was smaller than the dry model at all wind speeds, largely due to the decline in coat resistance (Table 2.7). The total resistance to heat transfer for the wet model was also found to be a linear function of the square root of wind speed:

$$r_{tot} = 485 - 86u^{0.5} \qquad \text{R}= 0.96 \qquad (2.26)$$

Observations revealed that the surface of the barn owl coat when wetted was incompletely saturated and therefore the rate of evaporation from the surface was less than the potential evaporation rate from a fully saturated surface. Having derived the resistances to vapour and sensible heat transfer, the actual rate of evaporation was estimated by calculating the energy balance of the plumage surface. At steady state the rate at which heat is gained by convection and radiation:

$$G + R_n = \rho C_p (T_a - T_c)/r_e \qquad (2.27)$$

will equal the rate at which latent heat (λE) is lost:

$$\lambda E = \rho C_p \{e(T_c) - e\}/r_{va} \qquad (2.28)$$

The actual rate of evaporation was calculated by adding the gain of sensible heat to the measured heat flux. From this it was determined that the ratio of actual to potential evaporation (ω) ranged between 0.52 in still air to 0.22 at 7 ms^{-1}. The actual rate of evaporation (λE_a) for incomplete saturation of the surface was therefore equal to:

$$\lambda E_a = \omega \rho C_p \{e(T_c) - e\}/r_{va} \qquad (2.29)$$

2.3.6 Total Heat Loss from the Model

Heat loss from the model increased by wetting the surface of the plumage, increasing wind speed and decreasing air temperature. At 20 °C with dry barn owl plumage the model had a heat loss of 56 Wm^{-2} (SE = 2.4) in still air. By wetting, heat loss increased by 32 % to 74 Wm^{-2} (SE = 4.0). For comparison the heat flux density through dry short-eared owl and tawny owl plumage was 51 and 55 Wm^{-2}, respectively. Heat loss from the model with wet plumage was greater than that from the model with dry plumage, at all wind speeds (paired t test $p > 0.002$). The heat flux density, G increased linearly with wind speed, u for dry and wet barn owl plumage samples (Figure 2.16) according to:

Dry Barn owl $G = 5.12u + 56.8$ R=0.96 (2.30)

Wet Barn owl $G = 6.37u + 77.6$ R=0.96 (2.31)

These equations indicate that there was more than a 60 percent increase in total heat loss for dry and wet plumages between 0 and 7 ms^{-1}. The presence of thinner plumage at the back of the model meant that there was a significantly greater heat loss from the back of the model than from the front with dry barn owl plumage samples, at all wind speeds other than 7 ms^{-1} (two sample t test $p = 0.025$). Similarly for wet barn owl plumage, heat flux densities at the back were significantly greater at all wind speeds ($p = 0.05$). The linear relationship between heat loss from the model and wind speed contradicted the result that the change in total thermal resistance was best described with the square root of wind speed. This differerence was thought to have been associated with the poor relationship between Nusselt and Reynolds numbers which introduced errors into the estimate of boundary layer resistance.

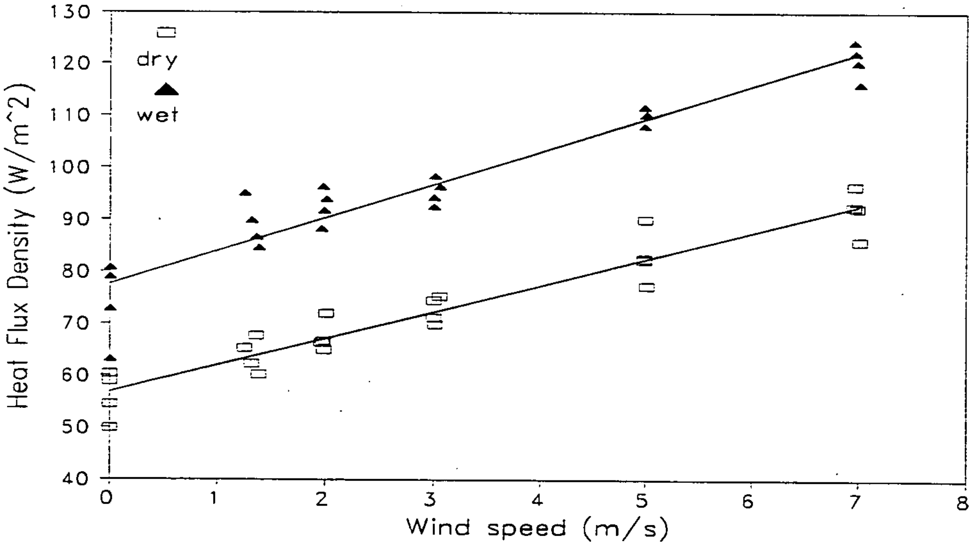


Figure 2.16. The effect of wind speed on the total heat loss from the model with dry and wet barn owl coats at an air temperature of 20 °C.

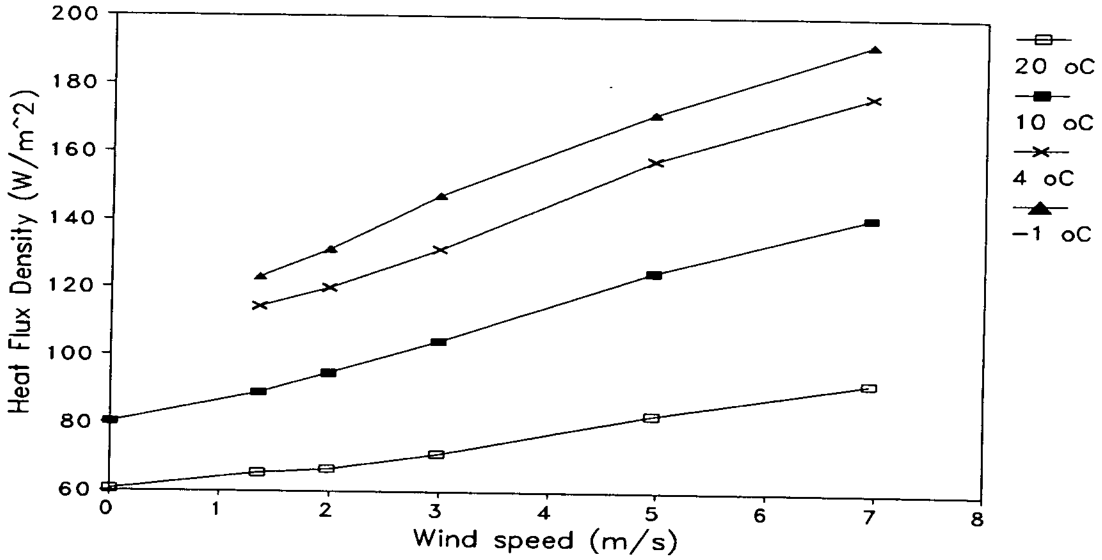


Figure 2.17. The effect of air temperature and wind speed on the total heat loss from the model with a dry barn owl coat.

Decreasing air temperature increased heat loss from the model such that at air temperatures of 20, 10 and 4 °C, heat loss increased to 60, 80 and 113 Wm^{-2} in still air (Figure 2.17). Heat loss was a linear function of both wind speed and air temperature with dry and wet barn owl coats over the temperature ranges -1 to 20 °C and 10 to 20 °C respectively and was described using multiple linear regression (Table 2.8). No values for still air at -1 °C were included in the analysis as air temperature could not be maintained at -1 °C without the wind tunnel fans running.

Plumage		**R**	**°C**
Dry Barn owl	$G = 119 + 8.63u - 3.58T_a$	0.98	-1 - 20
Wet Barn owl	$G = 110 + 5.77u - 1.49T_a$	0.98	10 - 20
Dry SE owl	$G = 129 + 5.97u - 4.64T_a$	0.94	10 - 20

Table 2.8. Multiple linear regression of total heat loss G (Wm^{-2}) with wind speed u (ms^{-1}) and air temperature T_a (°C) for the model with barn owl and short eared owl plumage.

2.4. DISCUSSION

2.4.1 Temperature Gradient Through Coats

Temperature profiles measured through barn owl coats indicated that the change in temperature with depth decreased towards the surface of the coat at all wind speeds. Non-linear temperature gradients have also been measured through white fox fur (*Aloplex lagopus*) by Scholander (1950) and through rabbit, horse and pig coats (Treagar, 1965). However, linear temperature gradients were measured through three avian plumages (Walsberg, 1988a), through sheep and rabbit coats (Cena and Monteith, 1975b) and through the fleece of a Clun forest ewe (Gatenby *et al*, 1983). Changes in gradient with depth through the coat may be due to: (i) the contact resistance between model and skin surface, (ii) a decrease in heat flux per unit area with distance from the skin surface on the curved body of the model (iii) the superficial thinning of coat elements and (iv) penetration of wind through the outer surface of the coat.

It is unlikely that the steep temperature gradient measured across the skin in this study was due to greater resistance of the skin rather than feathers. The apparently high resistance across this layer was because of incomplete thermal contact at the interface of the model and skin surface, a phenomenon reported for heat transfer between metal surfaces (Bayazitoglu and Ozisik, 1988). This result was also reported from measurements on animal coats by Scholander (1950).

The curvature of the model (or the body of an animal) results in a decrease in the heat flux per unit area of coat towards the surface of the coat. This is because the increase in area with depth will increase according to the ratio of internal to external radius. Combined with a greater density of coat elements near the skin surface, this would bring about larger temperature gradients close to the skin surface. Gatenby *et al* (1983) demonstrated that the skin temperature of a Clun forest ewe at a range of air temperatures always lay above the linear temperature gradient through the fleece. The heat flux density measured through coats mounted on flat plates will not decrease with depth as area remains constant and cannot account for changes in gradient in studies of that type. A decrease in the insulation of the coat towards the surface must therefore be responsible for a decrease in temperature gradient as a consequence of a reduction in the density of coat elements. The temperature profile in owl coats suggested that the density of feather elements was uniform to around 75 % of the depth from the skin surface, at which point the decrease in temperature gradient indicated a reduction in insulation due either to a change in density or structure of feather elements. Scholander (1950) attributed the decrease in gradient at the surface of white fox fur mounted on a heated flat plate to superficial thinning of the fur and showed that the uniformly dense caribou coat (*Rangifer arcticus*) exhibited no such decrease.

The temperature profile through barn owl coats did not change significantly in wind. At high wind speeds however the small change in temperature in the outer feather layers extended deeper into the plumage. Treagar (1965) reported a similar flattening of the temperature gradient with increasing wind speed in the outer layers of rabbit, horse and pig coats. It was judged that the total absence of a temperature gradient in the outer layer was the level to which the wind penetrated and that penetration increased with decreasing hair density of the coat.

Wetting the coat did not appear to change the temperature profile in barn owl coats at any wind speed and suggested that water did not penetrate inside the coat. Wetting did however decrease the surface temperature of the coat by evaporative cooling and increased the total temperature difference across the coat.

The surface temperature of owl coats was measured mid-way along the upper surface of the model and was described by multiple linear regression of air temperature and the square root of wind speed. The relationship between the surface temperature of the coat with the square root of wind speed demonstrated coupling of the surface to air temperature as the boundary layer was reduced. The surface can only cool to air temperature and therefore this relationship conflicts with measurements of the temperature difference across the coat which became constant at low wind speeds. The latter measurement was the average temperature difference across the coat at six locations on the model and was representative of the model as a whole. Difference between the two relationships may therefore indicate that the site where the gradient was measured was not fully coupled with the air stream.

2.4.2 The Radiative Temperature of Coats

Radiative temperatures of barn owl and short eared owl coats were greater than the temperature at the physical surface and indicated that radiation originated several millimetres below the surface. Radiation is emitted from the surface of feather elements which are at a range of temperatures determined by the temperature gradient between the skin and coat surface. The effective radiative temperature of plumage is therefore a function of the temperature profile through the coat and the structure of the coat which determines the degree of interception of radiation. The effective radiative temperature of plumage in this study was in agreement with the relationship derived by Cena (1974) in which the effective temperature of the coat (T_r) is given by:

$$T_{rc} = T_c - [a(1 - 1/p)] \qquad (2.32)$$

where T_c is the surface temperature (°C), a is the temperature gradient through the coat (°Ccm^{-1}) and p is the interception function of the coat (cm^{-1}). The decrease in radiative temperature with wind speed can therefore be considered to be due to the increase in temperature gradient and a possible change in the interception function as wind may flatten or open up the structure of the plumage.

In still air, the effective radiating surface was from a layer approximately 4 mm below the physical surface of barn owl plumage, and 2 mm for short eared owl plumage. Evans and Moen (1975) were able to show that the thermal depth of sharp-tailed grouse plumage (*Pedioecetes phasianellus*) in still air was 3 mm below the physical surface and declined to 8 mm at wind velocities above 3 ms^{-1}. This result was similar to that of barn owl plumage which had a thermal depth of 9 to 10.5 mm below the physical surface between 3 and 7 ms^{-1} but only 2 to 4.5 mm for short eared owl plumage.

Spraying water on the surface resulted in a decrease in surface temperature, a decrease in radiative temperature and an increase in the thermal depth of the model (assuming the emissivity of wet plumage was not significantly different from dry plumage). Following wetting, the plumage was calculated to be radiating from a depth corresponding to the physical surface. This suggested that the water layer became the radiative surface in still air, and at higher wind speeds the presence of water was sufficient to cause the thermal depth of the plumage to remain above that of dry plumage. Short eared owl plumage showed a similar decline in radiative temperature with increasing wind speed but determination of the thermal depth indicated that the depth remained constant over the range in wind speeds. Inter-specific comparisons must be tempered by the fact that this was one measurement at steady state, but as temperature gradients were similar, it would indicate that the wind did not alter the radiation interception function to the same extent as found in barn owl coats.

2.4.3 Coat Resistance

The resistance of dry barn owl coats ranged between 356 and 435 sm^{-1} in still air. This variation was most likely due to variation in condition of plumage from the four samples and from experimental technique. Differences in resistance due to preparation and storing cannot be ruled out, however, Webb and King (1984) demonstrated that freezing and thawing did not significantly affect the resistance of avian coats. There was no correlation in this study between feather mass per unit skin area as shown by Wathes and Clark (1981a) for extreme differences in plumage quantity in battery hens. It is interesting to note that the highest resistances were from female barn owls, but from the limited sample size, this observation remains inconclusive.

The resistance of barn owl coats in this study was greater than from dorsal samples of North American barn owls, with resistances of 182 - 200 sm^{-1} and 119 sm^{-1} for the screech owl (*Otus asio*), (Webb, Pers. com.). Mean coat resistances of barn owl, short eared owl and tawny owl plumage were compared with reported values from a range of different species (Figure 2.18). The resistance of owl coats was found to be marginally smaller than coats of similar depth and represented 39, 44 and 41 % of an equivalent depth of still air for the barn owl, short eared owl and tawny owl, respectively. This compared with 51 % (SE = 0.5) for previously reported plumages. Different experimental techniques may account for this small difference, as many previous measurements were made using plumage mounted on flat heated plates. Summary of the data also indicated that the insulation properties of downy chick plumage in still air was similar to adult plumage and represented 58 % (SE = 0.4) of an equivalent depth of air. For birds such as penguins, chicks posses thick coats and may have higher coat resistances than adult plumage in still air (Taylor, 1986).

Molecular conduction through air trapped within plumage accounted for 35 - 39 % of heat transfer within coats and the remaining heat transfer was due to radiation, conduction through feather elements and free convection within the coat. In this study it was estimated that radiation only accounted for 7 - 8 % of the total heat flux density through barn owl plumage and only 6 % in short eared owl and tawny owl plumage. Radiation within the coat does not result in high rates of heat transfer because of the tight packing of coat elements. On average 23 overlapping layers per cm of coat depth gave a radiative conductivity of 5.5 - 6 $mWm^{-1}{}^{o}C^{-1}$ based on mean coat temperature and an interception function of 14.2 cm^{-1}. Short eared owl and tawny owl coats had on average 25 and 30 layers of feather per cm of coat with interception functions of 20 and 22 cm^{-1} which gave marginally smaller conductivities of 4.1 and 3.9 $mWm^{-1}{}^{o}C^{-1}$. These results agreed with previous findings that radiative interception is high in avian coats.

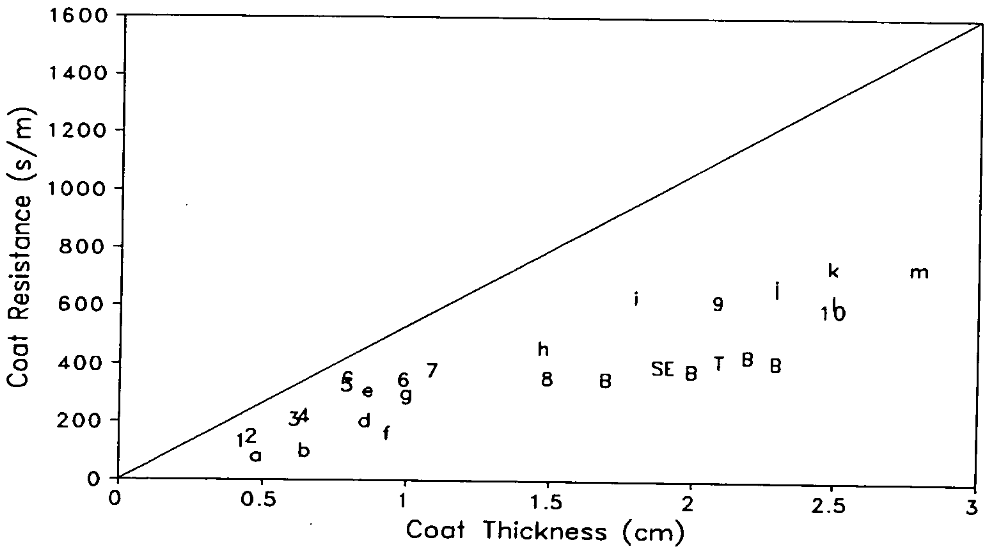


Figure 2.18. The relationship between coat resistance (sm^{-1}) and plumage depth (cm) for adult birds (a - m), chicks (1 - 10), barn owls (B), short eared owl (SE) and tawny owl (T) compared to the resistance of an equivalent depth of still air given by solid line. The source of values are given in Table 11.

Walsberg *et al* (1978) showed that pigeon plumage (*Columbia livia*) consisted of 26 layers cm^{-1} overlying the skin of which 0.67 was solid structure giving a mean radiative interception function of 17 cm^{-1} for breast and abdomen plumage. Dorsal plumage of Gambel's quail (*Callipepla gambelii*), crissal thrasher (*Toxostoma dorsale*) and house finch (*Corpodacus mexicanus*) was also reported to have interception functions of 20 to 42 cm^{-1} which gave radiative conductivities of 2 - 2.8 mWm^{-1}°C^{-1} or equivalent to 3 - 4 % of total heat transfer (Walsberg, 1988a).

Radiative interception functions of mammal coats are marginally smaller than in avian coats, depending on species. Cena and Monteith (1975b) calculated interception functions ranging from 4 - 5 cm^{-1} for sheep fleece to about 18 cm^{-1} for calf and deer coats and were able to demonstrate that radiative transfer amounts to 16 mWm^{-1}°C^{-1} for sheep fleece. This represented contributions of 5 and 15 percent of the total heat transfer for 4 cm and 2 cm fleeces, respectively.

The conductivity of coat elements was estimated to be 33, 33 and 35 mWm^{-1}°C^{-1} in barn owl, short eared owl and tawny owl coats, respectively which represented 45 - 50, 53 and 54 % of total heat transfer through plumages. This was in close agreement with Walsberg (1988) who estimated that conduction along the fibres accounted for 34 mW m^{-1}°C^{-1} or approximately 45 % of total heat flow in three avian coats.

Adults		**Depth (cm)**	r_c	**Technique**	**Author**
a	*Carpodacus mexicanus*	0.48	88	heated plate	Walsberg (1988)
b	*Toxostoma dorsale*	0.65	105	heated plate	Walsberg (1988)
c	*Eudyptula minor*	0.8	368	calorimetry	Stahel *et al* (1987)
d	*Calidris melanotos*	0.86	310	metal cast	Chappell (1980a)
e	*Phalaropus fulicarius*	0.87	318	metal cast	Chappell (1980a)
f	*Callipepla gambelii*	0.94	165	heated plate	Walsberg (1988a)
g	*Zonotrichia leucophrys* #	1.00	305	calorimetry	Robinson *et al* (1976)
h	*Pedioecetes phasianellus*	1.48	462	heated plate	Evans and Moen (1975)
i	*Pygoscelis antarctica* (dor)	1.8	640	heated plate	Taylor (1986)
j	*Pygoscelis papua* (dor)	2.3	682	heated plate	Taylor (1986)
k	*Pygoscelis antarctica* (ven)	2.5	746	heated plate	Taylor (1986)
l	Domestic hen	2.5	628	heated plate	Wathes and Clark (1981a)
m	*Pygoscelis papua* (ven)	2.8	747	heated plate	Taylor (1986)
Chicks					
1	*Calidris pusillus*	0.43	134	metal cast	Chappell (1980a)
2	*Calidris bairdii*	0.47	152	metal cast	Chappell (1980a)
3	*Charadrius fulicarius*	0.62	213	metal cast	Chappell (1980a)
4	*Calidris melanotos*	0.65	225	metal cast	Chappell (1980a)
5	*Pygoscelis antarctica* (8 days)	0.8	331	heated plate	Taylor (1986)
6	*Pygoscelis papua* (8 days)	1.0	349	heated plate	Taylor (1986)
7	*Pygoscelis antarctica* (11 days)	1.1	382	heated plate	Taylor (1986)
8	*Pygoscelis papua* (10 days)	1.5	358	heated plate	Taylor (1986)
9	*Pygoscelis antarctica* (21 days)	2.1	626	heated plate	Taylor (1986)
10	*Pygoscelis papua* (19 days)	2.5	599	heated plate	Taylor (1986)
11	*Pygoscelis papua* (27 days) *	4.0	782	heated plate	Taylor (1986)

Table 2.9. Coat resistance (r_c) of adult plumage of the house finch (*Carpodacus mexicanus*), crissal thrasher (*Toxostoma dorsale*), little penguin (*Eudyptula minor*), pectoral sandpiper (*Calidris melanotos*) grey phalarope (*Phalaropus fulicularis*), Gambel's quail (*Callipepla gambelii*), white crowned sparrow (*Zonotrichia leucophrys*), sharp-tailed grouse (*Pedioecets phasianellus*), chinstrap penguin (*Pygoscelis antarctica)*, pigeon (*Columbia livia*), domestic hen (Warren strain) and gentoo penguin (*Pygoscelis papua*) and for chicks including semi palmated sandpiper (*Calidris pusillus*), Baird's sandpiper (*Calidris bairdii*) and semipalmated plover (*Charadrius semipalmatus*). Numbering corresponds to that given in Figure 2.18. # a value of 100 sm^{-1} was subtracted for tissue resistance and *value not shown in Figure 2.18. A resistance of 100 sm^{-1} is equivalent to an insulation of 0.078 $W^{-1}m^2$ °C.

In mammalian coats, conduction through individual coat elements is considered to represent a very small proportion of total heat flow. Cena and Monteith (1975b) dismiss conduction as negligible because the cross section of hairs per unit area of skin of sheep and rabbit coats was only 0.01 and 0.03 %. Taking account of this and based on the fact that conductivity of coat elements was assumed to be no more than 5 times the conductivity of still air, the increase in conductivity attributable to conduction was unlikely to exceed 3 $mWm^{-1}{}^{o}C^{-1}$ or 10 % of the total heat flow through these coats. McArthur and Monteith (1980b) similarly agree that conduction is unlikely to be important in sheep fleece, as wool fibres occupy less than 5 % of available coat space.

Movement of air by free convection within the coat would appear to contribute only a small amount to the reduction in resistance of avian coats when the contributions of radiation and conduction are taken into account. Free convection contributed as little as 11 % to total heat transfer when the temperature difference across the barn owl coat was 20 ^{o}C. This agreed with measurements by Walsberg (1988) who showed that convection only accounted for 7 - 11 % in avian coats (with a 15 ^{o}C temperature difference) and both are in contrast with the importance of free convection in mammalian coats. Cena and Monteith (1975b) reported that the rate of heat transfer per unit temperature gradient through samples of sheep fleece and rabbit fur increased with the magnitude of the gradient and was close to the prediction for free convection from a flat plate. The additional heat loss could be attributed to the slow ascent of warm air inside the coat at a velocity around 0.01 ms^{-1}. McArthur (1980) also found that in fleece from a Clun forest ewe, free convection increased from 25 to 50 $Wm^{-1}{}^{o}C^{-1}$ with temperature differences of 8 and 25 ^{o}C.

The nature of heat transfer in avian coats may therefore be attributed to the tight packing of coat elements as seen from high radiative interception values. The overlapping matrix structure of avian plumage may reduce the importance of radiative and convective heat transfer within the coat but encourage transfer by conduction through the feather elements. This appears to be fundamentally different to mammalian coats in which free convection dominates and conduction is minimal.

2.4.4 The Effect of Wind Speed on Coat Resistance

The increase in conductance of dry and wet barn owl plumage in wind was consistent with the linear model applied by Campbell *et al* (1980) to reported values for 9 mammals, one bird coat and 3 human clothing samples. In this study, variation between coats obscured the result that linear regression of conductance with wind speed underestimated the conductance of single samples of plumage in still air. This may not be surprising because of the transition between free and forced convective regimes, and at low wind speeds the conductance appeared to show only a small increase when single barn owl and short eared owl coats were examined. Davis and Birkebak (1975) believed that conductance remains constant until a penetration velocity for the coat is reached, but it can be argued that the small changes in coat conductance may be due to mixing by buoyancy forces and to a mixed convective regime at low wind speeds rather than a failure of wind to penetrate the coat.

The change in conductance with wind speed indicated that the wind penetrated much deeper into the plumage at the front of the model than into the plumage at the back to the extent that at high wind speeds, any thermal advantage from thicker insulation at the front was lost. McArthur and Monteith (1980b) also found that the influence of wind on conductance was more pronounced on the windward than on the leeward side of a fleece-covered model sheep with coefficients of conductance between 0.038 and 0.024 $cms^{-1}ms^{-1}$ for windward and leeward sides of the model. This compared with values of 0.021 and 0.009 $cms^{-1}ms^{-1}$ for the front and back of the model in this study.

Previous studies on avian coats have indicated that the effect of wind speed on coat resistance is variable. Walsberg *et al* (1978) measured no consistent change in resistance of pigeon plumage (*Columbia livia*) mounted on a flat plate between 0.25 and 12 ms^{-1}. Using a similar technique, Taylor (1986) found that the resistance of chinstrap (*Pygoscelis antarctica)* and gentoo penguin (*Pygoscelis papua*) chick coats declined by 20 % at 1 ms^{-1} and 40 - 50 % at 10 - 15 ms^{-1} in wind parallel to plumage The resistance of coats from older chicks showed little change with wind speed up to a critical speed of 5.5 ms^{-1}. Feathered plumages had an apparent increase at high wind speeds but conflicting results with wind perpendicular to plumage showed a linear decline for all coats. A study by Stahel *et al* (1987) of the little penguin (*Eudyptula minor*) in a metabolism chamber indicated that the coat resistance was independent of wind speed at thermo-neutrality and declined marginally at high wind speeds only during cold stress. Chappell (1980a) showed that the resistance of arctic shorebird coats mounted on heated metal casts declined in proportion to the square root of wind speed while Robinson *et al* (1976) found that the combined tissue and coat resistance of white crowned sparrows kept in metabolism chambers also decreased in proportion to the square root of wind speed.

Differences in the relationship between coat resistance and wind speed reported in many studies may be due to variation in techniques and the degree of turbulence in wind tunnels. Examination of the relationship should be examined neglecting *a priori* assumptions on proportionality to wind speed or the square root of wind speed and should seek to identify a physical explanation for the relationship.

2.4.5 The Effect of Wetting on Coat Resistance

Wetting the surface of barn owl coats resulted in a decrease in resistance of 32 sm^{-1} (SE = 3.6) or 10 % (SE =1.1) at all wind speeds. Similar studies on wetting have usually measured a decrease in total resistance rather than coat resistance. However, changes attributed to wetting are likely to be comparable as changes in the radiative and boundary layer resistance will be small from decreased surface temperatures. Webb and King (1984) measured the effect of wetting five avian and 7 mammal coats. In this case the total resistance of the samples was reduced by approximately 50 % in still air following wetting. A similar decrease of 60 and 75 % was obtained by saturating the coats of wood rats (*Neotoma floridana*) and cotton rats (*Sigmodon hispidus*), (Webb *et al*, 1990) and the resistance of human clothing was found to decline by 64 %, following wetting at a wind speed of 4 ms^{-1} (Pugh, 1966).

The increase in heat transfer through wet coats may be due to (i) evaporation of water within the coat, (ii) conduction through a static layer of water surrounding individual coat elements, (iii) convective transfer within water contained in the coat, (iv) penetration of water into individual coat elements and (v) mechanical disruption of coat structure. In this study, examination of the coat following wetting at low wind speeds revealed that water had penetrated the top feather layers and the lower layers remained dry. The degree of wetting in this study may therefore have modified heat transfer only within the top layers of the coat but the high thermal conductivity of water (0.6 $Wm^{-1}{}^{o}C^{-1}$) which is approximately 25 times that of still air (0.026 $Wm^{-1}{}^{o}C^{-1}$) may have been significant in increasing the rate of heat transfer in this layer.

It is known that water penetrates into the feather shafts of birds giving rise to mechanical disruption (Rhijn, 1977) but it is not known to what extent this contributes to conduction of the feather element. Although conductance through individual feather elements is an important mechanism of heat transfer in avian coats, it is likely that in this study the degree of wetting was insufficient to increase the overall conductivity of feather elements. Wetting caused very little difference in the visual appearance of barn owl plumage and therefore it is was assumed that wetting caused little mechanical deformation of the coat structure. This was in agreement with the results of Webb and King (1984) who were able to show that mechanical deformation of the feather matrix by the weight and surface tension of water did not significantly reduce the resistance of avian coats.

The effect of wetting on the resistance of barn owl coats is difficult to assess for live birds because it is difficult to estimate (i) the degree to which coats become wetted and (ii) the ability of birds to resist the penetration of water by shaking and holding the feathers erect. Wetting in this study may be judged equivalent to light rain for a short period and therefore it was concluded that the reduction in resistance arising from this will be small. Wetting from contact with wet vegetation during hunting may be a more regular mechanism of wetting for the barn owl rather than interception of rain. If this is the case then contact with wet vegetation may bring about a greater reduction in coat resistance from an increase in penetration of water and by the mechanical disruption of plumage structure. The importance of this is suggested from photographs of barn owls in which the plumage on the legs and lower body became matted and compressed following hunting in wet vegetation (Mikkola, 1983).

Observations from the wetting experiment indicated that the physical structure of the coat acts as an efficient barrier to the penetration of water, as the water either remained in distinct droplets or ran off the surface. Birds would appear to be able to increase this further by shaking the plumage to remove free water. Stalmaster and Gessaman (1984) observed bald eagles (*Haliaeetus leucocephalus*) sleeking plumage following prolonged exposure to rain but it is not known whether the sensitive adjustment of feather posture as reported for responses to cold and heat stress (McFarland and Budgell, 1970) may also be used to reduce the penetration of water through plumage.

2.4.6 The Effect of Wind Speed on Boundary Layer Resistance

The relationship between Nusselt and Reynolds numbers for the bare model was similar to that derived for flow across a non-circular cylinder (Bayazitoglu and Ozisik, 1988) and for flow across smooth cylinders (summarised by Monteith and Unsworth, 1990). The cooling curve experiments indicated that the relationship was not significantly altered by considering flow across a horizontal cylinder compared with a vertical cylinder as derived in many of the above studies.

Nusselt numbers for the model with barn owl plumage were on average 30 % lower than those derived for the bare model and the difference was found to increase from 15 to 48 % with increasing wind speed. McArthur and Monteith (1980a) found that the fleece-covered trunk of a model sheep had 20 % lower Nusselt numbers at low wind speeds and attributed lower Nusselt numbers to the use of radiative temperature. This overestimates the boundary layer thickness because of the extra depth of air between the radiative surface and physical surface of the coat. In this study the surface temperature was used to calculate Nusselt numbers but variation according to coat thickness suggested that a change in shape may have accounted for smaller Nusselt numbers. Nusselt numbers for the model with the three thickest coats were close to that predicted using the relationship derived for a horizontal cylinder but, the thinnest plumage sample gave Nusselt numbers described by the relationship for the bare model.

Stahel *et al* (1987) found that the Nusselt numbers derived for heat transfer from the little penguin (*Eudyptula minor*) were also smaller than predicted by equations derived for the flow across smooth cylinders, but at critical Reynolds numbers when flow became turbulent, there was close agreement between the two. Wathes and Clark (1981b) were able to describe the heat transfer from a hen using spherical models but found that there was a doubling of the Nusselt number at high air speeds interpreted as the turbulence introduced from the roughness of the feather layer.

The consequence of smaller Nusselt numbers derived for the model with plumage covering was that the boundary layer resistance was larger than predicted by heat transfer from smooth cylinders. This effect may be offset by increased turbulence in natural conditions. McArthur and Monteith (1980a) reported that the Nusselt numbers for the bare trunk of a model sheep were on average 14 % greater out of doors, with a maximum difference of 38 %. Similarly, Mitchell (1976) found that the ratio of Nusselt numbers for spheres measured out of doors to Nusselt numbers for spheres in a wind tunnel was 1.0 to 2.2 and that this was increased as the ratio of height above surface to sphere diameter increased. In this study, the relationship between Nusselt and Reynolds numbers indicated that turbulence was low and therefore a correction for convective enhancement in natural conditions will be necessary.

2.4.7 Total Body Resistance

The total thermal resistance of the model barn owl can be compared with the total resistance of live birds if a value for the mean tissue resistance is included. The maximum tissue resistance expressed as an average of total body surface in birds is approximately 100 sm^{-1} (Table 2.10) which is similar to vasoconstricted tissue of mammals (Monteith and Unsworth, 1990). In this way, the total resistance to sensible heat loss in still air of a barn owl is estimated as 608 sm^{-1} and for a wet barn owl as 586 sm^{-1}. The corresponding resistances of the short eared owl and tawny owl are 612 and 631 sm^{-1}, respectively.

Resistance (sm^{-1})	Max	Min	
Eudyptula minor	2.53	1.55	Stahel *et al* (1987)
Domestic hen	0.90	0.64	Richards (1977)
Parus atricapillus	-	0.31	Hill *et al* (1980a)
Perisoreus canadensis	0.77	0.27	Veghte (1964)

Table 2.10. Maximum and minimum tissue resistances (sm^{-1}) calculated from body temperature, skin temperature and dry metabolic heat production of the little penguin (*Eudyptula minor*), the domestic hen, the black-capped chickadee (*Parus atricapillus*) and the gray jay (*Perisoreus canadensis*). Values were expressed as resistances based on surface area which was calculated using the relationship $Area = 8.11m^{0.667}$ between surface area (cm^2) and body mass (g) derived for birds by Walsberg and King (1978a).

The total resistance to sensible heat transfer in the barn owl was compared with resistances calculated from metabolic studies of owls. The rate of sensible heat loss was estimated by subtracting latent heat loss, which is around 4 Wm^{-2} for a range of owl species (Table 2.11), from the total metabolic heat production at an arbitrary temperature of 0 °C (to minimise errors from estimates of latent heat). In this way, the total resistance of barn owls in this study was estimated to be smaller than barn owls of body mass between 410 and 600 g and smaller than the total resistances of all owls measured by oxygen consumption (Table 2.12). A physical model was expected to underestimate total resistance; however, if the total resistance is compared with the measurements of total resistance of dead birds as determined by cooling curves (Herreid and Kessel, 1967), it can be seen that the estimates were not significantly different from a bird equivalent in body size to a barn owl (Figure 2.19).

Figure 2.19 indicated that there was a small increase of total resistance with increasing body size of barn owls as expected from increases of plumage thickness and a reduction in surface area to volume ratio. There was however, found to be no clear relationship between total resistance and body size within owls as a group and it was noticeable that small species had greater resistances than predicted. Conditions of captivity and different measurement techniques could account for this variation but differences may also be due to thermal adaptations of small species to cold climates.

Species	Mass (g)	λE (Wm^{-2})	Tair (°C)	
Otus trichopsis	120	3.7	7.5	Ligon (1969)
Micrathene whitneyi	46	2.9	10	Ligon (1969)
Tyto alba	561	3.5	2	Hamilton (1983, 1985c)
Speotyto cunicularia	138	6.3	0	Coulombe (1970)

Table 2.11. Minimum estimates of latent heat loss from the whiskered owl (*Otus trichopsis*), the elf owl (*Micrathene whitneyi*), the barn owl (*Tyto alba*) and the burrowing owl (*Speotyto cunicularia*) where 1g of H_2O is equivalent to 2500 J and the surface area was calculated using the relationship derived for birds by Walsberg and King (1978a).

	Species	Mass (g)	T_b	r_{tot}	
1	*Otus trichopsis*	100	36	898	Ligon (1969)
2	*Aegolius acadicus*	118	38	1013	Ligon (1969)
3	*Speotyto cunicularia*	138	37	772	Coulombe (1970)
4	*Otus asio*	166	38	882	Ligon (1969)
5	*Asio otus* (male)	230-247	39.5	700	Wijnandts (1984)
6	*Asio otus* (female)	252-211	39.5	656	Wijnandts (1984)
7	*Tyto alba*	410-588	40.4	648	Johnson (1974)
8	*Tyto alba*	488-578	37.8	797	Edwards (1987)
9	*Tyto alba (incub. female)*$^{+}$	490-592	39 *	869	Hamilton (1983, 85a)
10	*Tyto alba (post-incub. female)*	540-600	39 *	876	Hamilton (1983, 85a)
11	*Nyctea scandiaca*	2026	39 *	1342	Gessaman (1972)

Table 2.12. Total thermal resistance of the whiskered owl (*Otus trichopsis*), saw-whet owl (*Aegolius acadicus*), burrowing owl (*Speotyto cunicularia*), screech owl (*Otus asio*), long eared owl (*Asio otus*), barn owl (*Tyto alba*) and snowy owl (*Nyctea scandiaca*) at 0 °C estimated from oxygen consumption studies and one measurement from CO_2 ($^{+}$) production in a nest box. Latent heat loss was estimated as 4 Wm^{-2} and surface area using the relationship derived for birds by Walsberg and King (1978a). * assumed body temperature.

The total resistance of the model in this study was proportional to the square root of wind speed and represented a decline of 56 % between 0 and 7 ms^{-1}. This was similar to previous studies on the long eared owl where wind speed was calculated to reduce the total resistance from a mean of 652 sm^{-1} in still air to 538 (82 %), 518 (79 %) and 474 sm^{-1} (73 %) at wind speeds of 0.9, 1.2 and 1.8 ms^{-1} (Wijnandts, 1984) and from data on the snowy owl which indicated that the total resistance decreased form 1342 to 898 (67 %) and 799 sm^{-1} (60 %) at wind speeds of 4.47 and 7.47 ms^{-1} Gessaman (1972).

Robinson *et al* (1976) also found that the total resistance of white crowned sparrows declined with the square root of wind speed and represented a 24 % reduction at a wind speed of 1.68 ms^{-1}. In contrast Stahel *et al* (1987) reported a linear decline of the total resistance of the little penguin during cold stress, equivalent to a 25 % reduction at 4.7 ms^{-1}. Bakken (1991) examined the wind speed relationship of heated taxidermic mounts of 6 avian species and 4 mammals and found that the total resistances lay between proportionality to $u^{0.16}$ and $u^{0.61}$.

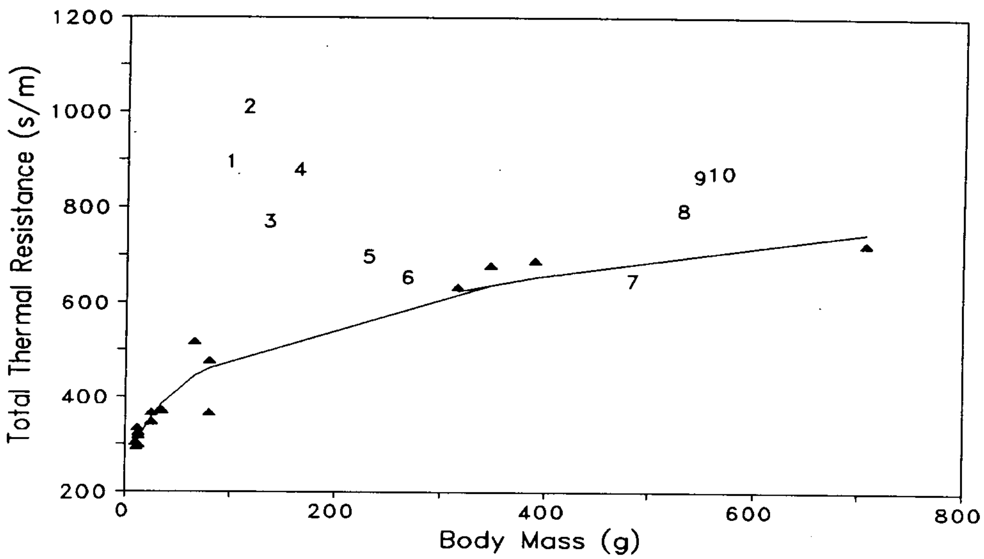


Figure 2.19. The relationship between total resistance to sensible heat loss and body mass for owls (numbers 1 - 10). This was compared with the relationship derived from cooling curves of dead birds ranging in size from 10.6 to 708 g (symbols and line: $r_{tot} = 176m^{0.22}$) by Herreid and Kessel (1967), converted to appropriate units where 100 sm^{-1} is equivalent to an insulation of $0.078W^{-1}m^2$ °C and surface area calculated using the relationship derived for birds by Walsberg and King (1978a).

2.4.8 The Effect of Air Temperature, Wind and Wetting on Total Heat Loss

The sensible heat loss from the model was compared with reported values of total metabolic heat production determined from rates of oxygen consumption, CO_2 production within the thermo-neutral zone and from feeding trials. (Table 2.13). Regression of heat loss with air temperature in this study estimated sensible heat loss to be 37 Wm^{-2} for a barn owl at the lower critical temperature of 23 °C. This was close to measurements of the standard metabolic rate within the thermo-neutral zone and considerably smaller than estimates of metabolisable energy of captive barn owls.

Mass(g)	**T_a (°C)**	**MR (Wm^{-2})**	**Method**	**Author**
540 - 600	23 - 30	43	Oxygen consumption	Hamilton (1983, 85a)
490 - 592	23 - 30	40	CO_2 production	Hamilton (1983, 85a)*
410 - 588	25 - 33	36	Oxygen consumption	Johnson (1974)
488 - 578	22.5 - 32.5	34	Oxygen consumption	Edwards (1987)
527 - 585	25	80	Mouse diet	Hamilton (1983,85b)
410 - 588	16 - 22	54	Beef heart diet	Johnson (1974)
483 - 566	-	75	Live mouse diet	Wallick and Barrett (1976)
333	15	87	Feeding trial	Wijnandts (1984)
358	7 - 13	100	Pheasant chick diet	This study (Appendix 1)
280	-	117	Feeding trial	Ceska (1980)
262	14	66	Cockerel chick diet	Kirkwood (1978)
350	TNZ	35	BMR all owls	Wijnandts (1984)
350	≈15	73	ME cage all owls	Wijnandts (1984)
	23	37	Heat transfer model	This study

Table 2.13. Metabolic rate (MR) of barn owls from gas exchange studies compared with metabolisable energy of caged birds and based on the regression equations ($kJbird^{-1}day^{-1}$) for all owls: $BMR = 1.435m^{0.759}$ and for metabolisable energy (feeding trials) $ME_{cage} = 8.63m^{0.578}$, Wijnandts (1984). Values were converted to heat flux densities assuming 1 litre of oxygen is equivalent to 20.1 kJ (Blaxter, 1989) and surface area was calculated using the relationship derived for birds by Walsberg and King (1978a). * Measurements made of females during incubation inside nest boxes.

Multiple linear regression of sensible heat loss from the model with wind speed and air temperature indicated that in still air, heat loss from the model was 2 to 4 times greater than the metabolic rate of barn owls and several other species of owls below the lower critical temperature (Table 2.14). This indicated the limitation of the model when considering total heat loss from a live bird and stressed the importance of physiological and behavioural mechanisms which are used to minimise heat loss at temperatures below the thermo-neutral zone.

There have been no reported studies on the metabolic response of the barn owl to wind speed. The standard metabolic rate of the long eared owl in a metabolism chamber has however, been found to increase by 18.9 - 35.7 % with wind speeds at 0.9 and 1.8 ms^{-1} for a range of air temperatures (Wijnandts, 1984). The effect of wind speed from the model indicated that an increase of wind speed between 0 and 2 ms^{-1} was predicted to increase sensible heat loss alone by 18 %. The heat production of snowy owls in outdoor aviaries was also found to increase by 60 and 79 % at wind speeds of 4.47 and 7.47 ms^{-1} (Gessaman, 1972) which was similar to a 63 % increase in sensible heat loss at 7 ms^{-1} in this study.

Species	**Mass (g)**	***c***	***m***	**Author**
Otus trichopsis	100	55.7	-1.11	Ligon (1969)
Aegolius acadicus	118	52.4	-0.74	Ligon (1969)
Speotyto cunicularia	138	65.8	-1.13	Coulombe (1970)
Otus asio	166	59.6	-1.62	Ligon (1969)
Asio otus (male)	230-247	76.8	-1.65	Wijnandts (1984)
Asio otus (female)	252-211	81.7	-1.77	Wijnandts (1984)
Tyto alba	410-588	84.4	-1.93	Johnson (1974)
Tyto alba	488-578	65.2	-1.35	Edwards (1987)
Tyto alba (incubating female)	490-592	61.9	-0.95	Hamilton (1983, 85a)
Tyto alba (post-incub. female)	540-600	61.4	-0.82	Hamilton (1983, 85a)
Nyctea scandiaca	2026	37.5	-1.04	Gessaman (1972)

Table 2.14. Linear regressions of metabolic rate (Wm^{-2}) with air temperature (°C) of the form $MR = c + mT_a$ where *a* is the metabolic rate at 0 °C (Wm^{-2}) and *m* is the temperature coefficient (Wm^{-2} $°C^{-1}$) for the whiskered owl (*Otus trichopsis*), saw-whet owl (*Aegolius acadicus*), burrowing owl (*Speotyto cunicularia*), screech owl (*Otus asio*), long eared owl (*Asio otus*), barn owl (*Tyto alba*) and the snowy owl (*Nyctea scandiaca*). Equations were converted to appropriate units assuming 1 litre of oxygen is equivalent to 20.1 kJ (Blaxter, 1989) and surface area was calculated using the relationship derived for birds by Walsberg and King (1978a).

The nature of the relationship between wind speed and metabolic rate of birds reported in the literature is variable. The metabolic rate was proportional to the square root of wind speed in the snowy owl (Gessaman, 1972) and was also found in a number of species, including white crowned sparrows (Robinson *et al*, 1976) and starlings (Kelty and Lustick, 1977). Hayes and Gessaman (1980) determined that the nature of the relationship is dependent on body size and that the relationship is better described with wind speed rather than the square root of wind speed for large raptors which agreed with the linear relationship reported for the 895 g little penguin (Stahel *et al*, 1987). Goldstein (1983) showed that the metabolic rate of Gambel's quail was proportional to wind speed and concluded that the increase in metabolic rate in birds (as measured from oxygen consumption in wind tunnels) can be equally well described by wind speed as by the square root of wind speed. Variation in the relationship most probably stems from the degree of turbulence in wind tunnels.

Species	**T_a °C**	**% Increase MR**	**Method**
Sturnus vulgaris	5 - 40	350 - 400	Immersion in detergent
Corvus frugilegus	2.5 - 24	54 - 73	15 hours (25% rain) and wind
Corvus frugilegus	2.5 - 24	23 - 35	15 hours (25% rain)
Haliaeetus leucocephalus	0 - 20	14 - 26	22.2 cmh^{-1} rain
Haliaeetus leucocephalus	0 - 20	0 - 15	6.1 cmh^{-1} rain
Tyto alba (model)	20	34	Sprayed and 0 - 7 ms^{-1} wind

Table 2.15. The increase in metabolic rate (MR) measured by oxygen consumption, following wetting of starlings (*Sturnus vulgaris*) by Lustick and Adams (1977) , rooks (*Corvus frugilegus*) by Swingland (1973) and bald eagles (*Haliaeetus leucocephalus*) by Stalmaster and Gessaman (1984), compared with the estimated increase of sensible heat loss for the model in this study.

The effect of wetting in this study was to increase the total heat loss from the model on average by 25 Wm^{-2} (SE = 1.5) or by 34 % (SE = 1.4) at all wind speeds. The increase in heat loss was due to a small reduction in coat resistance but was mostly dominated by evaporation at a rate equivalent to 0.22 and 0.52 of potential evaporation from a fully saturated surface. Lentz and Hart (1960) found that the increase in heat loss through the coats of new-born caribou fur measured on a hot plate apparatus increased by 30 % when wetted to the extent that most water was in the form of droplets on the surface (similar to this study). By fully saturating the surface, the rate of heat loss could be increased by 100 % compared with dry fur. A wetting experiment by immersion of starlings (*Sturnus vulgaris*) in a dilute detergent solution resulted in an increase in metabolic rate by almost a factor of 4 (Lustick and Adams, 1977). Saturation to this degree is clearly unrealistic for wild birds other than in extreme conditions and for birds contaminated with oil and as Lustick and Adams (1977) reported, could easily bring about death at moderate air temperatures. A more common form of wetting is likely to be partial saturation of the coat surface and therefore a realistic estimate of the elevation of metabolic rate would be closer to 30 % as estimated for the barn owl in this study. Experiments have indicated that the metabolic rate of bald eagles (*Haliaeetus leucocephalus*) increased by up to 26 %, depending on wetting regime (Stalmaster and Gessaman, 1984). Swingland (1973) also reported increases in metabolism of 23 - 35 % by the rook (*Corvus frugilegus*), while rain combined with wind increased metabolism by 54 - 73 % (Table 2.15).

2.5 SUMMARY

1. A heat transfer model was used to measure heat transfer through barn owl plumage. The mean coat resistance of 4 barn owl coats was 398 sm^{-1} and wetting the coat reduced coat resistance to 374 sm^{-1}. The conductance (reciprocal of resistance) increased linearly with increasing wind speed from 0 - 7 ms^{-1}. Individual coats however, showed non-linearity at low wind speeds.

2. Temperature gradients through the plumage were non-linear and were attributed to model design, superficial thinning of plumage and wind penetration. The effective radiating surface was approximately 4 mm below the physical surface and increased from 9 - 10.5 mm between 3 and 7 ms^{-1}. Water on the coat surface produced a significant fall in surface temperature and a reduction in thermal depth.

3. Heat transfer in barn owl coats occurred by conduction through the feather elements (45 - 50 %), by molecular conduction in air trapped within the coat (35 - 39 %), by radiation (7 - 8 %) and to a lesser extent, by free convection, only with large temperature differences (11 %).

4. Boundary layer resistance of the model decreased from 223 sm^{-1} in still air to 35 sm^{-1} at wind speeds of 7 ms^{-1}. Nusselt numbers for the model with plumage were 30 % lower than those derived for the bare model due to changes in shape. The boundary layer resistance was approximated by relationships between Nusselt and Reynolds numbers derived for smooth cylinders.

5. The total thermal resistance to sensible heat transfer for the barn owl was estimated as 608 sm^{-1} and was smaller than resistances calculated from metabolism studies of live owls. Sensible heat loss from the model at 23 °C was equal to 37 Wm^{-2}, within the range of values of standard metabolic rate. The temperature coefficient of the model was however 2 - 4 times greater than that for barn owls below the lower critical temperature and indicated the importance of physiological and behavioural mechanisms in reducing heat loss.

6. Heat loss from the model was a linear function of wind speed resulting in an increase in heat loss of 60 % at 7 ms^{-1}. Wetting the model increased heat loss by 34 % compared to dry conditions at all wind speeds and was in line with the rise of metabolic rate of birds in previous wetting experiments.

CHAPTER 3

DETERMINATION OF SURFACE TEMPERATURE OF THE BARN OWL USING INFRA RED THERMOGRAPHY

3.1. INTRODUCTION

Infra red (IR) thermography is a technique for converting a scene's thermal radiation pattern into a visible image. This technique allows the distribution of radiative temperature of a surface to be presented as an image divided into temperature bands on a grey or colour scale. Strong absorption of radiation by water vapour and carbon dioxide molecules present in the atmosphere restricts transmission of long wave radiation to two 'windows' of wavelength, 3 - 5 μm and 8 - 13 μm. The temperature measured by thermographic cameras is therefore determined by the flux of thermal radiation detected by semi-conductor sensors in the camera which are sensitive to wavelengths of transmitted radiation in these atmospheric windows.

Thermal imaging has been used extensively in civil, industrial, medical and military fields as reviewed by Burnay *et al* (1988). There has however been considerable interest in the use of this technique to examine the surface temperatures of animals. Veghte and Herreid (1965) demonstrated that the highest surface temperatures in the black-capped chickadee (*Parus atricapillus*), gray jay (*Periosoreus canadensis*), white-tailed ptarmigan (*Lagopus leucurus*) and the raven (*Corvus corax*) were around the eye-auricular region. Hill *et al* (1980a) also reported that the head and breast of black-capped chickadees were consistently the warmest areas. In these studies the surface temperature of most body regions was linearly related to air temperature and thermographic images showed that ptiloerection and postural adjustments were important mechanisms in altering the distribution of surface temperature. Thermograms of the Humbolt penguin (*Spheniscus humboltii*) by Despin *et al* (1978) indicated that flippers and feet were also important for temperature regulation.

IR thermography has been more often used to examine the surface temperature of mammals. Cena and Clark (1973) and Cena (1974) produced thermograms of domestic and zoo animals including the cow, rabbit, elephant, giraffe and zebra. The importance of vasoconstriction and dilation in the pinna of rabbits has been investigated extensively by Hill and Veghte (1976), Hill *et al* (1980b) and Mohler and Heath (1988). Mammal studies also include examination of heat loss in racoon dogs and foxes (Korhonen and Harri, 1986 and Klir and Heath, 1992) and thermoregulation in the Mongolian gerbil (*Meriones unguiculatus*) by Klir *et al* (1990). Thermography was again used to examine changes in temperature of foraging reptiles (den Bosch, 1983), thermoregulatory behaviour of lizards (Jones and Avery, 1989 and Tosini and Avery, 1993) and the effect of solar radiation on the temperature of active honey bees (Cena and Clark, 1972).

Application of thermography has largely been in the detection of patterns of surface temperature and has been less often used to estimate rates of heat loss. Veghte and Herreid (1965) and Hill *et al* (1980a) calculated heat loss by radiation and convection using thermographic measurements and recently Shuran and Nelson (1991) computed heat loss from thermographic images of humans to be within 2 - 7 % of the metabolic rate determined by indirect calorimetry.

In this study, IR thermography was considered to be a useful method to identify the major sites of heat loss on barn owls and quantify the total rate of heat loss in captivity. It was hoped that this would provide further information on the importance of behavioural thermoregulation which was missing from previous wind tunnel studies.

3.2. MATERIALS AND METHODS

An AGA 782 Thermovision system (AGEMA Infra Red Systems Ltd) was used to determine the radiative surface temperatures of live owls in captivity. This equipment consisted of a scanning thermographic camera with an Indium antimonide (InSb) photovoltaic detector cooled by liquid nitrogen (-196 °C) for wavelengths in the region 3 - 5.6 μm. The camera was fitted with a 7 ° lens which had a minimum focus distance of 1 m, a geometrical resolution of 1.1 mrad and the sensitivity of the system was reported by the manufacturers to be 0.1 °C at 30 °C. The camera was operated using the control system and images were recorded with a IVV-V300 Panasonic video recorder onto VHS tape. Recorded images were played back on a thermal imaging computer system (TIC-8000, AGEMA). This produced images with 10 colour temperature bands captured by freezing the image or by snapshot at 1/25 s for flight images. Emissivity of owl plumage was assumed to equal 0.98 according to measurements on animals by Hammel (1956) and emissivity of the epoxy coated surface of the heat transfer model was estimated to be 0.90, similar to rubber (Bayazitoglu and Ozisik, 1988). Image analysis included spot measurement, isotherm and histogram features. The area weighted mean temperature $\overline{T}$ (°C) of the image was calculated from histograms of the image where:

$$\overline{T} = \sum_{i=1}^{n} A_i T_i \Bigg/ \sum_{i=1}^{n} A_i \tag{3.1}$$

where A_i is the percentage of image area with mean temperature T_i (°C).

The sensitivity of the thermographic system was tested using the heat transfer model from previous studies (Section 2.2.1). The model was viewed by the camera at angles of 0, 20, 40 and 70° from the normal to the midpoint of the model surface. The temperature of the model was measured with six 42 s.w.g type T thermocouples (Dural Plastics Ltd) attached to the surface with a small section of Selotape. Images were also taken of the model covered with a plumage sample from a female barn owl. Wetting was also produced by spraying water at room temperature onto the surface of the plumage.

Surface temperature of a 9 year old female barn owl (captive bred) was examined inside an outdoor aviary (7 x 3 x 2 m) using the thermographic system. The owl was allowed to adjust to aviary conditions for several days before the study and was provided with a diet of dead, day-old, pheasant chicks (*Phasianus colchicus*). Images were recorded inside the aviary at a distance of 1 - 5 m from the owl. Air temperature was measured with a shielded 1 mm, type K thermocouple (RS Ltd). The design of the aviary was such that movement of air was negligible and measurements were made in almost complete darkness from 2000 - 2115 GMT on 14 August 1991.

In a second study, the system was used to obtain images of a male great grey owl (*Strix nebulosa*) and a female snowy owl (*Nyctea scandiaca*) in outdoor aviaries at Edinburgh Zoo. In this study, the camera was set up outside the aviaries at a distance of 3 - 5 m from the owls and air temperature was recorded as before. Images were recorded between 1530 and 1630 GMT on 13 February 1992 in low light conditions and with estimated wind speeds < 1 ms^{-1} in the aviaries. Air temperature was recorded with Campbell Scientific 21X and CR10 loggers in all studies.

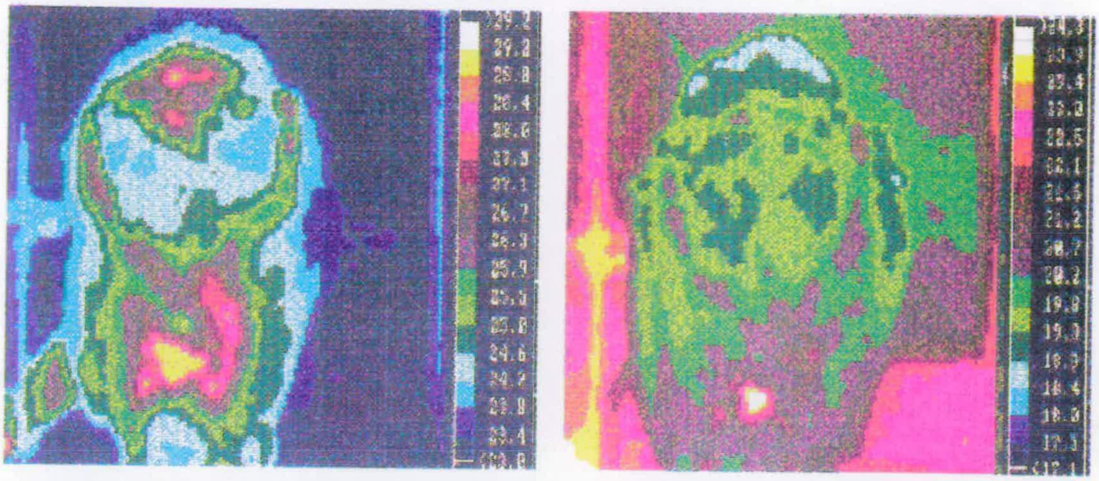
Rates of heat loss from the barn owl were estimated from heat transfer theory of free convection (Section 2.1.2.2). The boundary layer resistance of the perched barn owl was equivalent to a heated cylinder of characteristic dimension equal to a body length of 20 cm. Total sensible heat loss was calculated as the sum of heat loss by free convection and radiation excluding evaporation. Heat loss from images of barn owl wings when outstretched (not moving) were estimated by considering heat exchange from a vertical flat plate of characteristic dimension equal to a mean chord length of 15 cm. Heat loss from the wing was divided into two regions, representing the hot region overlying muscles and the cold region of primary and secondary flight feathers. The characteristic dimensions were 3 and 12 cm, respectively.

The characteristic dimension of a barn owl (as above) was estimated from the head to tail length on a road-killed female barn owl. The surface area of the barn owl (wings closed) was calculated from the area of a cylinder of mean body diameter (8.5 cm) giving an estimated surface area of 650 cm^2. The maximum surface area in flight was obtained by tracing the wing area (single wing = 530 cm^2) and extended tail (120 cm^2). The total surface area in flight was therefore obtained by doubling total wing and tail areas and adding this to the surface area of the main body section in flight (diameter = 7 cm). This gave an estimated total area in flight of 2880 cm^2. These areas should be distinguished from measurements made of wing span (88 cm) and total wing area (1310 cm^2) which were used to estimate flight costs of a 350 g barn owl with the aerodynamic model of Pennycuick (1989).

3.3. RESULTS

3.3.1 IR Thermography and Thermocouple Measurement

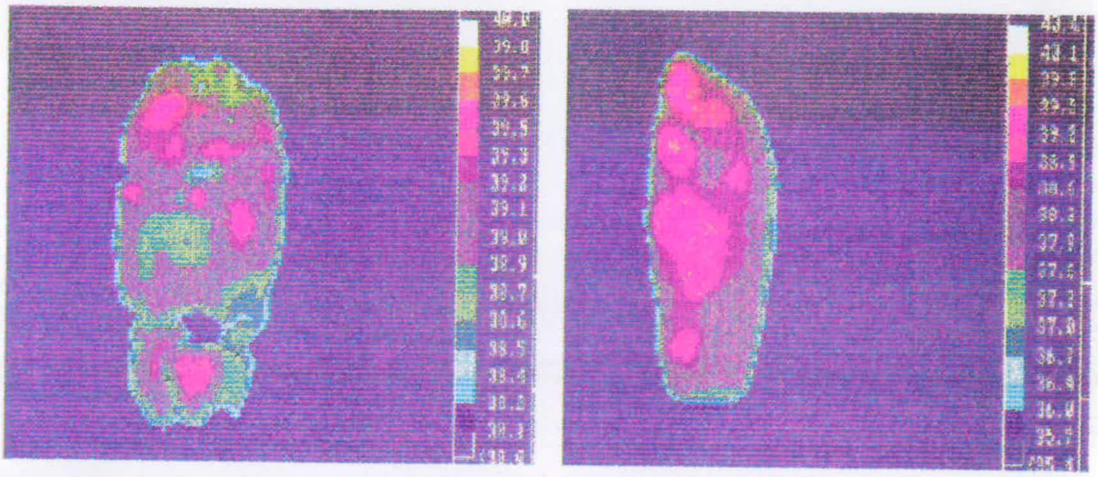
In air temperature of 23.7 ^oC (SE = 0.1), the core temperature of the model was 41.8 ^oC (SE = 0.01) while the surface temperature of the model measured by IR thermography ranged between 38.1 and 39.8 ^oC with a mean of 39.0 ^oC (SE = 0.1) (Figure 3.1 (i)). This compared with surface thermocouple measurements of 37.7 to 38.6 ^oC with a mean of 38.2 ^oC (SE = 0.1). The surface temperature of the model was non uniform with the exception of a narrow band towards the edge which was up to 1 ^oC colder than the centre area. This effect was seen in all images and increased in width on images taken from greater distances. Angle of view was found to produce differences in the temperature pattern of the model surface and differences between the centre and edge of the image increased to 4 ^oC at a viewing angle of 70^o (Figure 3.1 (ii)). The mean temperature of the model was seen to decrease by 0.6 ^oC with increased viewing angles 0 - 70^o, some of which may have been due to a 0.3 ^oC fall of model temperature measured by thermocouples throughout the measurement period (Table 3.1). The temperature of the model recorded by IR thermography was also seen to be 0.5 - 0.8 ^oC greater than from the mean of six thermocouples on the surface of the model (Table 3.1).



(i)

(ii)

Figure 3.2 IR images of model with (i) dry plumage and (ii) wet plumage, at air temperature of 23.7 °C.



(i)

(ii)

Figure 3.1 IR images of model viewed at angles of (i) 0°, and (ii) 70°, at air temperature of 23.7 °C.

	Temperature °C			
Angle °	**IR**	**S.E**	**TC**	**S.E**
0	39.0	0.1	38.2	0.1
20	38.7	0.1	38.0	0.1
40	38.5	0.2	37.8	0.1
70	38.4	0.2	37.9	0.2
Image				
Dry plumage	25.3	0.3	25.0	0.3
Wet Plumage	19.7	0.2	20.7	0.1

Table 3.1. Temperature measurement of the model by IR thermography (IR) and the average of six thermocouples on the surface (TC). Images were taken at angles of 0 - 70° from the normal to the midpoint of the model surface. Images of the model with a covering of barn owl plumage were taken at an angle of 0°.

The plumage-covered model had a mean surface temperature of 25.3 °C (SE = 0.3) (Figure 3.2 (i)) which was equivalent to the temperature of the plumage 2 mm below the surface (Figure 3.3). The IR image indicated that there were maximum temperature differences of 5 °C across the surface. This was considerably greater than the temperature variation on the bare model surface and reflected differences in plumage depth. The hottest area represented a thin area of feathering at the base of the tail and where the wings left the body there were lines of high temperature at either side of the model. The IR image taken after the plumage was wet (Figure 3.2 (ii)) showed that the surface had cooled below air temperature at 22.3 °C (SE = 0.1) to a mean of 19.7 °C (SE = 0.2). This was less than the temperature measured at the physical surface (Table 3.1) and was not consistent with the temperature gradient measured through the plumage (Figure 3.3).

3.3.2 Thermographic Images of the Barn Owl

IR thermography identified the major sites of heat loss from the live barn owl at air temperature of 17.5 °C (SE = 0.1). Figure 3.5 (i) showed the front view of the barn owl while perched, which indicated that areas around the eyes and facial disk were the warmest area of the body. Examination of the face and head region in detail (Figure 3.5 (iii)) revealed that the maximum temperature of the eye was 33.3 - 34.6 °C, which was considerably greater than the mean ventral head temperature of 23.9 °C (SE = 0.4).

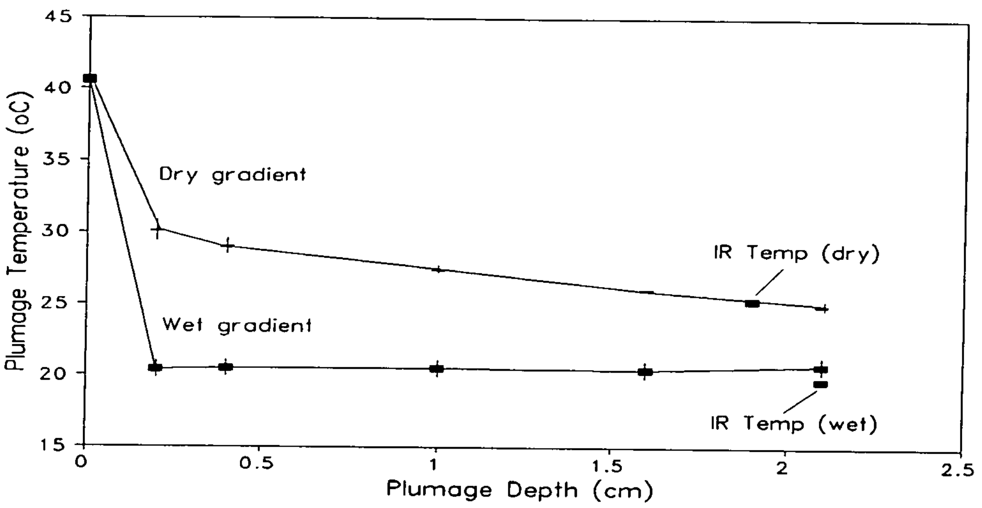


Figure 3.3. The temperature gradient through dry and wet plumage on the model as measured by thermocouples, indicating mean weighted temperature determined by IR thermography for dry and wet plumage. The mean temperature of wet plumage fell below thermocouple measurements. Vertical lines represent standard errors of measurement.

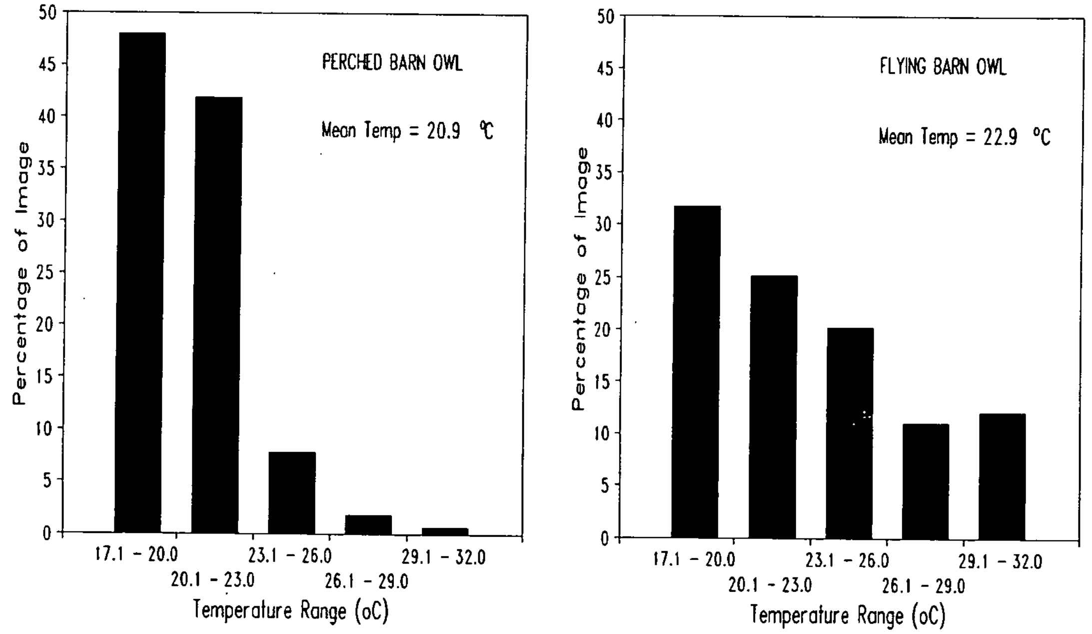


Figure 3.4. Temperature distribution of (i) a perched barn owl and (ii) a barn owl in flight in air temperature at 17.5 °C corresponding to images in Figures 3.5 (i) and (ii) and Figure 3.7. The mean surface temperature of the body was calculated as the area weighted surface temperature.

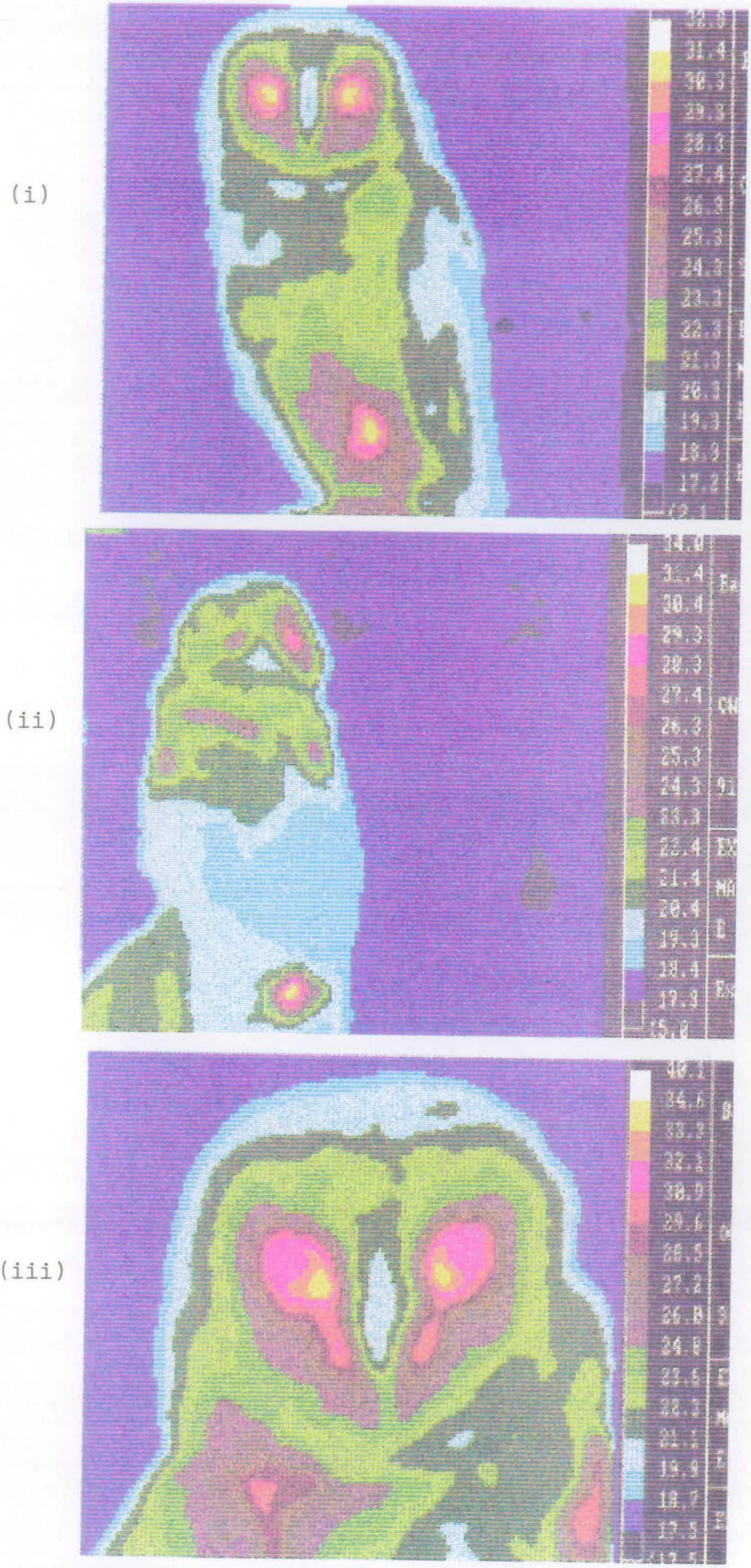


Figure 3.5 IR images of (i) ventral, (ii) dorsal and (iii) head of a barn owl, at air temperature of 17.5 °C.

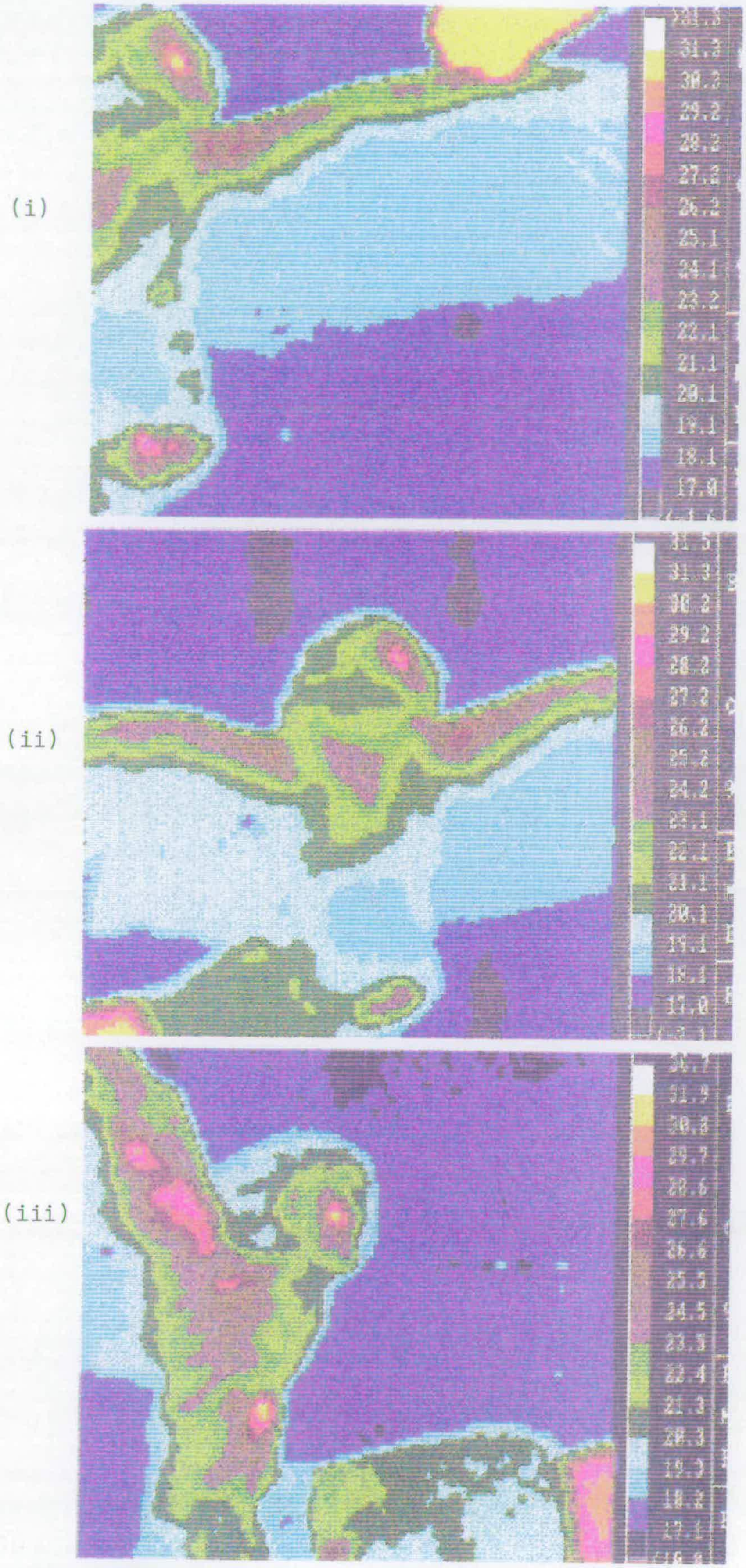


Figure 3.6 IR images of (i) right wing, (ii) both wings and (iii) underside of right wing, of a barn owl at air temperature of 17.5 °C.

Figure 3.5 (i) also identified a region on the lower ventral surface at 27.4 - 31.4 °C, which was significantly warmer than the temperature of surrounding plumage. This area corresponded to the brood patch and has a high rate of heat loss even though this female was not incubating at the time. The image of the owl (hand held) and viewed from the back (Figure 3.5 (ii)) showed that the mean temperature of the dorsal surface at 20.6 °C (SE = 0.5) was colder than the mean ventral surface at 21.8 °C (SE = 0.4). This image also shows a region of high temperature corresponding to the position of the metallic leg ring between the base of the tail feathers. This was probably an experimental artefact due to the difference between camera settings for plumage emissivity rather than the lower value for aluminium.

Images in Figures 3.5 (i) and (ii) were combined to give an estimate of 20.9 °C (SE = 0.5) for the area weighted surface temperature of the perched barn owl in air temperature of 17.5 °C. The temperature distribution was summarised in histogram form (Figure 3.4 (i)) and indicated the highly skewed distribution of surface temperature, with the highest temperatures (26.1 - 32 °C) representing less than 2 % of the total image area.

Figures 3.6 (i), (ii) and (iii) show the temperature distribution of wings while the barn owl was in the hand. Before the owl settled and the images were taken, the owl was seen to flap its wings vigorously. Figure 3.6 (i) shows an image of the dorsal surface of the right wing with a mean temperature of 20.0 °C (SE = 0.6). The image however clearly indicated that there was a small band of high temperature with mean 22.3 °C (SE = 0.7) overlying the musculature in the wing which represented about 30 % of the image area. Approximately 70 % of the wing was considerably colder and had a mean temperature of 18.9 °C (SE = 0.2) and Figure 3.6 (ii) of the dorsal surface demonstrated that a similar temperature pattern existed in both wings. The ventral side of the right wing was also examined following a period of vigorous flapping (Figure 3.6 (iii)) and indicated that the plumage overlying the main pectoral flight muscles was at 23.6 - 28.6 °C.

IR images of the barn owl during short periods of flight were obtained as it flew from a perch and are presented as flight sequences from right to left in Figures 3.7, 3.8 and 3.9. Figures 3.7 and 3.8 indicate that prior to flight the lower wing and tail were indistinguishable from air temperature and it was only the upper body and head which had temperatures significantly above air temperature. At the point of take-off there was a pulse of heat as the wings opened and the plumage temperature overlying the flight muscles was above 30 °C. In Figure 3.9 the heat produced by the leg muscles during take off increased the surface temperature of the legs to around 24 °C.

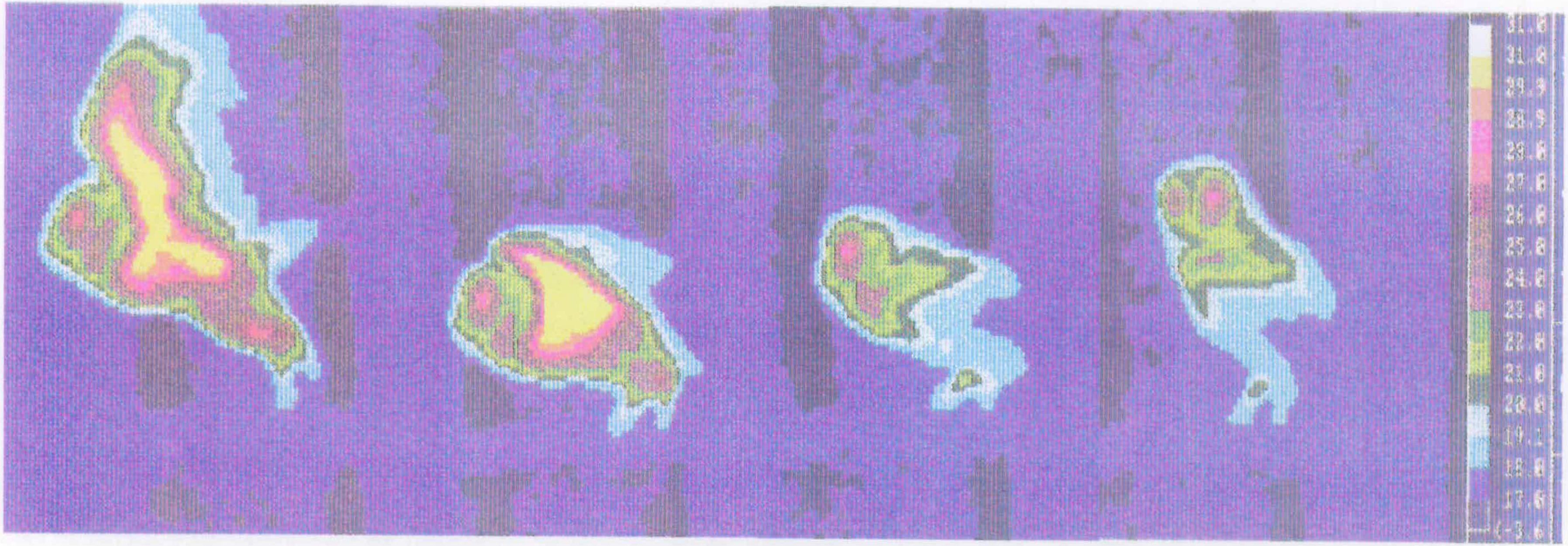


Figure 3.7 IR images of a barn owl in flight, at air temperature of 17.5 °C.

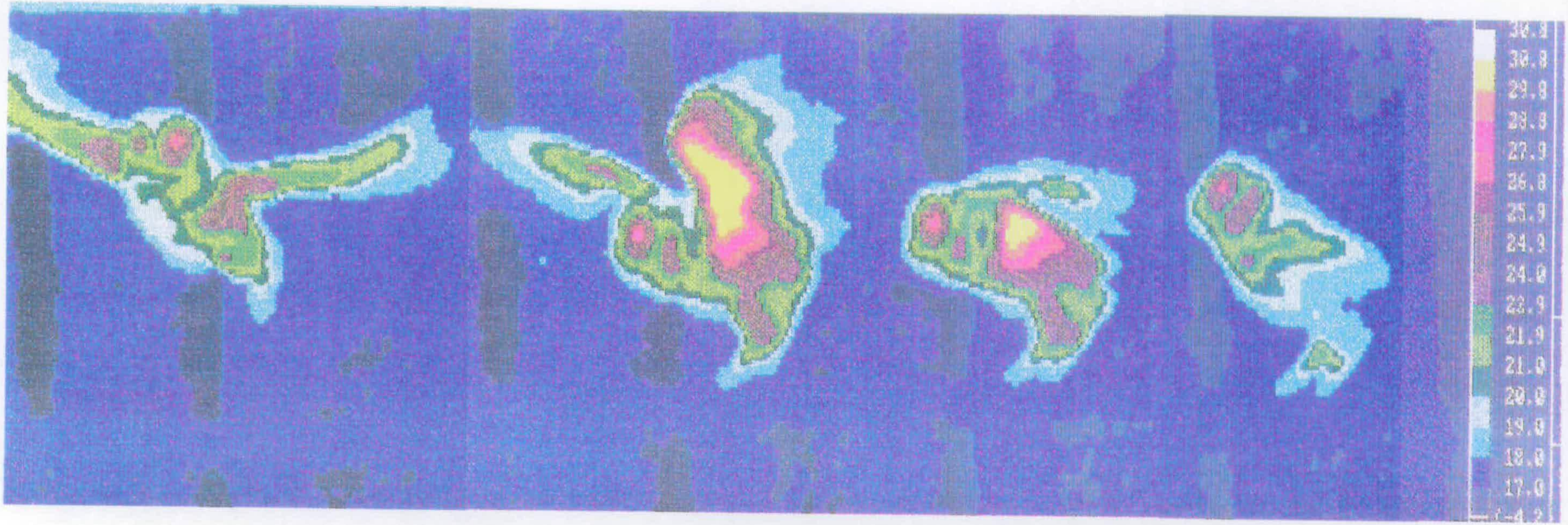


Figure 3.8 IR images of a barn owl in flight, at air temperature of 17.5 °C.

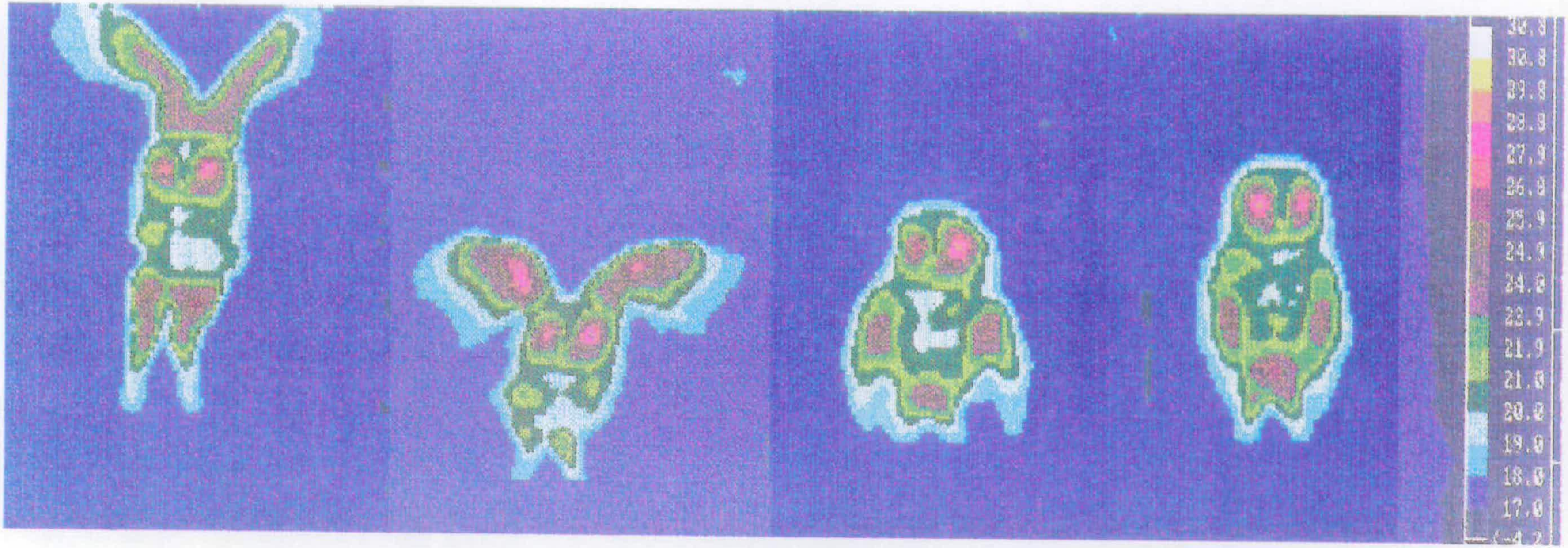


Figure 3.9 IR images of a barn owl in flight, at air temperature of 17.5 °C.

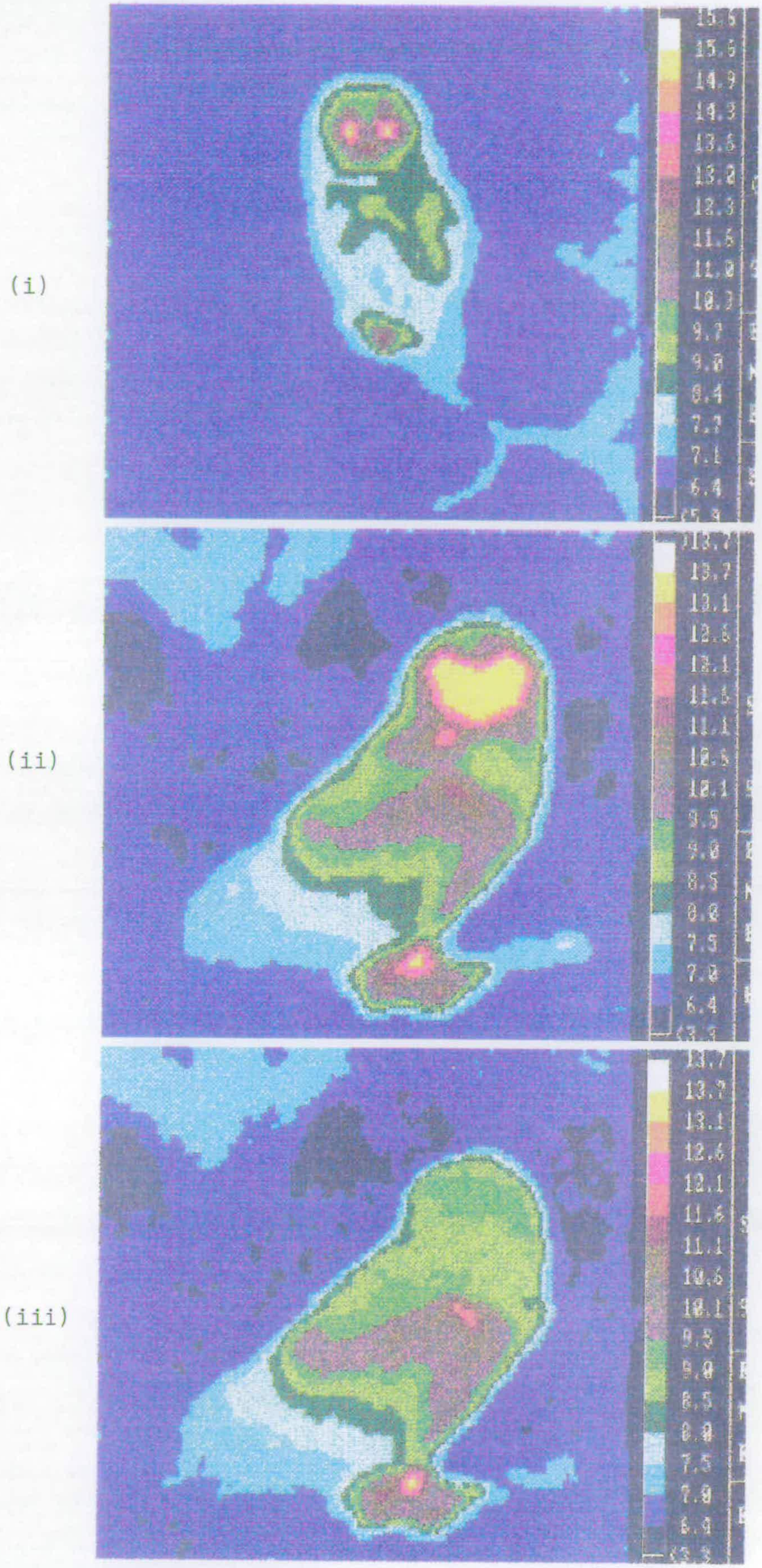


Figure 3.10 IR images of (i) great grey owl, (ii) snowy owl (front), and (iii) snowy owl (back), at air temperature of 6.7 °C.

The images of the barn owl in flight were on average 1.4 °C greater than images of the perched barn owl (Table 3.2). Flight images were characterised by a shift to a more even distribution of temperature such that approximately 20 % of the image area had temperatures 26.1 - 32.0 °C when the wing was fully stretched in flight (Figure 3.4 (ii)).

	Before Flight		**In Flight**	
	Mean °C	**S.E °C**	**Mean °C**	**S.E °C**
	21.0	0.5	21.0	0.4
	21.2	0.5	21.0	0.4
	19.9	0.4	22.1	0.3
	19.7	0.4	22.0	0.3
	19.7	0.4	20.8	0.4
	-	-	20.6	0.5
	-	-	23.3	0.3
	-	-	22.9	0.2
Mean	20.3	0.3	21.7	0.4

Table 3.2. The mean area weighted surface temperature of the barn owl determined by IR thermography before and in flight at air temperature of 17.5 °C.

3.3.3 Thermographic Images of Great Grey and Snowy Owls

The distribution of surface temperatures on the body of a great grey and a snowy owl in air temperature at 6.7 °C (SE = 0.1) was similar to the pattern on the barn owl. Figure 3.10 (i) shows a male great grey owl perched on the branch of a tree and indicates hot spots on the eyes at 14.9 - 16.2 °C and at 10.3 - 12.2 °C around the feet. The mean surface temperature of this image was 8.8 °C (SE = 0.1). Figure 3.10 (ii) shows a female snowy owl standing on the ground facing the camera and in Figure 3.10 (iii) standing with head turned away. The snowy owl had a noticeable heart shaped area of high temperature on the face between 13.1 and 13.7 °C and regions of elevated temperature overlying blood supply and tissue in the wings. The tips of the wings and tail are close to air temperature and the feet were significantly warmer than the ground surface with a hot region corresponding to its metal ring. The mean weighted temperatures of the front and back-facing snowy owl were 9.4 (SE = 0.1) and 8.9 °C (SE = 0.2) respectively.

3.3.4 Determination of Rates of Heat Loss from IR Thermography

The total sensible heat loss from the perched barn owl was estimated to be 31 Wm^{-2} at an air temperature of 17.5 °C (Table 3.3). The rate of heat loss from the head was calculated to be 66 Wm^{-2} which was more than double the rate of the whole body. Sensible heat loss from the wing was estimated to be 23 Wm^{-2} which was less than that from the body of the perched barn owl. However, the heat flux density from the hot area of the wing overlying muscles (56 Wm^{-2}) was almost five times greater than from the cold region of primary and secondary flight feathers (12 Wm^{-2}).

Region	$\overline{T}$	d	Nu	r_a	r_r	C	L	**Total**
Total Area	20.9	0.20	26	350	216	12	19	31
Head	23.9	0.06	10	270	212	29	37	66
Wing Area	20.0	0.15	20	350	217	9	14	23
Hot Region	22.3	0.03	7	200	214	29	27	56
Cold Region	18.9	0.12	14	400	218	4	8	12

Table 3.3. Estimation of convective C (Wm^{-2}), radiative R (Wm^{-2}) and total heat loss (Wm^{-2}) from the body surface, head and wing areas of the barn owl at an air temperature of 17.5 °C. The mean surface temperature determined by IR thermography $\overline{T}$ (°C) was used to calculate the Nusselt number (Nu) for free convection from a cylinder (body and head) or flat plate (wing) of characteristic dimension d (m) to give the boundary layer r_a (sm^{-1}) and radiative resistance r_r (sm^{-1}), (Monteith and Unsworth, 1990).

3.4. DISCUSSION

3.4.1 Measurement Errors with IR Thermography

Infra red thermography has been appreciated by animal physiologists for some time. Cena (1974) listed the advantages of thermography as: (i) the temperature distribution of a surface is seen almost instantaneously and in great detail, (ii) it allows measurement of animal coats with such small heat capacity that solid probes give false readings and (iii) measurements can be made in situations where proximity of the observer disturbs the object being measured. The disadvantages of thermography are that it has a relatively low precision of point measurement and relatively poor accuracy in determining absolute temperatures. This study was in general agreement with these conclusions as will be discussed.

The errors associated with temperature measurement were assessed from images taken from the heat transfer model. This identified an apparent fall in temperature at the outer edge of images associated with the degree of curvature. Watmough *et al* (1970) observed a decrease in temperature and a loss of image at the edges on images of the human face, and determined that radiation interception by the detector surface resulted in a fall in effective emissivity of the object where the surface is highly curved. For a surface with emissivity of 0.98, the associated temperature error was independent of viewing angle up to about 30^{0} but increased from 0.5 to 3 ^{o}C at 30 to 70^{0} and was greater than 4 ^{o}C at angles above 70^{0}. This could account for temperature differences of 4 ^{o}C across the model surface in this study as viewing angle was increased to 70^{0}. Similar curvature effects were also noted on the images of owls and was reported by Hill *et al* (1980a) on images of the black-capped chickadee (*Parus atricapillus*).

Temperatures recorded by IR thermography were 0.5 - 0.8 ^{o}C greater than those measured by thermocouples placed on the surface of the bare model. This difference may have been due to a combination of: (i) the uneven coverage of the model surface with thermocouples, (ii) incomplete contact between the thermocouple and the model surface and (iii) an incorrect emissivity value for the model surface. Images identified temperature variation of up to 2 ^{o}C between hot and cold regions on the model surface which suggested that the difference between the two techniques was due to inadequate coverage of the area with thermocouples. Indeed, Mohler and Heath (1988) recorded differences of ±3 ^{o}C between IR thermography and thermocouple measurements on the pinna of rabbits (*Oryctolagus cuniculus*). It was difficult to assess the degree of error associated with thermocouple attachment and choice of emissivity. The relatively small difference between the two methods however, would indicate that IR thermography provided a reasonably accurate measurement of temperature.

IR thermography also demonstrated that radiation was emitted from an effective surface which lies several millimetres below the tips of feather elements and agrees with the findings of Cena (1974) as discussed in Section 2.4.2. Wet plumage had a mean temperature which was less than thermocouple temperature at all depths within the coat. A change in the emissivity of the surface associated with wetting was not accounted for in image analysis and may have been a source of error.

3.4.2 Major Sites of Heat Loss on Owls

The highest surface temperatures measured on the barn owl were from the regions around the eyes, facial disk, lower abdomen and on the areas overlying musculature on the wings. This temperature distribution was also similar in images of the great grey and snowy owl. Identification of these major sites of heat loss were in general agreement with previous thermographic studies on birds. The maximum recorded eye temperature of the barn owl was 33.3 - 34.6 °C. Veghte and Herreid (1965) showed that the temperatures from the eye-auricular region were -18 to 25 °C for air temperatures -40 to 20 °C for birds ranging in size from the black-capped chickadee to the raven, while Hill *et al* (1980a) recorded eye temperatures above 30 °C on black-capped chickadees at an air temperature of 10 °C.

Overall, the head of the barn owl, great grey and snowy owl was the warmest region of the body due to the high temperature of the eyes and facial disk. Hill *et al* (1980a) reported that the head of the black-capped chickadee was consistently the warmest part of the body at 8 - 10 °C above ambient temperature which was similar to head temperatures in this study. The rate of heat loss from the head alone was calculated to be more than two times greater than from the total body surface of the barn owl. As the head was estimated to represent around 30 % of the surface area of the owl when perched, it is clear that the head is a major site of heat loss for owls. This agrees with the finding that heat loss from the head of the sharp-tailed grouse (*Pediocetes phasianellus*) was 4 times greater per unit area than on the body (Evans and Moen, 1975). Reduction of head area by retraction into the body is therefore seen to be an important mechanism of reducing heat loss. Barn owls and other owls are noticeably hunched when roosting, with eyes and facial disk 'closed up' and thereby benefit by minimising exposure of these areas of high temperature. At night, sharp-tailed grouse decrease head area from 20 to 5 % of total surface area (Evans and Moen, 1975) and many birds place the head under a wing to cover up regions of high temperature (Veghte and Herreid, 1965 and Hill *et al*, 1980a).

A notable area of heat loss on the barn owl was from a region of plumage overlying the brood patch. The female barn owl in this study was not incubating at the time which suggested that this area remains an area of high heat loss outside the period of incubation due either to a relatively high blood supply in this area or to thinner feathering than surrounding areas. It is known that during incubation the brood patch becomes highly vascularised to provide maximum transfer of heat from bird to eggs (Drent, 1975). The temperature of this region (27.4 - 31.4 °C) in this study compared with a reported brood patch temperature of 39.3 °C on an incubating female barn owl and 38.0 °C on the corresponding abdominal skin of a male (Howell, 1964). The combination of warm face and brood patch therefore accounted for the 1.2 °C temperature difference between ventral and dorsal surface. Hamilton (1983) found that ventral surfaces of barn owls were 1.8 - 2.0 °C warmer at 5 - 15 °C and showed that the surface temperature was linearly related to air temperature. Data from previous thermographic studies were examined by linear regression and were compared with measurements of the barn owl at 17.5 °C and at 6.7 °C for great grey and snowy owls (Table 3.4).

Regression equations derived from thermographic studies overestimated the mean surface temperature of the three species of owls examined in this study. The mean surface temperature of the barn owl, however, agreed closely with measurements taken by Hamilton (1983) using an infra red thermometer. This may have suggested that the insulation of owls was greater than in other species of similar body size but the low air temperatures in many of the previous studies probably induced vasodilation to prevent freezing in tissues and would account for higher temperatures than in this study.

3.4.3 Heat Loss from the Barn Owl in Flight

Images of barn owl wings showed that the temperature distribution was related to underlying tissue. The warmest areas of the wings were those overlying the main flight muscles and were around 3 °C warmer than the primary and secondary feathers. This temperature difference indicated that heat loss was almost 5 times greater from the leading edge of the wing than from the cooler wing feathers. Images of flying barn owls indicated that the temperature of flight muscles increased to around 30 °C. This was close to measured wing temperatures of 31.5 - 32.5 °C in the great black-back gull (*Larus marinus*) flying in a wind tunnel at an air temperature of 15 - 19 °C (Berger and Hart, 1974) while Hart and Roy (1967) implanted heat flow disks over the pectoral muscles in pigeons (*Columbia livia*) and measured an increased heat flow from 58 Wm^{-2} at rest to 327 Wm^{-2} in short flights at 17.5 °C.

IR images of the barn owl in flight showed that the surface temperature was on average 1.4 °C greater than in resting images. Although this may have been due to changes in field of view it agreed with a rise in core temperature of 1 - 2 °C from increased energy production associated with flight (Berger and Hart, 1974).

Energy expenditure during flight has been estimated from oxygen consumption of birds flying in wind tunnels, by measuring the mass change of birds during long flights and using the doubly labelled water technique for free ranging birds (Masman and Klaassen, 1987). These measurements have also been successfully used to validate aerodynamic flight models (Tucker, 1973, Rayner, 1979 and Pennycuick, 1989). Muscular efficiency (power output / power input) has not been determined precisely for any avian species but estimates suggest that it is 15 - 25 % (Tucker, 1968, Masman and Klaassen, 1987 and Pennycuick, 1989). The implication of this is that 75 - 85 % of muscular work is converted to heat and is potentially available for thermoregulation. The metabolic rate at minimum power output for a 350 g barn owl in flight was calculated using the computer program of avian flight by Pennycuick (1989) which assumed a conversion efficiency of 0.23. This gave a flight requirement of 19.2 W (69.1 kJ hour^{-1}) at a flight speed of 7.8 ms^{-1} or equivalent to almost 13 times basal metabolic rate (BMR). This estimate was close to generalised relationships of 12.1 BMR for non passerines (Kendeigh *et al*, 1977), 16.2 BMR for the kestrel (*Falco tinnunculus*) and 3.6 - 22.6 BMR for a range of species (Masman and Klaassen, 1987) but considerably greater than 8.3 BMR for the long eared owl (*Asio otus*), (Wijnandts, 1984).

It appears that flight metabolism of this magnitude fully substitutes thermostatic costs. Good experimental evidence to demonstrate the independence of flight metabolism with temperature is lacking, however. Recent studies on exercise metabolism have however shown that in Gambel's quail (*Callipepla gambelii*), walking at 1.5 ms^{-1} substituted for the heat production of a bird at rest in the same air speed over a range of temperatures (Zerba and Walsberg, 1992). Free ranging verdins (*Auriparus flaviceps*) were also shown to partially substitute activity for heat production (Webster and Weathers, 1990). The ability of barn owls to dissipate high levels of heat production in flight was seen to be achieved by a reduction in thermal resistance.

Species	Temp. Range	Equation	Surface Temperature	
			17.5 °C	6.7 °C
Black capped chickadee [a]	-34 to 20	$\overline{T} = 0.85T_a + 14.1$	29.0	19.8
Black capped chickadee [b]	-22 to 27	$\overline{T} = 0.78T_a + 8.6$	22.2	13.8
Gray Jay [a]	-37 to -8	$\overline{T} = T_a + 13.0$	30.5	19.7
White tailed ptarmigan [a]	-34 to -8	$\overline{T} = T_a + 9.4$	26.9	16.1
Raven [a]	-8 to -41	$\overline{T} = 1.2T_a + 9.3$	28.0	17.3
Barn owl [c]	**5 to 25**	$\overline{T} = 1.04T_a + 1.3$	**19.5**	**8.3**
Sharp tailed grouse (head) [d]	?	$\overline{T} = 0.54T_a + 19.0$	28.4	22.6
Sharp tailed grouse (body) [d]	?	$\overline{T} = 0.87T_a + 5.2$	20.4	11.0

Table 3.4. Linear regressions of mean surface temperature $\overline{T}$ (°C) with air temperature T_a (°C) from thermography studies by Veghte and Herreid (1965)[a] (calculated using original data) and by Hill *et al* (1980a)[b] and using an infra red thermometer by Hamilton (1982)[c] (combining dorsal and ventral measurements) and Evans and Moen (1975)[d]. Surface temperatures corresponding to air temperatures of 17.5 and 6.7 °C were calculated for comparison with this study.

Assuming that 77 % of flight metabolism is dissipated as heat, the metabolic heat production of the barn owl was calculated to be 370 Wm^{-2} using the relationship between surface area and body size for birds (Walsberg and King, 1978a), evaporation at rest (Hamilton, 1983, 1985c) and an estimated rise in body temperature of 1 °C. These calculations indicated that the resistance to sensible heat transfer in flight was approximately 100 sm^{-1}, around 80 % smaller than the estimated resistance at rest (Section 2.4.7). This agreed with 58 - 86 % reductions in thermal resistance of other species using the data of Tucker (1968) and Berger *et al* (1971) for the budgerigar (*Melopsittacus undulatus*) and black duck (*Anas rubripes*), where metabolic rate and water loss were measured (Table 3.5). Zerba and Walsberg (1992) measured reductions in resistance of only 29 - 53 % for the Gambel's quail during exercise, which suggests that changes in resistance may be greater in flight. The thermal resistance of a barn owl at 7 ms^{-1} was estimated as 387 sm^{-1} (including tissue resistance, Section 2.3.6) which predicted that equivalent air speeds would not reduce resistance to the same extent as a bird in active flight. The higher surface temperatures of barn owls in flight demonstrated that thermal resistance was reduced considerably during flight and the increase in heat loss was likely to be associated with changes in boundary, coat and tissue resistances.

Species	T_{air}	T_{body}	***M Heat***	λE	r_{tot}	***Ratio***
	°C	**°C**	Wm^{-2}	Wm^{-2}	sm^{-1}	$\frac{r_{flight}}{r_{rest}}$
Budgerigar (flight)	20	42	280	54	130	0.42
Budgerigar (rest)	20	41	100	12^{+}	310	-
Black duck (flight)	19	42 *	570	96 •	60	0.14
Black duck (rest)	19	41 *	70	3 •	420	-
Barn owl (flight)	20	40	370	120	100	0.16
Barn owl (rest)	20	39	-	-	$608^{\otimes}$	-
Barn owl (rest)	Estimate in 7 ms^{-1} wind speed				$387^{\otimes}$	0.26

Table 3.5. Rates of metabolic heat production in the budgerigar (Tucker, 1968) and black duck (Berger *et al*, 1971) compared to the estimated sensible heat loss for a 350 g barn owl (*Tyto alba*) during flight (Pennycuick, 1989). Metabolic heat production was 77% of the flight metabolism and expressed as a heat flux density (*M Heat*) using the relationship between body mass and surface area derived by Walsberg and King (1978a). Latent heat loss (λE) was estimated from total water loss in the budgerigar ($^{+}$) and respiratory water loss in the black duck ($^{\bullet}$) and evaporative loss of resting barn owls (Hamilton, 1983, 1985c) where 1 g H20 is equivalent to 2500 J. Total resistance to sensible heat loss (r_{tot}) was calculated from [$r_{tot} = \rho Cp(T_b - T_a)/MHeat$] and from model results ($^{\otimes}$) to give the ratio between resistance in flight and at rest. Body temperature (*) at rest for the black duck was estimated from the mean of 4 *Anas* spp. (McNab, 1966) and was assumed to increase by 1 °C in flight.

3.5 SUMMARY

1. IR thermography was used to examine the distribution of surface temperature on a captive barn owl, great grey owl and snowy owl. Comparison with conventional thermocouple measurement of a heated model indicated that curvature of surfaces decreased the surface temperature recorded on thermographs, but accuracy was sufficient to detect overall patterns of temperature.

2. The highest surface temperatures on a barn owl were recorded from regions surrounding the eyes, facial disk, lower abdomen and areas overlying musculature on the wings. These patterns were also observed on great grey and snowy owls and were in general agreement with previous measurements. Based on these temperatures, heat loss was estimated to be two times higher from the head than the from the entire body surface.

3. Images of the barn owl in flight were dominated by surface temperatures around 30 ^{o}C on the main pectoral muscles and along the leading edge of the wing. These high temperatures were considered with respect to the reported rises in core temperature and the increase in total energy expenditure during flight.

4. The minimum power output of a 350 g barn owl in flight was estimated to equal 19.2 W (69.1 kJ hour^{-1}) with the aerodynamic model of flight by Pennycuick (1989), using wing measurements from a dead barn owl and assuming a muscular efficiency of 23 %. This estimate was equal to 13 x BMR which was in line with previous metabolic estimates.

5. Total heat loss in flight was calculated to increase from around 50 Wm^{-2} at rest to 370 Wm^{-2} in flight and suggested full thermostatic substitution. The high surface temperatures of the barn owl demonstrated the significant fall in thermal resistance, where resistance to sensible heat loss was estimated to decrease by 80 % during flight. Changes in the boundary layer, the plumage resistance and blood flow were therefore presumed to be responsible for the high rate of heat exchange during flight.

CHAPTER 4

HEAT LOSS, THERMAL RESISTANCE AND MICROCLIMATES OF PREY

4.1. INTRODUCTION

Investigation of barn owl energetics requires an understanding of the ability of barn owls to match energy requirements with food intake. The barn owl is a highly specialised predator and in SW Scotland has been shown to rely predominantly on one species of small mammal, the field vole *Microtus agrestis,* which alone contributes around 50 to 65 % of the weight of prey eaten (Taylor, In press). Environmental factors such as air temperature and wind speed which increase metabolic demands for owls may also be expected to influence the behaviour of prey because of the high rates of heat loss associated with a high surface area to volume ratio of small mammals. It is therefore necessary not only to consider the direct effects of temperature and wind speed on energy requirements of owls but the influence of these variables on the activity of field voles and hence availability of prey.

The field vole is the only species of the genus *Microtus* on the British Mainland and is found on rough ungrazed grassland including young forestry plantations. Adults reach up to 120 mm and body mass shows a seasonal maximum of around 40 g in males and 30 g in females. Field voles are strictly herbivorous, feeding on green leaves and grass stems. The breeding season extends from March / April to September / October, producing a seasonal increase in population size and in addition there are pronounced multi-annual cycles in northern parts of the range (Gipps and Alibhai, 1991).

Knowledge of the behaviour of field voles comes largely from studies of activity and feeding patterns of voles in captivity by Davis (1933), Hansson and Grodzinski (1970), Hansson (1971), Erkinaro (1961, 1970, 1973), Lehman (1976) and Nygren (1978) and from trapping studies in the field (Baumler, 1975). These studies suggest that there are short term and circadian rhythms of activity together with long term seasonal changes in timing of activity. Davis (1933) reported a 2 - 4 hour activity rhythm which Lehman (1976) demonstrated to be essentially a pattern of feeding and rest. Field voles have also been shown to be more active at night with peaks in activity around sunset and shortly before sunrise (Davis, 1973 and Nygren, 1978). It appears, however, that the circadian rhythm shifts seasonally, such that voles in captivity are more active during the day in winter (Erkinaro, 1961, 1970) and capture rates of field voles have been reported to be greatest during the day in winter (Baumler, 1975).

The reason for a seasonal shift towards increased activity during the day in winter is not known but it has been suggested that it is a response to cold nocturnal winter temperatures. The high metabolic rates associated with the small body size of field voles indicate that avoidance of low temperatures may be an important mechanism to reduce overall energy demands. Hansson and Grodzinski (1970) have shown that the metabolic rate of field voles in captivity doubles between temperatures typical of summer and winter. Experiments in captivity also indicate that low temperatures combined with high wind speeds increase metabolic rates and reduce the insulation of mice (Chappell, 1980b) and suggest that weather conditions have an important influence on the activity of small mammals.

This study was therefore an attempt to understand the activity pattern of field voles by examining the implications of weather on insulation and heat loss and to provide greater knowledge of the weather conditions experienced by field voles in the wild. From this it will be possible to examine the effect of environmental conditions not only on energy requirements of barn owls but on the activity patterns of prey and thereby identify critical periods when high energy requirements may also be matched by low prey availability.

4.2. MATERIALS AND METHODS

4.2.1 Heat Transfer Study of the Field Vole

4.2.1.1 Design and Construction of Model

A simple model was designed and constructed to estimate heat loss from field voles and to examine the thermal resistance to heat transfer provided by fur and the boundary layer. The model consisted of an electrically heated solid core over which the pelage of a field vole was fitted. Heat loss from the model was examined in a series of experiments with the use of a small wind tunnel.

The model was constructed from a solid copper cylinder of length 6 cm and maximum diameter of 1.5 cm, which was machined to give a body core which tapered at the front and back. The surface of the copper was electrically insulated by covering the surface with a thin layer of double sided adhesive tape, over which 0.12 mm diameter constantan wire was wound. The wire was secured at the rear with epoxy adhesive and 10 / 0.1 mm multi core extension wires were soldered to the ends. The body was coated with a thin layer of lacquer and a 38 s.w.g, type T thermocouple junction (Dural Plastics and Engineering Ltd) and a 3 kΩ (@ 25 ^{o}C) thermistor were inserted into a 3 mm diameter hole drilled into the centre of the cylinder (Figure 4.1).

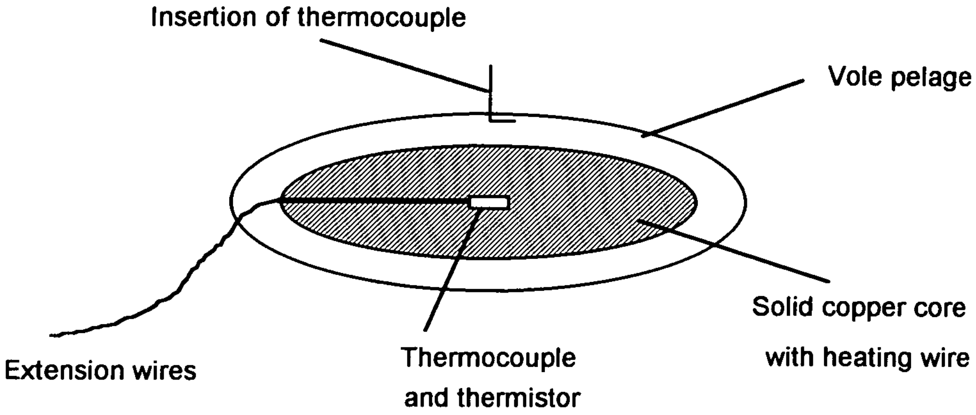


Figure 4.1. Design of heat transfer model of field vole *Microtus agrestis*.

The pelage (skin and fur) from a 13 g field vole was removed following standard taxidermic techniques (Metcalf, 1987). All traces of fat and blood were removed from the skin before placing over the surface of the copper core. This was then secured with adhesive (Bostik Super Glue 4), ensuring that there was good thermal contact between the skin and core. The model was heated using a three-mode temperature controller unit constructed according to Bakken (1983). This was tuned to the core temperature of 38 ^{o}C, with the centrally located thermistor acting as one arm of a resistance bridge and the set-point measured with the thermocouple inserted in the model. The heat flux density from the model, G (Wm^{-2}) was determined according to:

$$G = V^2 / R \times A \qquad (4.1)$$

where V is the heater voltage, R is the resistance of the heater wire (30.6 Ω @ 38 ^{o}C) and A is the surface area of the model (m^{2}). External surface area was calculated as that of a cylinder based on the mean diameter of the model. This was determined from the circumference at several positions along the model by placing a loop of thread around the model and avoiding compression of fur. The thread was cut when the circumference was met and the length measured to 0.1 mm with callipers. The depth of fur on the model was also measured by carefully inserting a metal needle through the fur, marking the depth with a pen and measuring this depth with callipers.

4.2.1.2 Wind Tunnel Design and Experimental Method

A wind tunnel capable of delivering low wind speeds of the magnitude experienced by small mammals was constructed from a 40 cm section of 5 cm diameter perspex piping. At the head of the pipe a section of baffles designed to reduce turbulence was inserted 7 cm from the end of the pipe. These were produced from 4 cm lengths of plastic drinking straws which had been aligned together to form a cylindrical section. A 12 V electric fan was fitted to the head of the tunnel and wind speed was controlled by varying the voltage from a stabilised power supply (Farnell L30 B). A simple working section consisted of an insulated polystyrene base with cardboard sides, both of which were matt black in colour (Figure 4.2).

The model was placed on the working section of the wind tunnel and held approximately 1 cm from the surface on two plastic supports. Five 42 s.w.g, type T thermocouple junctions were placed just below the surface of the vole fur (Figure 4.1) and two additional thermocouples measured air temperature and surface temperature of the working section.

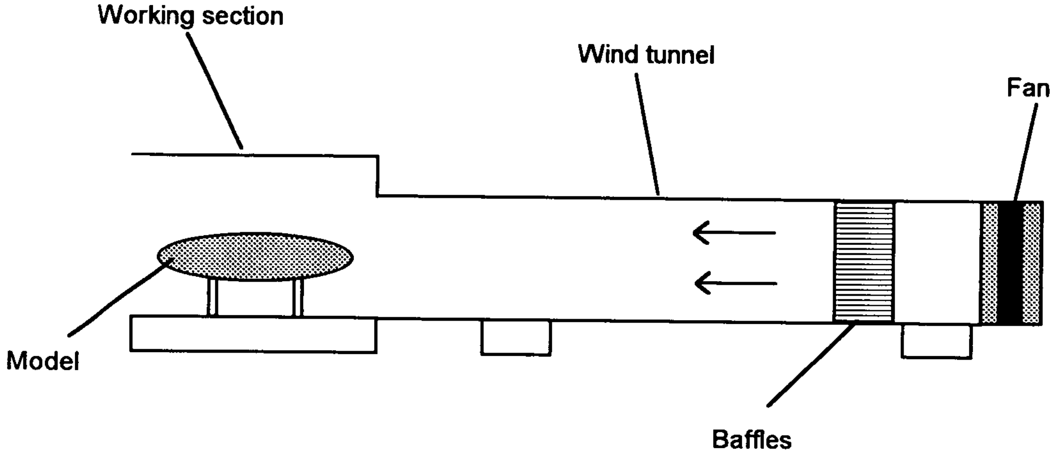


Figure 4.2. Diagram of mini wind tunnel showing position of heat transfer model of the field vole.

Wind speed was measured at the front and rear of the model with a hot-wire anemometer (AVM 501 PSI, Proster Scientific Instruments) which had been calibrated at low wind speeds (Section 4.2.2.2). Temperatures and heater voltage were recorded with a one minute averaging program on a Campbell Scientific 21X logger with a 32 channel multi-plexer using an external thermistor temperature reference. Measurements of heat loss from the model were made at steady state over a range of wind speeds and in still air following wetting from a mist spray at room temperature.

4.2.2 The Microclimate of Field Vole Habitat

4.2.2.1 Field Measurements

The microclimate of field vole habitat was examined during the months February to April 1992 using automatically recording instrumentation within the study area at Eskdalemuir. A suitable area of field vole habitat was selected in an area of *Molinia caerulea - Juncus effusus* rough grassland in a forest ride. A 1.7 m mast accommodated 2 cup anemometers (A100R, Vector Instruments Ltd) located on projecting arms at a height of 1.7 and 0.45 m above the ground surface. The lower anemometer was at a height corresponding to the maximum height of the vegetation.

Five entrances to tunnel systems were identified by the presence of faeces and caches of partially eaten vegetation. At each of these entrances a thermocouple junction was secured and a second was inserted 10 - 20 cm inside the grass tunnel. Thermocouples were 0.2 mm welded tip, type K (RS Ltd) which had been weatherproofed with a thin covering of epoxy adhesive and were soldered to 7 / 0.2 mm multi core extension wire. Radiation errors associated with junction diameter were calculated to be negligible according to Monteith and Unsworth (1990). The thermocouple junctions were configured in parallel to give a mean temperature for entrance and tunnel sites.

Solar radiation was measured at the entrance to a vole tunnel in the centre of a grass tussock using a mini pyranometer (Li-cor LI-200SZ) and the wind speed at the entrance to a vole tunnel was measured with a hot wire anemometer (AVM 501 PSI Ltd) which was set approximately 1 cm above the ground surface and secured with a clamp adjacent to the tunnel. The hot wire anemometer was powered with two 8.5 V regulators run from two 12V 24 Ah lead-acid batteries (Yuasa NP24-12B). The anemometer was calibrated before use (Section 4.2.2.2) and was not found to have drifted throughout the study, by checking the output when the anemometer was covered. At no time during field checks was the hot wire found to be wet.

Outputs from the instruments were recorded on a Campbell Scientific CR10 logger as 10 minute averages. Thermocouples used an external thermistor reference on the logger panel and the hot wire anemometer was sampled with an execution interval of 0.25 seconds. The logging program converted the voltage output from the anemometer to wind speed and corrected for temperature effects. Supply voltage of the anemometer was also recorded. Measurements were compared with the data collected from the meteorological station set up at the beginning of the study and additional snowfall records were obtained from Eskdalemuir Meteorological Observatory.

4.2.2.2 Calibration of Hot Wire Anemometer

The hot wire anemometer was calibrated at low wind speeds and the effect of air temperature and supply voltage were examined. The calibration procedure involved moving the anemometer at constant rates over a known distance to give an independent measure of wind speed. A moving platform arrangement which consisted of an aluminium trolley which ran freely on bearings along smooth rails was modified for this purpose. The speed of the trolley was controlled by a step motor working a plastic tracked belt connected to the centre of the trolley. The step rate of the motor was controlled by a BBC microcomputer which was programmed to move the motor at half steps at known execution intervals. The mean distance moved for a half step of the motor was measured and therefore the trolley could be run back and forth over a range of speeds between 5 and 50 cms^{-1}. A plastic enclosure was placed over the top of the calibration apparatus and ensured still air conditions during calibrations.

The anemometer was mounted vertically on the trolley and was calibrated from the mean of 5 runs at each wind speed. The voltage output from the anemometer was logged with a Campbell Scientific 21X logger with measurement execution intervals of 0.1 s at low wind speeds and at 0.05 s for wind speeds greater than 35 cms^{-1}. This ensured that the sampling frequency was well within the response time of the anemometer. Output from the anemometer was determined by rejecting acceleration and deceleration readings at the start and the end of each calibration.

The voltage output from the hot wire anemometer showed a curvilinear increase with increasing wind speed. A third order polynomial was fitted to the mean output mV at each wind speed giving wind speed u (cms^{-1}) from:

$$u = 3.39 + 0.059mV + 7.5\times10^{-7}mV^2 + 2.3\times10^{-7}mV^3 \qquad R = 1.0 \quad (4.2)$$

The effect of air temperature on anemometer output was examined by placing the anemometer and control box inside a cooled incubator (Gallenkamp IH 270). The anemometer was clamped at the base of a vertically mounted plastic tube fitted with a 12 V electric fan (Micronel Ltd) run from a stabilised power supply (Farnell L30B). Using the known calibration of the anemometer at 20 ^oC, the supply voltage to the fan was adjusted to give known wind speeds by monitoring a digital volt meter (Beckman Industrial DM78). These voltages were then converted to wind speed settings between 0 and 50 cms^{-1} from 1 to 20 ^oC. Air temperature inside the incubator was measured with a 0.2 mm welded tip, type K thermocouple which was recorded together with anemometer output at steady state on a 21X Campbell Scientific logger. The anemometer functioned well over the range of air temperatures but it was found that the anemometer had a mean temperature coefficient of -7 mV^oC^{-1} (SE = 0.21) which was consistent at all wind speeds.

The effect of supply voltage on anemometer output was investigated by allowing the voltage provided by 9V alkaline cells to decrease with continuous use. The anemometer was mounted in air flow of approximately 10 cms^{-1} using the wind tunnel arrangement and the mean battery voltage, anemometer output and air temperature were recorded as 15 minute averages over 48 hours. The output from the anemometer fell rapidly with decreasing battery voltage within 24 hours continuous operation. 9V batteries were therefore replaced with a supply from two 8.5 V regulators run from two 12V, 24 Ah lead acid batteries which gave satisfactory operation for 10 days in the field.

4.3 RESULTS

4.3.1 Heat Loss and Thermal Resistance of Model

In still air, heat loss from the model vole was 73 Wm^{-2} (SE = 0.3) and increased to 225 Wm^{-2} (SE = 2.7) following wetting. The heat flux G (Wm^{-2}) from the model increased linearly with increasing wind speed, u (ms^{-1}) according to:

$$G = 72.6 + 18.4u \qquad R=0.98 \qquad (4.3)$$

Heat transfer by radiation was calculated using the Stefan-Boltzmann equation (Equation 2.14) using measured surface temperatures and an emissivity of 0.98 for fur (Hammel, 1965). Subtraction of radiative loss from the total gave the convective loss and indicated that radiation and convection represented 39 and 61 % of the total heat loss in still air (Figure 4.3). Heat loss by radiation decreased linearly over the range in wind speeds while convection showed a corresponding increase. At the highest wind speed of 0.85 ms^{-1}, radiation accounted for only 18 % of total heat loss while convection accounted for 82 %.

Vole fur on the model was estimated to be 5.8 mm thick (SE = 0.6) and had a resistance in still air of 242 sm^{-1} (SE = 0.5). Wetting the fur brought about a 55 % reduction in coat thickness to 2.6 mm (SE = 0.3) and significantly reduced resistance by 67 % to 79 sm^{-1} (SE = 1.15) (two sample t test $p > 0.01$). The resistance of dry fur was reduced significantly to 234 sm^{-1} (SE = 0.94) by a wind speed of 0.2 ms^{-1} ($p > 0.025$) but thereafter remained constant at all wind speeds (Figure 4.4).

The boundary layer resistance of the model, r_a (sm^{-1}) declined linearly with increasing wind speed according to:

$$r_a = 144 - 103u \qquad R = 0.98 \qquad (4.4)$$

Examination of the relationship between Nusselt and Reynolds numbers indicated that Nusselt numbers increased linearly with increasing Reynolds numbers in the range 340 - 1460, according to:

$$Nu = 0.01Re + 5.12 \qquad R = 0.99 \qquad (4.5)$$

Although the relationship was linear, Nusselt numbers were similar to those predicted by the logarithmic relationship derived for smooth cylinders (Monteith and Unsworth, 1990) but at high Reynolds numbers were greater than from the relationship derived for a heated metal cast of a masked shrew (*Sorex cinereus*) with similar diameter (Chappell, 1980b), (Figure 4.5).

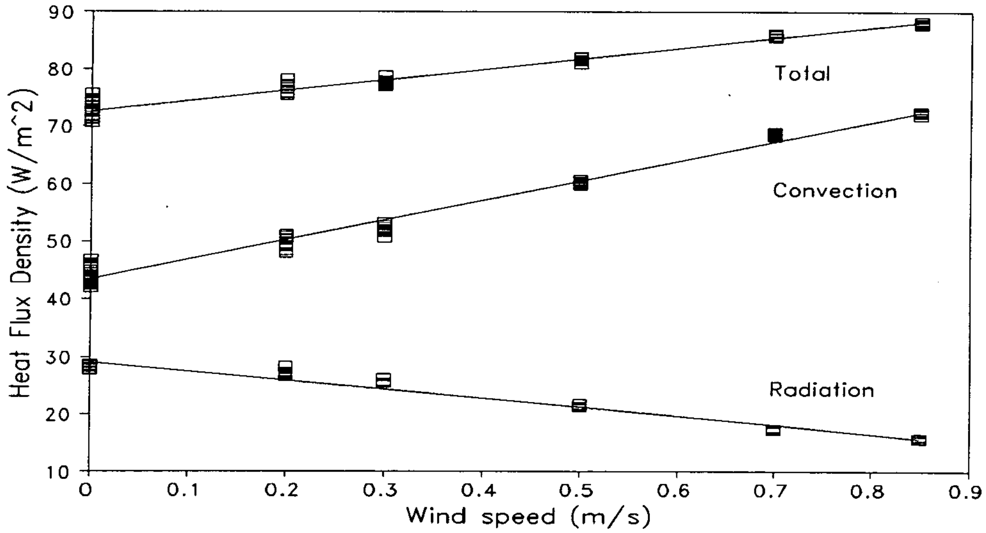


Figure 4.3. The effect of wind speed on total, convective and radiative heat loss from the model vole in steady state conditions.

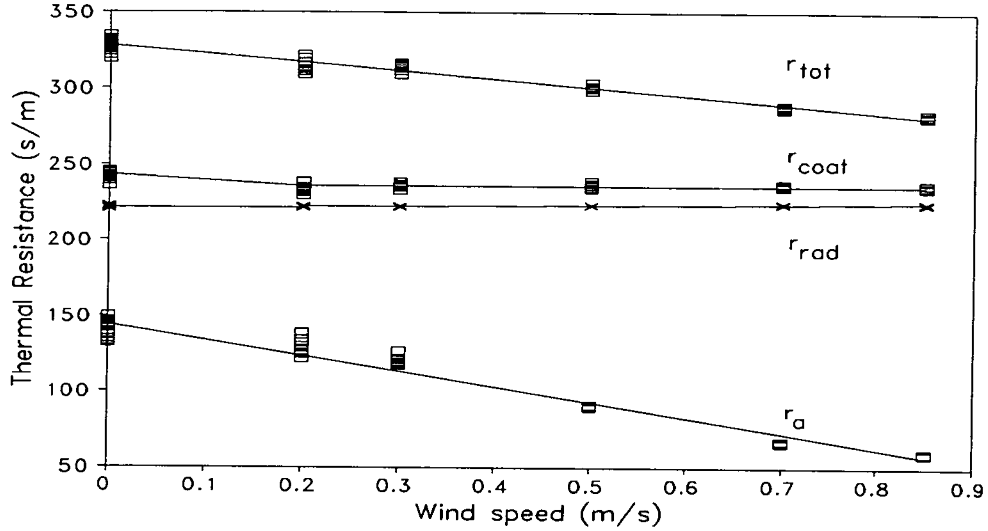


Figure 4.4. The effect of wind speed on thermal resistances (sm^{-1}) of the model vole at steady state. Linear regression lines are plotted for the total resistance (r_{tot}) and the boundary layer resistance (r_a). Lines are plotted through the mid point of data values for the coat resistance (r_{coat}) and the radiative resistance (r_{rad}).

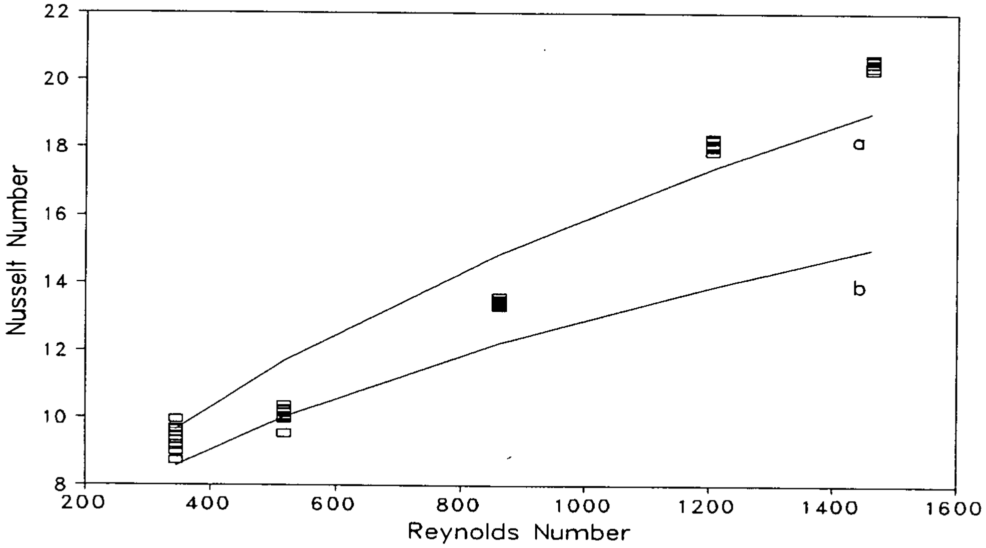


Figure 4.5. The relationship between Nusselt and Reynolds numbers for the model vole. This is compared with the relationship derived for smooth cylinders (line a), (Monteith and Unsworth, 1990) and for a heated metal cast of a masked shrew (*Sorex cinereus*) (line b) with similar diameter, (Chappell, 1980b).

Coat and boundary layer resistances were combined with the radiative resistance (which remained constant at 223 sm^{-1} (SE = 0.5)) to give the total resistance of the model (Table 4.1). Total resistance declined from 328 sm^{-1} (SE = 0.74) in still air to 282 sm^{-1} (SE = 0.22) at 0.85 ms^{-1} according to:

$$r_{tot} = 328 - 55.8u \qquad R = 0.98 \qquad (4.6)$$

Wind Speed (ms^{-1})	r_c (sm^{-1})	r_a (sm^{-1})	r_r (sm^{-1})	r_{tot} (sm^{-1})
0	242 (0.46)	141 (1.1)	221 (0.12)	328 (0.74)
0.2	234 (0.95)	129 (1.5)	222 (0.04)	315 (1.24)
0.3	236 (0.46)	120 (0.8)	222 (0.03)	314 (0.67)
0.5	236 (0.40)	90 (0.2)	223 (0.02)	301 (0.46)
0.7	235 (0.24)	67 (0.1)	224 (0.02)	288 (0.30)
0.85	235 (0.21)	59 (0.1)	224 (0.03)	282 (0.22)

Table 4.1. Thermal resistances of the model vole, including coat (r_c), boundary layer (r_a), radiative (r_r) and total thermal resistance (r_{tot}) at wind speeds from 0 to 0.85 ms^{-1}. Values in brackets are standard errors of measurements from the model at steady state.

4.3.2 Vole Microclimates

The microclimate of vole habitat was described by measurements of temperature, solar radiation and wind speed. Measurements were made between 11 February and 3 April 1992 during which continuous records of temperature and solar radiation were obtained for 50 days and wind speed was measured for 36 days between 28 February and 3 April. Throughout the study period there were only 5 days when <0.2 mm of rain was recorded (this excluded 2 days with no rainfall data). There were 9 days on which snow was lying at 9 am, 20 days of snow or sleet and 9 days during which hail or ice pellets were recorded falling. These reports identified three main periods of snowfall from 15 - 20 February, 11 - 16 March and 1 - 3 April.

The data was summarised as hourly averages and were used to calculate daily averages and maximum and minimum hourly values of temperature, solar radiation and wind speed (Table 4.2). An hourly summary of weather variables was also determined for periods excluding periods of snow cover.

Measurement	Daily Mean	Hourly Max	Hourly Min
Tunnel Temperature (°C)	4.7	12.0	-3.3
Entrance Temperature (°C)	4.2	11.0	-6.6
Solar Radiation at Noon (Wm^{-2})	17.9	40.0	0 *
Wind speed (ms^{-1})	0.13	0.29	0

Table 4.2. Microclimate of vole habitat from 11 February to 3 April 1992, summarised as the daily mean and hourly maximum and minimums of vole tunnel and entrance temperatures and 1200 GMT solar radiation at the entrance to a tunnel where * denotes minimum radiation when instrument was buried beneath snow. Wind speed was measured at the entrance to a vole tunnel between 28 February and 3 April 1992.

The mean daily temperature of vole habitat was similar to air temperature measured nearby at 9 m over the sitka spruce plantation. On average, the temperature inside the tunnels was only 0.5 °C above the temperature measured at the entrances, but during a period of snow cover the temperature of the tunnel was more than 3 °C warmer. The temperature of vole habitat in the absence of snow cover exhibited a typical pattern of diurnal warming and nocturnal cooling similar to the diurnal change in air temperature measured above the forest (Figure 4.6). Relative temperature differences indicated that the temperature inside vole tunnels was greater than the air temperature during the day and night, with the exception of a single period during early evening. This was seen as a time lag between the cooling rate of air and the cooling rate of the surface during the afternoon and early evening. The rapid change in temperature at the surface with respect to air temperature was clearly seen from temperature measurements at the entrances to vole tunnels which remained below air temperature throughout the night.

The effect of snow cover was to insulate vole habitat from large changes in air temperature, especially during the night. The potential benefits of higher temperatures for voles beneath the snow were seen from measurements made during the period of snowfall between 1 and 3 April (Figure 4.7). During this period, snow was recorded falling on each day and was recorded lying at Eskdalemuir on 2 April. From examination of air temperature, it was estimated that snow fell during the afternoon of 1 April and a field visit on 3 April verified that the site remained covered by an estimated 5 cm of snow. This indicated that the temperature of vole habitat remained relatively stable and above air temperature under snow. In the grass tunnels the temperature was found to be as much as 3 °C above air temperature during the coldest period of the night.

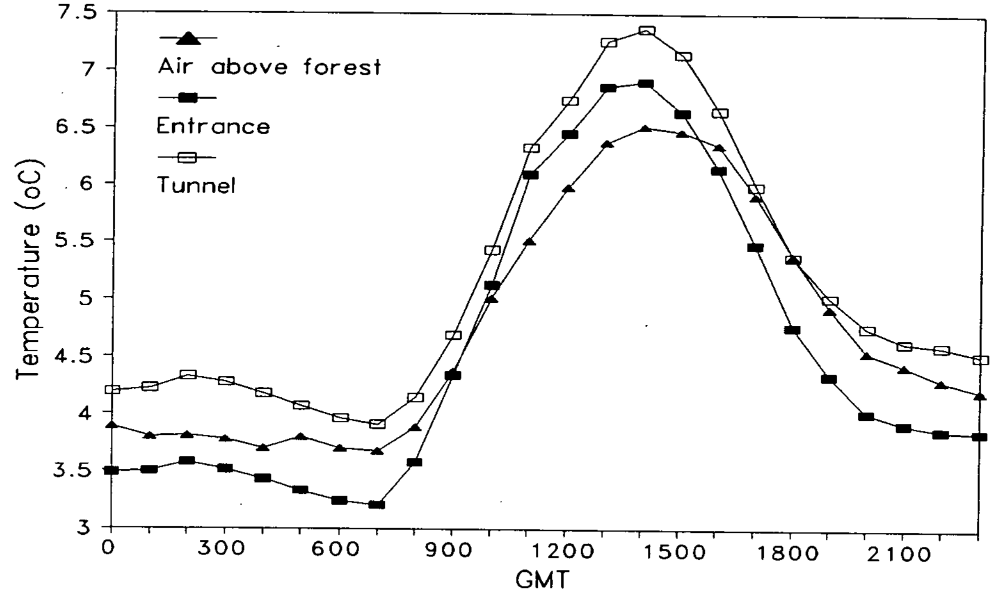


Figure 4.6. The mean temperature of vole habitat in *Molinia - Juncus* vegetation measured at the entrance and inside tunnels from February to April 1992 during periods with no snow cover. These measurements are compared with the temperature of air measured nearby at 9 m over a sitka spruce plantation.

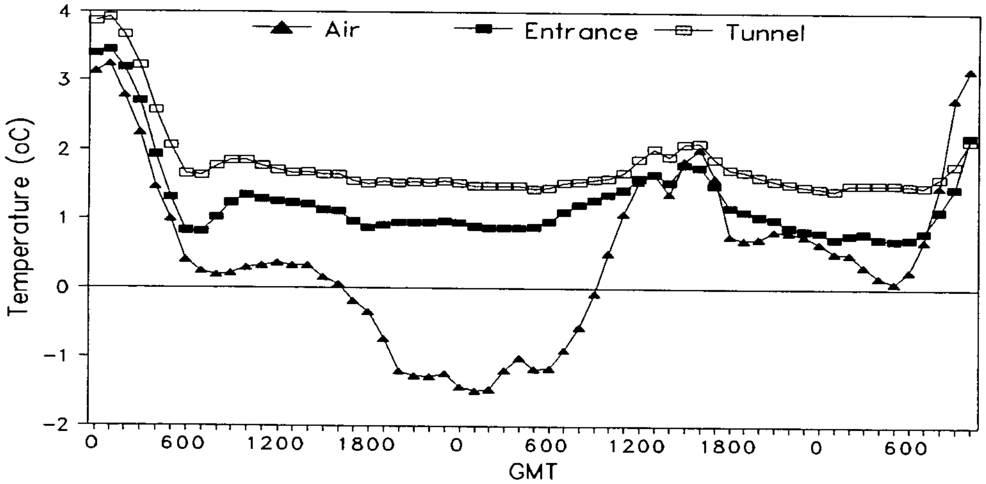


Figure 4.7. The temperature of vole habitat measured during a period of snow cover from 1 - 3 April 1992. The temperature measured at the entrances and inside tunnels remained relatively constant above air temperature.

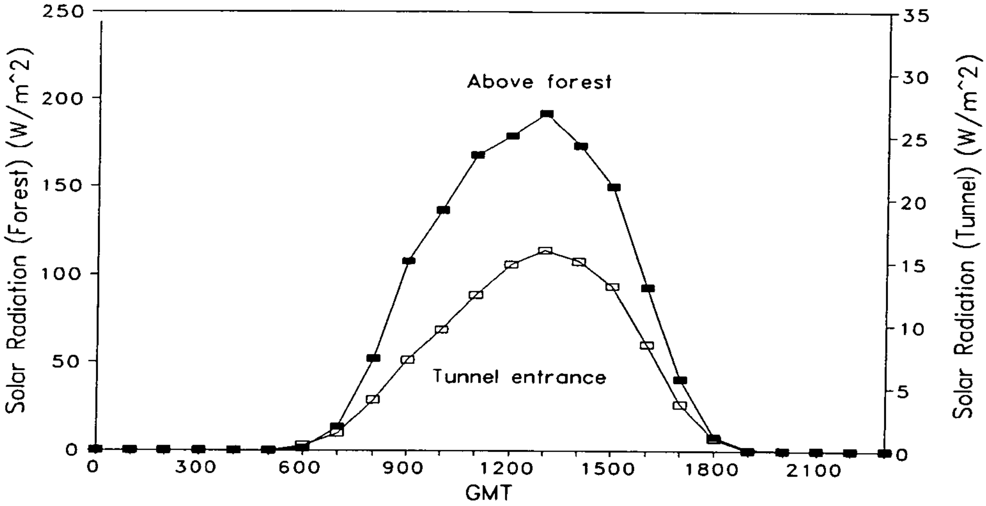
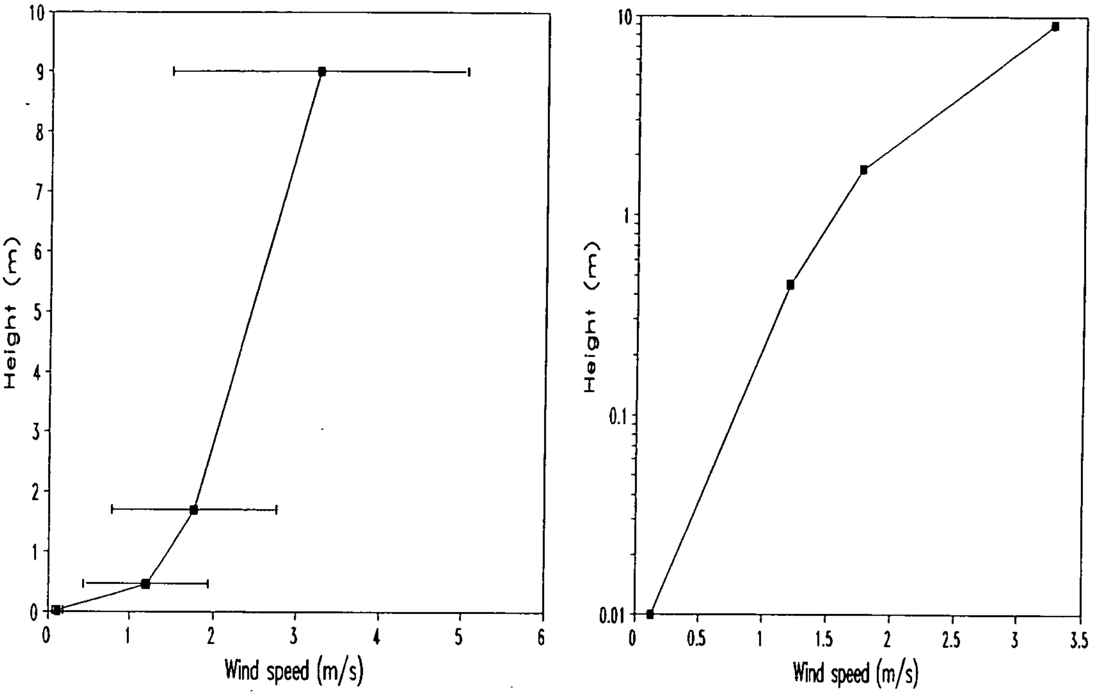


Figure 4.8. Comparison between solar radiation measured at the entrance to a vole tunnel amongst *Molinia - Juncus* vegetation and nearby at 9 m, over a sitka spruce plantation.

Solar radiation within the grass tussock vegetation showed a diurnal pattern corresponding to the flux above the forest (Figure 4.8), however, the flux represented only 8 % of total solar radiation. On average, the maximum radiation flux at solar noon was found to be 17.9 Wm^{-2} but there was considerable day-to-day variation, ranging from a maximum of 40 Wm^{-2} to a minimum of 0 Wm^{-2} with snow cover (Table 4.2).

The mean daily wind speed recorded at the tunnel entrance throughout the entire study period was 0.13 ms^{-1} and the maximum hourly wind speed was 0.29 ms^{-1} (Table 4.2). This compared with a daily mean of 1.16 ms^{-1} and a maximum hourly wind speed of 3.23 ms^{-1} at 0.45 m above the ground surface. A mean hourly wind speed of 0 ms^{-1} was recorded at the tunnel entrance for 95 hours or 11% of the study period and it was clear that the wind speed measured at this position was closely coupled to wind at greater heights above the surface. The change in wind speed with height above the surface was examined by plotting the height against the mean hourly wind speed (excluding days of snow cover), (Figure 4.9). The wind profile indicated a rapid increase in wind speed above the surface of the ground, above *Molinia - Juncus* vegetation in the forest ride and above the sitka spruce plantation.

The mean wind speed in vole habitat, above the grassland and above the forest showed a strong diurnal pattern. Mean hourly wind speed was relatively constant throughout the night, dropped to a minimum around dawn, increased to a maximum around solar noon and then decreased throughout the afternoon and early evening (Figure 4.10).



(i) (ii)

Figure 4.9. Wind profiles, plotted as height against mean hourly wind speed on (i) linear and (ii) logarithmic scales of measurement height. Measurements were made using a hot wire anemometer at 1 cm above the ground surface at the entrance to a vole tunnel and using cup anemometers at 0.45 and 1.7 above *Molinia - Juncus* vegetation in a forest ride and at 9 m, over a sitka spruce plantation. Error bars in (i) are standard errors of wind speed for February to April excluding snow periods.

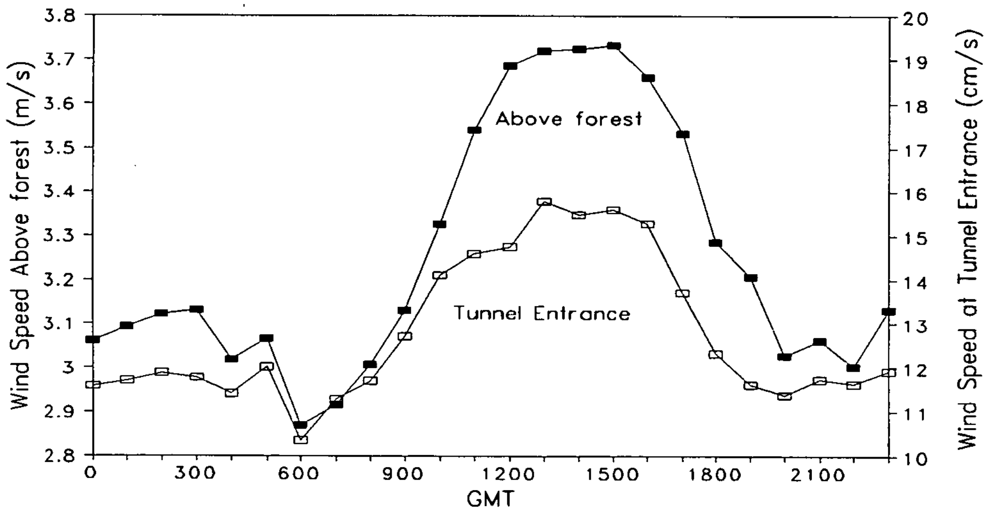
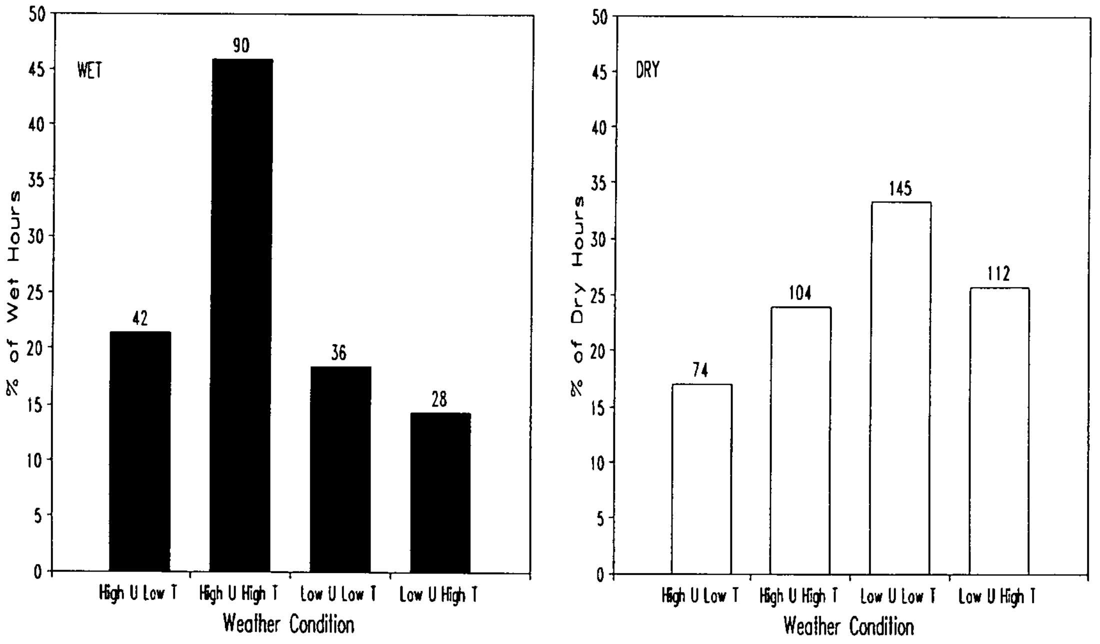


Figure 4.10. Mean hourly wind speed measured at the entrance to a vole tunnel and at 9m, over a sitka spruce plantation between 28 February - 3 April 1992 during periods of no snow cover.

The wind speed at the entrance to the tunnel was not always zero during periods of snow cover. Checking the data on days on which snow was recorded lying at 9 am indicated that on 2 days (1 cm and 4 cm snow depth) the wind speed at the tunnel entrance was 0 cms^{-1}. A day with a trace amount of snow had a mean hourly wind speed of 9 cms^{-1} and on a day with 1 cm of snow the wind speed was 13.7 cms^{-1}. This variation in wind speed may therefore have indicated incomplete covering of the anemometer by snow.

The effect of weather patterns on the energetics of field voles was examined by calculating the simultaneous occurrence of rainfall with high or low temperature and wind speed between 28 February and 3 April, excluding periods of snow cover. The weather over this period was divided into hours in which rain or no rain was recorded and again divided if the temperature and wind speed at the entrance to vole tunnels was greater or less than the mean wind speed and temperature, averaged over the entire period (Figure 4.11). Data was analysed for 631 data hours during periods free from snow cover of which 196 were wet and 435 were dry hours. The analysis suggested that wet hours were characterised by higher than average wind speeds and temperatures while dry hours were characterised by lower than average wind speeds and temperatures.



(i) (ii)

Figure 4.11. The combination of weather conditions between 28 February and 3 April 1992 during periods of no snow cover. The number of hours in each category are given above the bar.

4.4 DISCUSSION

4.4.1 Heat Loss and Thermal Resistance of the Field Vole

4.4.1.1 Heat Loss from the Field Vole

Measured rates of heat loss from the model were compared with metabolic rates of the field vole from oxygen consumption studies in captivity. Hansson and Grodzinski (1970) determined the relationship between the rate of oxygen consumption and body mass for the field vole at temperatures below the thermo-neutral zone. When expressed as a flux density this gave a value of 98 Wm^{-2} for a 13 g vole at 20 °C. Latent heat loss was estimated from measurements on deer mice (*Peromyscus maniculatus*) which showed an increase in the ratio of latent heat loss to metabolic heat production from 0.05 to 0.35 between 0 and 30 °C (Chappell and Holsclaw, 1984). Subtraction of latent heat loss at 20 °C gave an estimated dry metabolic heat production of 78 Wm^{-2} for a field vole. This was close to the value of 73 Wm^{-2} determined with the model in this study (Table 4.2).

Temperature °C	**Estimates From the Model** G (Wm^{-2})	λE (Wm^{-2})	$G + \lambda E$ (Wm^{-2})	**Measured Metabolic Rate** (Wm^{-2})
0	149	8	157	163
10	110	14	124	138
20	73	20	93	98
30	32	14	46	41

Table 4.3. Comparison between the metabolic rate of a 13 g field vole *Microtus agrestis* estimated from heat transfer theory in this study with the metabolic rate calculated from oxygen consumption studies by Hansson and Grodzinski (1970). The dry metabolic heat production (G) was calculated from heat transfer theory and evaporative heat loss (λE) was estimated from measurements on deer mice (*Peromyscus maniculatus*) by Chappell and Holsclaw (1984).

The thermo-neutral zone of metabolism for the field vole was reported to be 32 - 35 °C (Rigaudiere and Delost, 1964) and the metabolic rate of field voles was reported to increase linearly between 30 and 0 °C (Hansson and Grodzinski, 1970). The effect of temperature on metabolic rate was calculated from Equation 2.1 based on the body temperatures of field voles in captivity by Hansson and Grodzinski (1970), with a total resistance of 328 sm^{-1} determined in this study and including an estimate of latent heat loss as above. This indicated that estimates of thermal resistance with the heat transfer model gave comparable estimates of the metabolic rate of field voles, as determined in captivity (Table 4.3).

In this study, heat loss from the model increased linearly with wind speeds up to 0.85 ms^{-1}. Chappell and Holsclaw (1984) showed however that the rate of oxygen consumption in deer mice increased linearly with the square root of wind speed. Their results predicted a 50 % rise in metabolic rate at 0.85 ms^{-1} which was greater than the 22 % increase in non evaporative heat loss measured with the model. It is clear from measurements in the field that wind speeds as high as 0.85 ms^{-1} are ecologically unrealistic for the field vole and therefore metabolic increases of this magnitude are unlikely to occur.

4.4.1.2 Coat Resistance of the Field Vole

Vole pelage was found to have a resistance of 242 sm^{-1}. The insulation provided by the coat represented on average 73 % of an equivalent depth of still air which was considerably larger than reported for a range of small Arctic mammals by Chappell (1980b) and for western chipmunks (*Eutamias* spp.) by Heller and Gates (1971), (Figure 4.12). In these previous studies, coats provided on average 30 % of the insulation of an equivalent depth of still air which was considerably less than other mammal coats (Monteith and Unsworth, 1990). The resistance per unit coat depth of 4.2 - 3.5 scm^{-2} for the field vole in this study was however closer to reported values for larger mammals.

Wind decreased coat resistance at 0.2 ms^{-1} but had no effect at speeds greater than this. Analysis of the ratio between the Grashof number and the square of the Reynolds number (G_r/Re^2) indicated that the transition between free and forced convection occurred at 0.14 ms^{-1}. The decline in resistance between 0 and 0.2 ms^{-1} was most probably due to closer coupling of the fur surface with air temperature, rather than any penetration or compression by wind. The absence of any decline in coat resistance with increasing wind speed did not agree with a decrease which was proportional to the square root of wind speed for a range of small mammal coats (Chappell, 1980b) or according to linear reductions, for a range of animal coats (Campbell *et al*, 1980). Wind speeds in this study were considerably less than in previous studies and indicated that wind was not able to penetrate the dense fur of the field vole at these low wind speeds.

Wetting the model reduced the depth of fur by compression and reduced the resistance of the coat by 67 %, comparable with reductions of 60 and 75 % in wet coats of the wood rat (*Neotoma floridana*) and wet cotton rat (*Sigmodon hispidus*), (Webb *et al*, 1990) and with 50 % reductions following wetting of a range of mammal coats (Webb and King, 1984).

4.4.1.3 Boundary Layer Resistance of the Field Vole

The boundary layer resistance of the model was similar to the resistance of other small mammals and fitted the relationship between resistance and body size for small mammals less than 150 g (Figure 4.13). Linear reduction of boundary layer resistance with increasing wind speed was also in agreement with the data of Chappell (1980b) for metal casts of small Arctic mammals and for models of western chipmunks (*Eutamia* spp.), (Heller, 1972).

The relationship between Nusselt and Reynolds numbers in this study was linear rather than the familiar logarithmic relationship derived for smooth cylinders. Values were, however, close to those predicted for a cylinder of similar dimensions (Monteith and Unsworth, 1990). Chappell and Holsclaw (1984) have shown that relationships derived for cylinders and spheres predict accurately the Nusselt numbers of deer mice (*Peromyscus maniculatus*) at low wind speeds in captivity. This therefore suggests that the approximation of small mammals as simple geometric shapes, such as cylinders, estimates reasonably accurately the boundary layer resistance at wind speeds encountered in the wild. The deviation from a logarithmic relationship in this study may be due to a high degree of turbulence associated with wind tunnel design, as Campbell *et al* (1980) report that the exponent of the Reynolds number tends towards unity for heated cylinders with a surface which is rough enough to make the boundary layer turbulent.

	Name		Depth (mm)	r_c (sm^{-1})
1	Western chipmunk[1]	*Eutamias minimus*	2.5	65
2	Western chipmunk[1]	*Eutamias alpinus*	3.3	120
3	Masked shrew[2]	*Sorex cinereus*	3.3	72
4	Least weasel[2]	*Mustela nivalis* (female)	3.4	45
5	Masked shrew[2]	*Sorex cinereus*	3.5	78
6	Least weasel[2]	*Mustela nivalis* (female)	3.5	49
7	Western chipmunk[1]	*Eutamias amoenus*	3.7	62
8	Western chipmunk[1]	*Eutamias speciosus*	3.9	52
MA	Field vole[3]	*Microtus agrestis* (sleek)	4	142
9	Brown lemming[2]	*Lemmus sibiricus*	4	79
10	Least weasel[2]	*Mustela nivalis* (male)	4	58
11	Tundra vole[2]	*Microtus oeconomus*	4.5	66
12	Brown lemming[2]	*Lemmus sibiricus* (baby)	5	79
13	Short tailed weasel[2]	*Mustela erminae* (female)	5	72
14	Brown lemming[2]	*Lemmus sibiricus*	5.5	114
MA	Field vole[3]	*Microtus agrestis*	5.8	242
15	Short tailed weasel[2]	*Mustela erminae* (female-winter)	6	93
16	Varying lemming[2]	*Dicrostonyx torquatus* (summer)	6.5	99
17F	Tundra vole[2]	*Microtus oeconomus*	6.5	79
18F	Brown lemming[2]	*Lemmus sibiricus*	8.0	144
19	Brown lemming[2]	*Lemmus sibiricus* (winter)	8	95
20	Varying lemming[2]	*Dicrostonyx torquatus* (winter)	8.5	107
21	Varying lemming[2]	*Dicrostonyx torquatus* (winter)	9.5	139
22	Brown lemming[2]	*Lemmus sibiricus* (winter)	9.5	124
23	Brown lemming[2]	*Lemmus sibiricus* (winter)	10	124
24	Varying lemming[2]	*Dicrostonyx torquatus* (winter)	10.5	143
25F	Varying lemming[2]	*Dicrostonyx torquatus*	12.3	117
26F	Varying lemming[2]	*Dicrostonyx torquatus*	13.8	159
27F	Brown lemming[2]	*Lemmus sibiricus*	14.5	136
28F	Varying lemming[2]	*Dicrostonyx torquatus*	15.2	177

Table 4.4. The coat resistance of small mammals as determined by pelage-covered heated metal casts from Heller and Gates (1971)[1], Chappell (1980b)[2] and this study of the field vole (*Microtus agrestis*)[3].

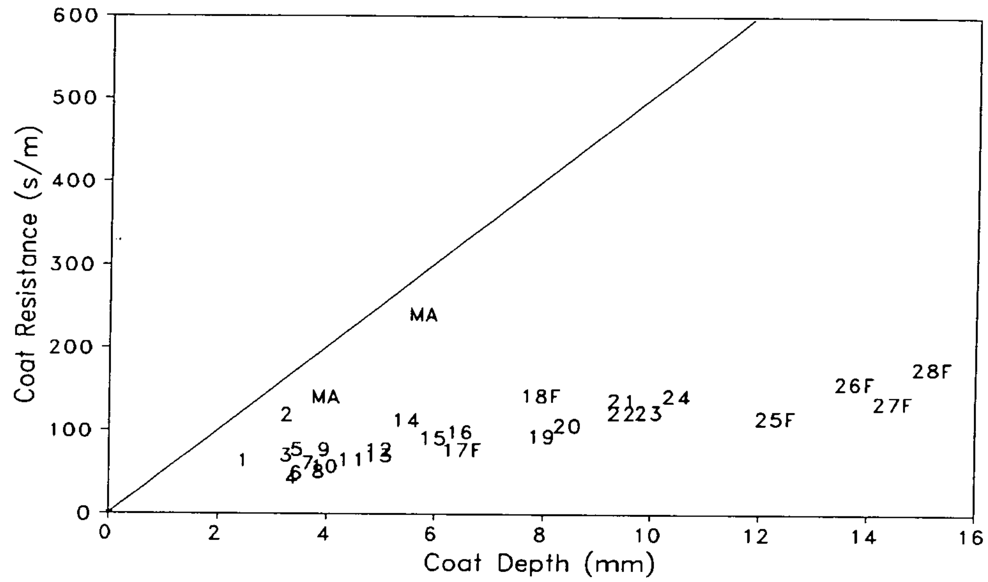


Figure 4.12. The relationship between coat resistance and pelage depth of small mammals as measured by pelage-covered heated metal casts. Species are numbered 1- 28, letter F denotes measurement of fluffed fur, and MA for the field vole (*Microtus agrestis*) in this study. The solid line represents the resistance of an equivalent depth of still air and the sources of data are given in Table 4.4.

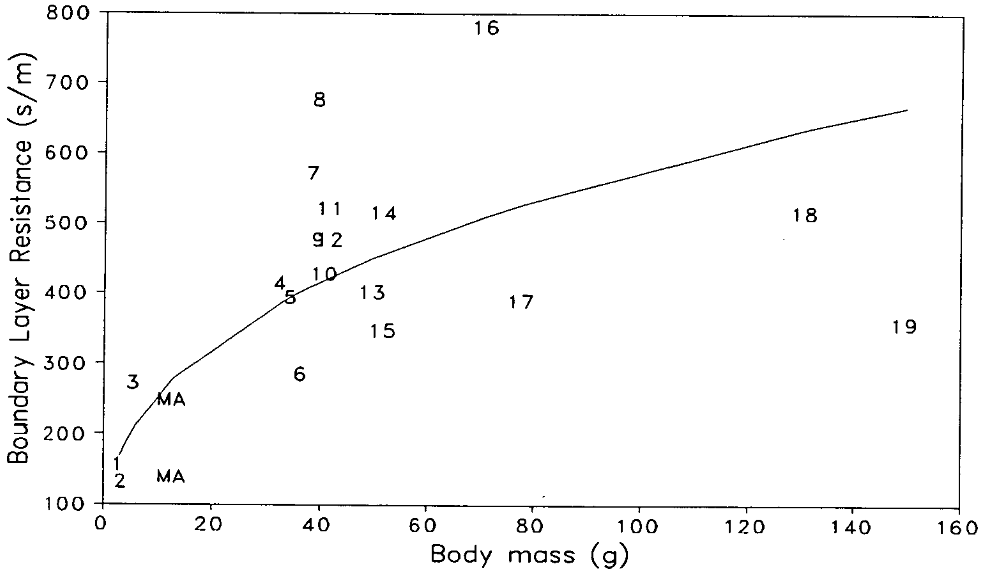


Figure 4.13. The boundary layer resistance of small mammals determined by pelage-covered, heated metal casts. Species are identified with numbers 1 - 19 and MA for the field vole (*Microtus agrestis*) in this study. Solid line is: $r_a = 111m^{0.36}$ determined by log-log regression (R = 0.76). The sources of the data are given in Table 4.5.

	Name		Mass	r_a (sm^{-1})
1	Masked shrew[1]	*Sorex cinereus*	3.2	157
2	Masked shrew[1]	*Sorex cinereus*	3.7	133
3	Brown lemming[1]	*Lemmus sibiricus*	6	274
MA	Field vole[2]	*Microtus agrestis*	13	250
MA	Field vole[2]	*Microtus agrestis*	13	141
4	Brown lemming[1]	*Lemmus sibiricus*	33	416
5	Western chipmunk[1]	*Eutamius minimus*	35	396
6	Brown lemming[1]	*Lemmus sibiricus*	37	287
7	Western chipmunk[3]	*Eutamius alpinus*	39	573
8	Varying lemming[1]	*Dicrostonyx torquatus*	40	679
9	Least weasel[1]	*Mustela nivalis*	40	478
10	Tundra vole[1]	*Microtus oeconomus*	41	430
11	Western chipmunk[3]	*Eutamius amoenus*	42	522
12	Brown lemming[1]	*Lemmus sibiricus*	42	478
13	Varying lemming[1]	*Dicrostonyx torquatus*	50	403
14	Brown lemming[1]	*Lemmus sibiricus*	52	516
15	Varying lemming[1]	*Dicrostonyx torquatus*	52	349
16	Western chipmunk[3]	*Eutamius speciosus*	71	782
17	Least weasel[1]	*Mustela nivalis*	78	391
18	Short tailed weasel[1]	*Mustela erminea*	131	516
19	Short tailed weasel[1]	*Mustela erminea*	150	358

Table 4.5. The boundary layer resistance of small mammals of body mass < 150 g as determined by pelage-covered heated metal casts from Chappell (1980b)[1], this study of the field vole (*Microtus agrestis)*[2] and from Heller and Gates (1971)[3].

4.4.1.4 Total Thermal Resistance of the Field Vole

The total thermal resistance of the field vole to sensible heat loss was estimated by the addition of tissue resistance to the total resistance of the model. Typical tissue resistances of mammals are 30 sm^{-1} for vasodilated tissue and 100 sm^{-1} when vasoconstricted (Monteith and Unsworth, 1990). Including these values, the total resistance of a field vole was estimated to range from 360 to 430 sm^{-1}. From the data of Hansson and Grodzinski (1970) the total thermal resistance of field voles below thermo-neutrality was calculated to be approximately 310 - 350 sm^{-1} which was close to the minimum resistance estimated in this study.

The linear decline in total thermal resistance (excluding tissue) in this study was a reflection of the linear relationship between boundary resistance and wind speed, as discussed above. Chappell and Holsclaw (1984) reported that the total as well as the boundary resistance of deer mice decreased in proportion to the square root of wind speed suggesting that total thermal resistance is also controlled by changes in the boundary layer in live animals. Chappell and Holsclaw's study, however, indicated that although small mammals are not able to change the functional relationship between resistance and wind speed they have the ability to increase total thermal resistance by peripheral vasoconstriction and pelage adjustments.

4.4.2 Microclimate and Behaviour of Field Voles

During February to April 1992 in SW Scotland the temperature of field vole habitat remained below the thermo-neutral zone of metabolism. The temperature of the tunnels and entrances to the tunnels showed strong diurnal changes in the absence of snow cover. These findings are somewhat different from studies on other species of small mammals which suggest that the temperature within the burrows and nests of small mammals remain relatively stable throughout the day and night. Hayward (1965) reported that the nest of *Peromyscus* spp. remained at a constant 10 °C despite a diurnal temperature change of 4.6 - 19.8 °C. Stark (1963) found that the nest temperature of *Microtus californicus* was similar to soil temperature and as a consequence the voles were not subject to daily and seasonal extremes of temperature.

The diurnal pattern of temperature observed in this study was due to the position of thermocouples above soil surface. This is likely to be representative, as the distribution of runways used by field voles is dominated by a network of tunnels through the base of the vegetation. Where field voles do burrow beneath the ground surface it would be expected that the temperature would show less diurnal variation and be equal to soil temperature several centimetres below the surface. The minimum height of the vegetation at this period in the year may also have contributed to greater daily temperature changes. The close coupling of the surface with air temperature may be a seasonal phenomena and it would be expected that the increase in vegetation height in the summer would result in a decoupling or insulation of vole habitat from changes in air temperature.

The measurements in this study were of tunnel rather than nest temperatures (which have been reported elsewhere) and therefore represent temperatures experienced by voles when foraging. Temperatures of field vole nests are likely to be greater than the temperature at entrances and inside tunnels due to the greater insulation provided by nest material and local heating effects from the vole's own body heat. Hayes *et al* (1992) found that individual field voles were able to produce a local heating effect in captivity which was linearly related to outside temperature and which provided a rise of 7 °C at outside temperatures of 0 °C. Measurements of oxygen consumption (of voles separated but not huddling) indicated that higher temperatures from local heating resulted in energy savings of 14 %. Local heating effects of 5 - 10 °C in artificial hay nests of the bank vole (*Clethrionomys glareolus*) in an outdoor enclosure were also recorded by Cotton and Grifiths (1967) and both studies indicated that this heating effect was increased if there were more than one individual in the nest at any one time. Hayes *et al* (1992) determined that huddling behaviour of groups of five field voles resulted in a reduction in oxygen consumption of 23 %, of which, 55 % was due to the local heating effect of the huddling group. Extrapolations from laboratory studies to wild populations of field voles should, however, be made with caution, as it is known that field voles, especially adult males, are generally aggressive towards other individuals. Energy savings associated with huddling may therefore be significant only in nests of females with offspring or amongst juveniles. Undoubtedly, local heating effects and reduced body surface area while resting in the nest reduce the metabolic demands for individual field voles.

The insulating effect of snow cover on the underlying soil surface is well known (Oke, 1978) and it is therefore clear that snow cover insulates small mammals from severe temperature changes. Johnson (1951) documented that a distinct air space of as much as 5 cm was present beneath snow and red backed voles (*Clethrionomys rutilis*) in Alaska were observed using this area beneath the snow. Measurements taken in areas used by small mammals in this subnivean air space or at the base of snow 70 - 85 cm deep, ranged between -3 and 6 °C for air temperatures of -45 to -10 °C. Similar measurements in southern Sweden by Coulianos and Johnels (1963) indicated that with 20 cm of snow cover the temperature within the subnivean air space remained above 0 °C for 14 consecutive days despite minimum temperatures as low as -22.5 °C and maximum fluctuations of 25 °C. Snow cover in this study was less than 10 cm but the temperature remained above freezing despite a minimum air temperature of -1.5 °C.

The short term activity rhythm of 2 - 4 hours found to occur in captive field voles by Davis (1933) has been shown by Lehman (1976) to consist of a short period of feeding and a relatively long period of rest. Daan and Slopsema (1978) demonstrated that short term activity rhythms occur in other members of the Microtinae and that the length of the activity rhythm increases with body size. This suggests that the short term rhythm is correlated with metabolic requirements and that it is an adaptation for efficient bacterial degradation of the low quality food shown to be eaten by voles (Hansson, 1971). The consequence of small body size therefore forces field voles to remain periodically active even during conditions which may be unfavourable.

Field voles must also remain active to feed because small body size limits the amount of energy which can be stored as fat. The total amount of fat in field voles was found to be 0.1 - 1.6 g and decreased to a minimum of 8 % of lean body weight during winter (Evans, 1973). This quantity of fat is only sufficient to provide energy for a relatively short period of time. In this study, the mean daily temperature in vole tunnels was 4.7 °C and therefore it is reasonable to assume that the temperature in nests may be around 15 °C. Evans (1973) reported that 18 - 22 g voles during winter had a mean fat content of 0.42 g which would yield 16.6 kJ (based on the energy equivalent of 39.5 kJg^{-1} Schmidt-Nielsen, 1990) The resting metabolic rate of a vole remaining in the nest would be 0.77 W (Hansson and Grodzinski, 1970) and would therefore indicate that a field vole could last only 6 hours on metabolism of fat reserves alone. This is likely to be an overestimate, as field voles which died of starvation in captivity were only able to metabolise half of their fat reserves (Evans, 1973). Incomplete metabolism of fat reserves to this degree would provide sufficient energy for 3 hours at resting metabolic rate and considerably less at a metabolic rate required for feeding activity. In addition, the rapid cooling rates of dead redback voles (*Clethrionomys rutilis*), (Morrison and Tietz, 1957) would suggest that once metabolism was insufficient to maintain homeostasis the body temperature would fall to lethal limits in a matter of minutes.

Davis (1933) and Nygren (1978) have shown that the activity pattern of field voles in captivity is essentially nocturnal. These studies were limited to only a few months and it was demonstrated by Erkinaro (1961, 1970) that field voles are most active during the night in summer but become more active during daylight hours in winter. Intermediate patterns were observed in the Spring and to a lesser extent in the Autumn. The rise in capture rates of field voles during the day in winter found by Baumler (1975) also appears to provide supporting evidence that an increase in daytime activity during winter also occurs in the wild. The energy savings associated with greater diurnal activity for field voles in winter may be critical owing to a combination of low food supply, poor food quality, low fat reserves and temperatures well below the thermo-neutral zone. The change in mean hourly temperature of vole habitat suggested a 10 % increase in metabolism between maximum day and minimum night temperatures and the range of minimum night temperatures during this season of the year show the benefit of greater activity during the day.

In synchrony with the diurnal rise in temperature there was also found to be a rise in mean wind speed measured at the entrances to vole tunnels. The peaks in activity of field voles around sunset and before sunrise reported by Davis (1933) and Erkinaro (1961) suggest that voles could benefit on average from the low wind speeds at these times. The magnitude of this change, however, indicated that any energy savings associated with behaviour adapted to the mean pattern of wind speed are likely to be small and the day-to-day variation in wind speed demonstrated that it is an unreliable environmental cue for adaptation. Responses to short term fluctuations in wind speed could lead to energy savings. The maximum wind speed of 0.29 ms^{-1} would increase heat loss from a field vole by an estimated 7 % which could be significant combined with low temperatures. However, studies using sand transect techniques of the masked shrew (*Sorex cinereus*) by Doucet and Bider (1974) and of *Peromyscus* spp by Marten (1973) found no correlation between activity and wind speed. The increase in activity of field voles around sunset and sunrise may be associated with minimising the number of short term activity periods during daylight hours when risk of predation is greatest (Daan and Slopsema, 1978) and the mean hourly wind speed measured in this study indicated that field voles are operating in wind speeds where heat transfer by free convection dominates. This suggests that the strong decline in wind speed towards the surface of the vegetation allows voles to operate essentially independently of wind speed.

Results from the model indicated that reduction of insulation by wetting could lead to lethal levels of metabolism in field voles. It is not known to what extent voles become wet in the wild. Voles active in tunnels and within the vegetation are unlikely to be exposed to direct rainfall and are more likely to become wet by contact with wet vegetation. This leads to the hypothesis that activity of field voles would be unaffected by rainfall as a consequence of high energy demands associated with wetting. Several studies have in fact shown that small mammals are more active during rain (Doucet and Bider, 1974, Vickery and Bider, 1981 and Gauthier and

Bider, 1987) and suggest that this was associated with predator avoidance. The noise of rainfall will interfere with detection of sounds and wetting of the vegetation may reduce the sound of small mammals on the moist surface and wash away sent trails. Vickery and Bider (1981) and Gauthier and Bider (1987) demonstrated that the variation in activity was not explained by rain alone but by the combination of rain, warm and moon-less nights, suggesting avoidance of acoustic, olfactory and visual detection was important.

In this study it was shown that periods of rain are closely associated with warm temperatures while dry periods are associated with low temperatures. This is caused by the predominant air flow which brings warm, wet Atlantic depressions while dry, cold periods are caused by anticyclonic conditions at this time of year. It would therefore appear that field voles may potentially benefit from a reduction in predation during periods of rain and a reduction in energy demands with relatively warm temperatures associated with rainfall. In contrast dry periods may have high risks of predation and therefore activity during these times may show responses during periods of relatively high temperature.

Findings from this chapter indicate that high metabolic requirements associated with small body size forces field voles to remain active in conditions of high energy demands. The microclimate of vole habitat, however, allows voles to operate almost independently from wind speed, while snow cover insulates the grass tunnels from severe temperatures and therefore the behaviour of voles may respond to seasonal changes in temperature and patterns of rainfall. The implications of these factors to a predator such as the barn owl are that during periods of high energy requirement, prey periodically remain active and are thereby vulnerable to predation. The response of aerial predators to activity patterns of voles has been reported in previous studies (Raptor Group RUG/RIJP, 1982, Wijnandts, 1984). It has been suggested that daytime foraging in barn owls may be adapted to the seasonal shift of field vole activity in winter, which will be discussed in Chapter 6.

4.5 SUMMARY

1. Sensible heat loss of a field vole was estimated to be 73 Wm^{-2} at 20 ^oC using a simple heat transfer model. Heat loss increased linearly with increasing wind speed and showed a threefold increase following wetting. These measurements predicted increases in metabolic rate of 46 - 157 Wm^{-2} from 30 to 0 ^oC, similar to previous studies of voles in captivity.

2. The coat resistance of the field vole was 242 sm^{-1} and represented 73 % of an equivalent depth of still air, considerably greater than 30 % in a range of other small mammals but in line with values for coats of larger mammals. At 0.2 ms^{-1} coat resistance was marginally reduced but thereafter was unaffected by wind speeds up to 0.85 ms^{-1}. Wetting the coat decreased coat thickness and reduced resistance by 67 % to 79 sm^{-1}.

3. The boundary resistance of the model was 141 sm^{-1} in still air and comparable with values for small mammals < 150 g. Linear reductions in boundary resistance were associated with a linear relationship between Nusselt and Reynolds numbers. The total resistance (including tissue) to sensible heat transfer for a field vole was estimated to be 360 to 430 sm^{-1}.

4. The microclimate of field vole habitat in SW Scotland was examined from February - April 1992. The mean temperature at the entrances and inside grass tunnels used by voles was 4.2 and 4.7 ^oC respectively. Strong diurnal temperature changes existed but during periods of snow cover temperatures remained constant and were up to 3 ^oC greater than outside air temperature.

5. Solar radiation at tunnel entrances represented 8 % of solar radiation measured above a sitka spruce plantation nearby. Mean daily wind speed at the tunnel entrance was 0.13 ms^{-1} and ranged between 0 and 0.29 ms^{-1}. Wind speed exhibited a diurnal pattern and was coupled to wind speed above the vegetation.

6. The high metabolic rate of field voles associated with large surface area to volume ratios and low fat reserves may help to explain 2 - 4 hour activity - rest cycles and daily and seasonal changes in activity of this species. Periodically active prey during unfavourable environmental conditions may therefore increase prey availability when metabolic requirements of barn owls are also high.

CHAPTER 5

MICROCLIMATE AND HEAT LOSS OF ROOSTING BARN OWLS

5.1 INTRODUCTION

The cost of maintenance metabolism, which includes both basal and thermostatic requirements in birds is an important determinant of the total energy available for other activities such as foraging and reproduction. It has been estimated from a range of species that maintenance metabolism typically accounts for 40 - 60 % of total energy expenditure of free living birds (Walsberg, 1983). Reductions in maintenance costs are relatively insensitive to behavioural changes other than through the selection of microclimates which reduce the cost of thermoregulation.

Studies of the energy savings associated with selection of favourable microclimates have largely concentrated on diurnal birds which select roost sites to avoid cold nocturnal conditions. However, the importance of favourable microclimates in daytime roosts of nocturnal birds such as owls has been neglected. Ligon (1969) speculated that physiological modifications in metabolism and temperature regulation may be correlated with nocturnal periods of activity, as owls active at night would require less augmentation of metabolic rate by shivering than diurnal species which are inactive at this time. Muscular activity at night contributes to thermoregulation in owls and the advantages of higher air temperatures during the day may reduce thermostatic demands while inactive. Incubating barn owls in North America have been found to benefit from higher air temperatures inside nest boxes and were sheltered from wind inside large grain silos used for roost and nest sites (Hamilton, 1983). Barrows (1981) reported that spotted owls (*Strix occidentalis*) selected daytime roosts to reduce heat stress in summer and to obtain thermal benefits from solar radiation in winter while Wijnandts (1984) found that wind speeds inside long eared owl (*Asio otus*) roosts were 75 % lower than in open fields.

The barn owl in SW Scotland roosts and nests predominantly in disused farm buildings and tree holes and elsewhere in Europe occupies similar sites as well as church towers and occasionally cliff sites (Taylor, 1991, Bunn *et al* 1982). There are several anecdotal observations of barn owls roosting in conifers (Anderson, 1946, Ash and Walpole-Bond, 1946) and also within dense reed beds (Ash, 1954). Barn owls roost in these sites throughout the day but it has also been found by radio-tracking, that barn owls frequently spend short periods in buildings between foraging at night (Taylor, in press). The choice of these sites therefore suggests that the roosting behaviour of barn owls is an adaptation to reduce the cost of metabolic heat production.

The thermal benefits associated with the selection of particular micro-habitats by birds have been quantified from micro-meteorological measurements in the field combined with biophysical models of heat loss and were reviewed by Walsberg (1985) and recently, by Reinersten (1988). Nocturnal roosts in trees or dense vegetation generally provide small radiative savings and large reductions in convective heat loss due to a decrease in wind speed, in a number of studies which include crows (*Corvus corone*) and rooks (*Corvus frugilegus*) in deciduous woods (Swingland, 1973, 1977), starlings (*Sturnus vulgaris*) in pine woods (Kelty and Lustick, 1977), reed buntings (*Emberiza schoeniclus*) using winter roosts in reed beds (Warrilow *et al*, 1978), winter roosts of American robins (*Turdus migratorius*) in fir trees (Walsberg and King, 1980), dark eyed juncos (*Junco hyemalis*) in cedar and yew trees (Webb and Rogers, 1988), the Phainopepla (*Phainopepla nitens*) in small trees (Walsberg, 1986), American goldfinches (*Carduelis tristis*) in spruce woods (Buttemer, 1985), ruffed grouse (*Bonasa umbellus*) in mixed cedar canopies (Thompson and Fritzell, 1988) and bald eagle (*Haliaeetus leucocephalus*) roosts in deciduous and coniferous trees (Stalmaster and Gessaman, 1984 and Keister *et al*, 1985).

The higher temperatures and sheltered conditions under bridges used by roosting dippers at night were estimated to provide significant metabolic savings (Shaw, 1979). Local heating of natural cavities from metabolic heat production has been found to occur in roosts of a number of *Parus* spp. (Andreev in Reinersten, 1988) and in nest boxes of house sparrows (*Passer domesticus*), (Kendeigh, 1961). Many small species such as these, also benefit from a decrease in exposed surface area of the body in communal roosts (Guntert *et al*, 1988). The insulating effects of snow provide conditions for significant local heating effects. Snow cover allowed capercaillie (*Tetrao urogallus*) to heat snow burrows to temperatures within thermo-neutral limits (Marjakangas *et al*, 1984) and was estimated to provide large metabolic savings for willow grouse (*Lagopus lagopus*), (Korhonen, 1989).

Communal roosting of large aggregations of birds has been shown to have no overall effect on the temperature of the roost site. Higher temperatures in these roosts are associated with the choice of site topography, as in starling roosts (Yom-Tov *et al*, 1977) and by brambling (*Fringilla montifringilla*) flocks which avoid roosting in the cold valley bottom during winter (Jenni, 1991). Communal roosts such as these, however, are often situated at some distance from feeding areas and studies of the roosts of jackdaws (*Corvus monedulla*), (Gyllin *et al* (1977) and bald eagle roost sites (Buehler *et al*, 1991) suggest that flight cost often outweighs typical thermostatic savings.

Investigation of the cost of incubation has also led to detailed measurements of microclimate. Kendeigh (1963) showed that exposure of the nest box of the house wren (*Troglodytes aedon*) to sunshine reduced energy requirements for incubation. Large nests of the sociable weaver (*Philetairus socius*) reduced the range of nocturnal and seasonal temperature and humidity fluctuations (White *et al*, 1975 and Bartholomew *et al*, 1976). Exposure to solar radiation, low wind speeds and elevated air temperatures provided significant thermal benefits in the nests of white crowned sparrows (*Zonotrichia leucophrys*), (Walsberg and King, 1978b), winter nests of verdins (*Auriparus flaviceps*), (Buttemer *et al*, 1987) and monk parakeets (*Myiopsitta monachus*), (Caccamise and Weathers, 1977). Vinuela and Sunyer (1992) also reported that black kite (*Milvus migrans*) nests were sited to reduce exposure to rain and prevailing winds.

In view of the metabolic savings associated with exploitation of favourable microclimates in roost sites and the lack of information on the microclimate of owls, the microclimate of a barn owl roost and nest site was examined throughout the year. The savings associated with roost site selection were estimated with a biophysical model of heat loss which used measurements of roost and nest microclimate together with local meteorological measurements.

5.2 MATERIALS AND METHODS

5.2.1 Field Measurements

Local meteorological data and measurements of the microclimate of the barn owl roost were obtained from December 1990 to April 1992. Meteorological measurements were taken from instruments mounted at the top of a 9 m tri-pole mast above a Sitka spruce (*Picea sitchensis*) plantation. Tree height was 5 - 7 m and the mast was approximately 30 m from the roost building. Wind speed and wind direction were measured with a cup anemometer and a wind vane mounted horizontally (models A100R and W200P:1030, Vector Instruments Ltd). Temperature and relative humidity were recorded using a Skye 103 sensor (Skye Instruments Ltd) fixed inside a gill radiation shield (Campbell Scientific Ltd) and solar radiation was measured with a pyranometer sensor (200SZ Licor Ltd) which was levelled and held above all instruments. The instrument leads were routed to a waterproof junction box at the top of the mast and connected to a multi-core signal cable which ran directly to a weatherproof box containing loggers, on the forest floor.

Rainfall was measured in the forest ride, 10 m from the roost site with a Casella 0.2 mm tipping bucket rain gauge (225 mm funnel diameter) with Goldcrest logging system. A 1.3 mm tipping bucket and combined collecting gauge (125 mm funnel diameter, Casella Instruments) was positioned nearby and used as a back-up system.

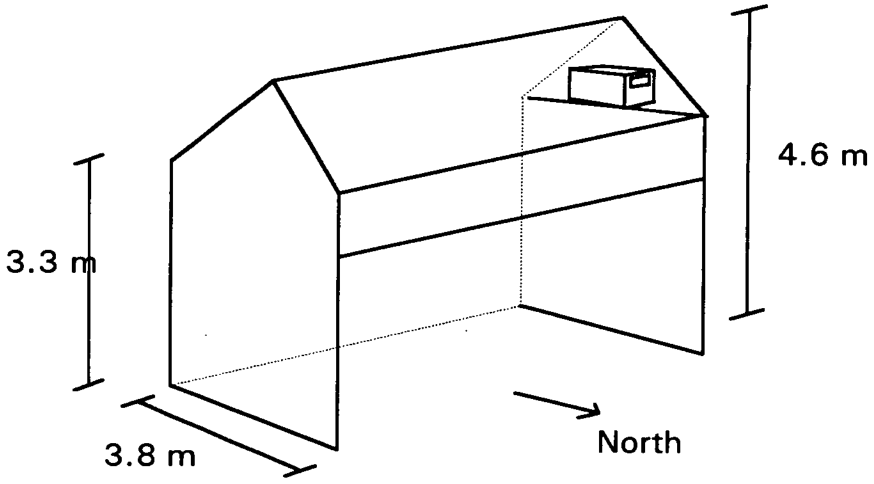


Figure 5.1. The barn owl roost and nest site indicating position of the nest box.

The microclimate of the building used as roost and nest site was determined from measurements of: (i) air temperature and relative humidity within the roost building, (ii) air temperature and surface temperature inside the nest box and (iii) surface temperature of the walls, roof and floor of the building. Air temperature and relative humidity were measured with a second temperature-humidity sensor and radiation shield, which was fixed below the roof. Measurement of air temperature inside the nest box was made with three 0.2 mm type K welded tip thermocouples (RS Ltd) mounted inside the roof of the nest box and wired in parallel to give the average air temperature inside the box. A second set of 5 junctions, welded to 7 mm diameter copper disks (RS Ltd) were again wired in parallel and secured to the interior surfaces of the nest box roof and sides. Both sets of thermocouples were connected to 7/0.2 mm extension cables (RS Ltd).

The temperature of each inside surface of the building was measured with five type T thermocouple junctions configured in parallel and each wired to an isothermal reference junction buried 50 cm below the soil surface on the roost floor (Figure 5.2). Measurement junctions were soldered to 0.5 mm thick copper disks of 15 mm diameter which had been painted black and sealed with epoxy adhesive to prevent corrosion. These were mounted on wall surfaces by applying a thin layer of heat sink compound to ensure good thermal contact with the surface before fixing with a central screw. This configuration determined the difference in temperature between each surface and the temperature of the reference junction which was measured with a 0.2 mm type T thermocouple junction (TC Ltd) connected directly to the logger. Connecting cables from all three sets of measurements were carefully secured to the roost interior and routed to a weatherproof box outside the roost.

Air temperature and humidity, wind speed, wind direction, solar radiation, roost box temperatures and isothermal reference temperature were averaged over 15 minutes and stored on a Campbell Scientific 21X logger. A Campbell Scientific CR10 logger also recorded mean surface temperatures of the building and rainfall from the 1.3 mm tipping bucket gauge every 10 minutes. Loggers were powered by external 12 V 24 Ah lead acid batteries (Yuasa NP24-12B) which provided continuous operation of the logger for a 2 week period. At the end of this period, data was retrieved from the loggers using a Toshiba T1200 portable computer and batteries were replaced. This system allowed continuous measurement of weather conditions and roost microclimate without the need to disturb the birds in the roost throughout the study period.

5.2.2 Calibration of Instruments

The Skye 103 temperature-humidity sensors were calibrated before use in a Gallenkamp cooled incubator against a Guild-line standard platinum resistance thermometer (PRT). Relative humidity readings were checked by placing the sensor inside a flask containing a saturated solution of sodium chloride (75 % RH) and a second, containing alumino silicate granules (0 % RH). The instrument was then adjusted following 12 hour equilibration to within 0.5 % of the reference. Thermocouples were calibrated in an ethylene glycol temperature controlled bath against the PRT above. The thermocouple junctions measuring surface temperature of the roost were calibrated by placing the reference junction in a thermos of ice broth and measuring junctions in the temperature controlled bath. The anemometer was calibrated between wind speeds of 1 to 10 ms^{-1} in the wind tunnel (Section 2.2.1). The manufacturer's calibration was used for pyranometer measurements.

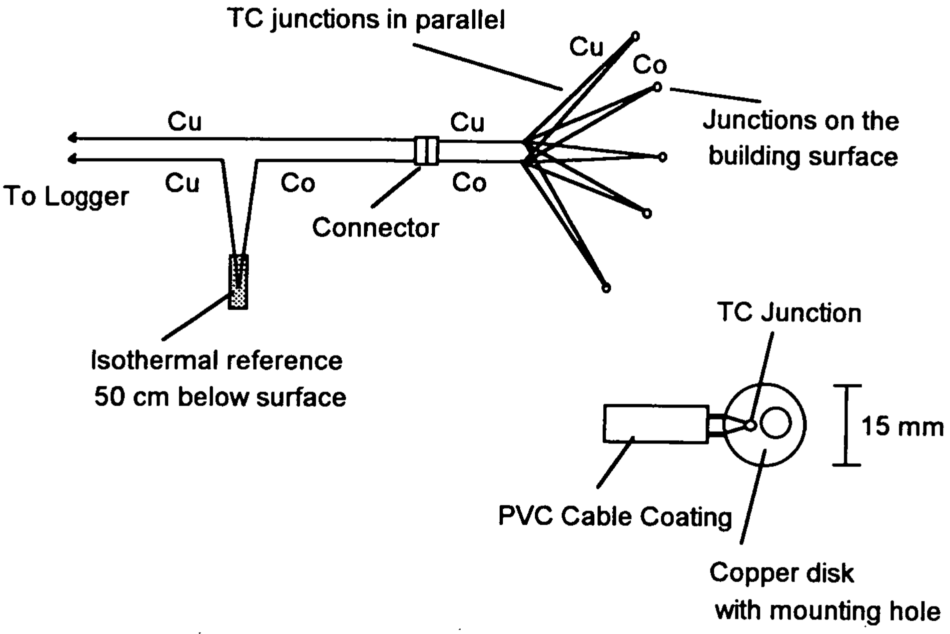


Figure 5.2. Diagram (not to scale) of thermocouple junctions wired in parallel which measured the temperature of surfaces in the roost building. Five sets of these were used to measure the temperature of each building surface. The diagram also shows a detail of the junction for surface mounting.

5.2.3 Biophysical Model of Roosting Barn Owls

5.2.3.1 Energy Balance

The metabolic heat production was estimated for owls roosting in the building, the sitka spruce plantation nearby and in the open, using mean night and daytime measurements of temperature, wind speed and solar radiation. This was calculated using a biophysical model based on that of Robinson *et al* (1976) and Mahoney and King (1977) where the metabolic heat production of a bird, M (Wm^{-2}) is given by:

$$M = \rho Cp(T_b - T_e)/r_{tot} + \lambda E \qquad (5.1)$$

where T_b and T_e are core body temperature and equivalent temperature respectively, r_{tot} is the total resistance to heat loss and λE is the latent heat loss from cutaneous and respiratory evaporation.

The equivalent blackbody temperature is calculated from:

$$T_e = T_a + R_{ni} \cdot \rho Cp / r_e \qquad (5.2)$$

where the net isothermal radiation, R_{ni} (Wm^{-2}) is defined as the net radiation of an animal surface that is at air temperature, T_a:

$$R_{ni} = R_{abs} - \varepsilon\sigma T_a{}^4 \qquad (5.3)$$

and R_{abs} is the total radiation absorbed at the surface of the bird and is determined from the balance of long wave and short wave radiation absorbed.

Latent heat loss from barn owls was calculated by fitting an exponential curve to the data of Hamilton (1985c) for the rate of evaporation, E (mg H_20 per g of body mass per hour) in post incubating barn owls:

$$E = 0.41 \times 10^{0.03T_a} \qquad (5.4)$$

which was converted to latent heat loss where 1 mg of water is equivalent to 2.5 J, and expressed as a flux density for a 350 g barn owl using the relationship between body size and surface area of birds derived by Walsberg and King (1978a).

5.2.3.2 Thermal Resistance

The total thermal resistance of a barn owl to sensible heat loss was determined with a maximum tissue resistance of 100 sm^{-1} (Section 2.4.6) and using values of coat resistance from experimental results (Section 2.3.3.2) where the conductance, $1/r_c$ (cms^{-1}) of dry and wet plumage was linearly related to wind speed:

$$1/r_c = 0.0205u + 0.232 \qquad \text{dry} \qquad (5.5)$$

$$1/r_c = 0.0246u + 0.262 \qquad \text{wet} \qquad (5.6)$$

Heat exchange by convection for barn owls roosting in the building, tree and open sites was determined following the treatment of Nusselt, Grashof and Reynolds numbers (Section 2.1.2.2) as approximated by a vertical cylinder of characteristic dimension 0.2 m. Free convection was assumed to be the dominant mode of heat transfer at wind speeds < 0.1 ms^{-1} and in these conditions the relationship between Nusselt and Grashof numbers (Monteith and Unsworth, 1990) was used:

$$Nu = 0.58Gr^{0.25} \qquad (5.7)$$

where the surface temperature of an owl was estimated from thermography studies (Section 3.3.2) to be 3.4 ^{o}C above air temperature. In conditions of forced convection the relationship derived in Section 2.3.4 for a vertical cylinder was used:

$$Nu = 0.55Re^{0.51} \qquad (5.8)$$

Although wind speed was never measured within the roost building, inspections suggested that conditions within the roost were dominated by free convection. Wind speed at mid tree height in the plantation was estimated to be 20% of wind speed above the canopy (Green, 1991). Wind speed in open sites was determined from the wind profile at 1m above the surface reported in Section 4.3.2 to be 50 % of above canopy wind speed.

5.2.3.3 Radiation Analysis

Long wave radiation absorbed within the roost site was determined by modelling the exchange of radiation between the building surfaces and the owl. Radiative exchange L (Wm^{-2}) between two surfaces with unit emissivity can be calculated from:

$$L = F_{12}\sigma(T_2^{\,4} - T_1^{\,4}) \qquad (5.9)$$

where the shape factor F_{12} is the fraction of total radiation from surface 1 which falls on surface 2, with radiative temperatures T_1 and T_2, respectively. The roost was considered to act essentially as blackbody surroundings as the distance between owl and building surfaces was such that reflected radiation can be discounted. The amount of radiation absorbed by an owl was calculated by approximating shape factors according to the study of Cornwell (1977) which considered exchange of radiation between a plane surface and a sphere.

As an approximation, the shape factor was calculated from the ratio of the projected area of the wall surface ($A\cos\phi$) to the total area of radiative exchange of the owl ($4\pi x^2$):

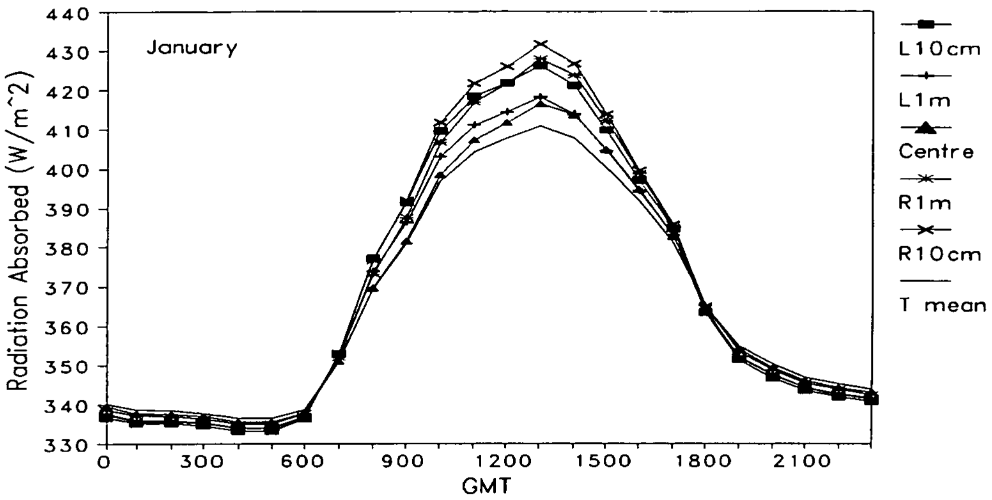
$$F_{s1} \approx \frac{A\cos\phi}{4\pi x^2} \tag{5.10}$$

where ϕ is the angle between a line (x) drawn from the owl to the centre of the wall surface and the normal to the surface. Radiation absorbed by an owl was derived entirely from inside the building and therefore the sum of the shape factors is equal to unity, such that:

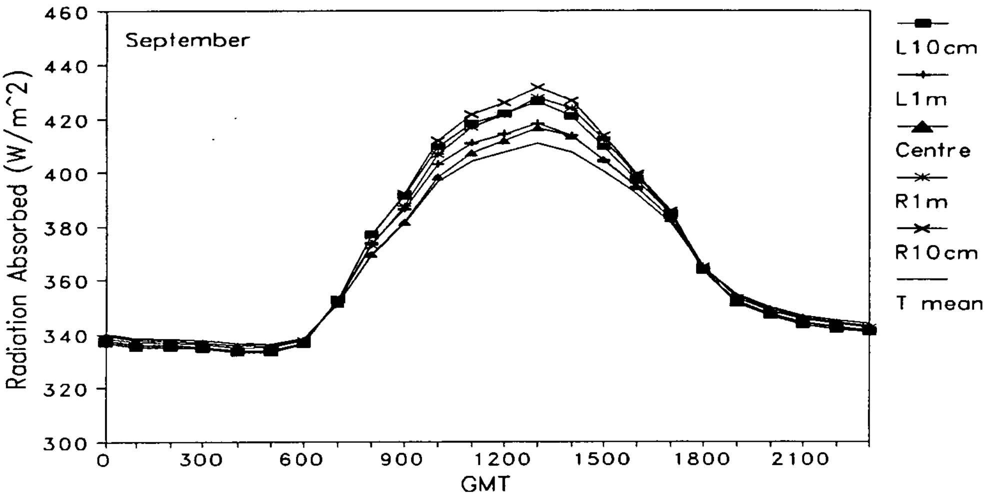
$$F_{1O} + F_{2O} + F_{3O} + F_{4O} + F_{5O} + F_{6O} = 1 \tag{5.11}$$

where F_{no} represents the shape factor between the building surface and the owl, where 1 - 6 are left wall, right wall, floor, back wall, front and roof surfaces, respectively. Shape factors for each surface were calculated according to Equation 5.10 with the exception of the roof surface which was determined by $1-\sum F_{no}$. Shape factors were estimated for favoured roosting locations on the beams 3.3 m above the floor at 0.1 m and 1m from the left and right walls and in the centre of the building.

The corresponding shape factors are given in Table 5.1 and indicated that roosting owls exchanged radiation predominantly with the roof surface and nearest wall surfaces. Roosting in the centre of the building resulted in a more even exchange with all surfaces. Radiation absorbed was compared with values from black body surroundings calculated with the mean surface temperature of the building. This indicated that radiation absorbed by an owl at night was relatively insensitive to position but during the day, differences were associated with the variation in surface temperature of the building from solar heating. Values calculated using the mean surface temperature were found to be similar to shape factor determinations but consistently underestimated the total radiation absorbed (Figure 5.3).



(i)



(ii)

Figure 5.3. The effect of roosting position during (i) January and (ii) September 1991 on the estimated radiation absorbed by a barn owl in the roost building calculated using the shape factor analysis for individual surfaces which was compared with values determined using the mean surface temperature of the roost (T mean).

An owl in a tree roost or in the open exchanges radiation with the sky and surroundings (e.g. vegetation, rocks etc.). The amount of radiation emitted from the sky is largely dependent on the water vapour content of the air and the degree of cloud cover. Relationships between air temperature and radiative temperature of the sky have been empirically determined in a number of studies (reviewed in Campbell, 1977 and Monteith and Unsworth, 1990). These studies indicate that as an approximation, the radiative temperature of a clear and cloudy sky are 20 K and 11 K below air temperature (measured at screen height). For the purposes of this study, days and nights were classed as clear when cloud cover was ≤ 3 oktas and with ≥ 4 oktas were assumed to be cloudy, using records of cloud cover for 0000 and 1200 GMT from Eskdalemuir Meteorological Observatory.

	Position from Left Wall (m)				
	0.1	**1**	**2.8**	**4.5**	**5.4**
Left wall	0.14	0.24	0.22	0.06	0.04
Right wall	0.04	0.06	0.22	0.24	0.14
Floor	0.07	0.11	0.15	0.11	0.07
Back wall	0.06	0.09	0.12	0.09	0.06
Front	0.01	0.03	0.07	0.03	0.01
Roof	0.68	0.47	0.22	0.47	0.68

Table 5.1. Shape factors determined for a barn owl roosting in the rafters of the roost building at 3.3 m above the ground for positions at the left side, centre and right sides of the building.

Radiation absorbed by an owl roosting in the sitka spruce plantation was assumed to consist of long wave only and was weighted with a sky view factor of 0.25, which is a typical value for avian roost sites in vegetation (Walsberg, 1986 and Webb and Rogers, 1988). The remaining radiation absorbed by an owl in this site originates from the surroundings which were assumed to be at air temperature and therefore long wave radiation absorbed, L_{abs} was calculated from:

$$L_{abs} = a_l\left(0.25\sigma T_{sky}{}^4 + 0.75\sigma T_a{}^4\right) \qquad (5.12)$$

where a_l is the long wave absorptivity of owl plumage (emissivity = 0.98, as measured for animal coats by Hammel, 1956) and T_{sky} and T_a are the radiative temperature of the sky and air temperature, respectively.

An owl in an open site was assumed to exchange radiation equally with the sky and the surroundings and was calculated according to:

$$L_{abs} = a_l\left(0.5\sigma T_{sky}{}^4 + 0.5\sigma T_a{}^4\right) \qquad (5.13)$$

5.2.3.4 Solar Radiation

During the daytime, solar radiation will be absorbed by an owl in the open. Total solar radiation received on a horizontal surface, S_t (Wm^{-2}) consists of beam S_b and diffuse components, S_d such that:

$$S_t = S_b + S_d \tag{5.14}$$

On a clear day, the amount of diffuse radiation is dependent on the degree of molecular scattering and aerosol attenuation. This can be determined theoretically but in this study the ratio of diffuse to total solar radiation on clear days was estimated with the empirical relationship derived by Unsworth and Monteith (1972) for clear days in the English Midlands:

$$S_d / S_t = 0.1 + 0.68\,\tau_a \tag{5.15}$$

when solar elevation ψ is less than 60° and where τ_a is the turbidity coefficient. The turbidity coefficient was estimated from records at Eskdalemuir to have a mean of 0.27 (0.15 - 0.33, over a 6 month period). With increasing cloud cover, the ratio of diffuse to total radiation increases and reaches unity when sun is fully obscured, but the absolute level of S_d is maximum when cloud cover is about 50 %. In this study, measurements were made of total solar radiation and therefore S_b and S_d were estimated by dividing days into cloudy and clear, from 1200 GMT records of cloud cover. Days were classed as clear when cloud cover was ≤ 3 oktas and the ratio of diffuse to total radiation was therefore calculated as above. Days with ≥ 4 oktas were assumed to be cloudy and as an approximation all solar radiation received was assumed to be diffuse. This may have underestimated solar radiation on days of incomplete cloud cover but overall the number of days in this category during each month represented a small proportion of the total.

The amount of solar radiation absorbed by an owl when perched in the open was estimated to be equal to that of a vertical cylinder, using the shape factor analysis of Gates (1980), Campbell (1977) and Monteith and Unsworth (1990). In this way the mean flux, $\overline{S_b}$ (Wm^{-2}) received from the direct beam was calculated from:

$$\overline{S_b} = \frac{A_h}{A} . S_b \tag{5.16}$$

where A_h/A is the ratio of shadow area to total area and for a vertical cylinder is given by:

$$A_h/A = \frac{(2x\cot\psi)/\pi + 1}{2x+2} \qquad (5.17)$$

where $x = h/r$ is the ratio of height (20 cm) to radius (4.2 cm) and ψ is the angle between the solar beam and the horizontal surface. This was taken to equal the mean daily solar elevation for the 15 th day of each month calculated from computed hourly elevations with the meteorological tables of Beer (1991), (Table 5.2).

Month	**Sunrise**	**Sunset**	ψ	A_h/A
Jan	830	1600	9	1.26
Feb	730	1700	15	0.74
Mar	630	1800	21	0.52
Apr	500	1900	28	0.37
May	400	2000	31	0.33
June	330	2030	33	0.31
July	400	2000	31	0.33
Aug	430	1930	29	0.36
Sept	530	1800	23	0.47
Oct	700	1700	17	0.65
Nov	730	1600	11	1.02
Dec	830	1530	7	1.62

Table 5.2. Time of sunrise and sunset (to the nearest half hour) for each month and the mean hourly solar elevation of the study site at 55°10' N 3°12' W computed using meteorological tables (Beer, 1991). The shape factor A_h/A was determined for a vertical cylinder.

Diffuse radiation can be considered to be isotropic and therefore the mean diffuse absorbed by a vertical cylinder, $\overline{S_d}$ (Wm^{-2}) is given by:

$$\overline{S_d} = (S_d + \rho_s S_t)/2 \qquad (5.18)$$

where ρ_s is the albedo of the surface (grass =0.24, Monteith and Unsworth 1990).

The total solar radiation absorbed $\overline{S}_{abs}$ was therefore determined by summing the beam and diffuse fluxes:

$$\overline{S}_{abs} = a_s\left(\overline{S}_b + \overline{S}_d\right) \tag{5.19}$$

where a_s is the mean short wave absorptivity of barn owl plumage (0.34) which was determined by measuring the reflectivity of plumage samples from the dorsal and ventral surfaces of adult male and female barn owls (Appendix 2).

The biophysical model was examined to determine the sensitivity of changes in resistances to estimates of total heat loss from barn owls. As described in Section 5.2.3.3, determination of radiation absorbed with shape factors was in close agreement with values calculated using the mean surface temperature of the roost building. Overestimation of the radiation absorbed by 10 % was found to produce a 10 % increase in total heat loss. By using a constant value of radiative resistance it was found that estimates of heat loss were insensitive to changes in surface temperature such that an increase of 5 °C resulted in an increase of only 0.2 % in total heat loss. A decrease in the boundary layer resistance of 20 % brought about an increase in total heat loss of 3 %; a decrease in body resistance of 20 % brought about an increase of 14 %, and a combined decrease in both these resistances produced an increase of 18 % in total heat loss.

5.2.4 Energy Requirements During Incubation

The energy requirements of a female barn owl during incubation was determined following the work of Hamilton (1983) in which the energy required to maintain eggs at constant temperature was calculated with the formula of Kendeigh (1963) and the metabolic heat production of the incubating female was estimated using the model of heat loss for incubating birds by Walsberg and King (1978b).

Kendeigh (1963) estimated heating costs during incubation from the product of mass, heat capacity, temperature difference across eggs and the rate of cooling of eggs in the nest. Clearly it is erroneous to consider warming eggs in steady state conditions and therefore the formula incorporated an empirical term to account for the cost of rewarming eggs by the proportion of time the bird is absent from the nest. The formula was converted to appropriate S.I. units in this study to determine the amount of heat supplied to eggs (in this case, each day) by an incubating barn owl, E_{incub} (J) according to:

$$E_{incub} = n.m.c_{egg}.b.\left(T_{egg} - T_{nest}\right).i.(1 - p.a) \qquad (5.20)$$

where *n*, *m*, *c* and *b* are the clutch size (6); mean mass of barn owl egg (17.9 g, Taylor, in press); specific heat capacity of the egg (3.36 $Jg^{-1}{}^{o}C^{-1}$, Kendeigh 1963) and the cooling rate of eggs (2.4^{o}C $hour^{-1}$ per ^{o}C fall in temperature, Hamilton 1983). T_{egg} is egg temperature during incubation equal to 34.2 ^{o}C (Howell, 1964) and T_{nest} is the temperature of the nest below the eggs. $(T_{egg} - T_{nest})$ was found to be 3.5, 2.8 and 1.3 ^{o}C at air temperatures of 5, 15 and 25 ^{o}C by Hamilton (1983). Substitution of T_{egg} at these temperatures gave a linear approximation of $T_{nest} = 0.1.T_a + 30$ which was used in this study. $[i.(1 - p.a)]$ is used to account for *p*, the proportion of the clutch surface which is covered by the bird (pers. observation of 0.5 by Hamilton, 1983) and *a*, the proportion of time spent incubating over the time interval, *i* (24 hours) assumed to equal 1 for the barn owl.

With this model, estimates of energy required were most sensitive to changes in the temperature gradient between egg and nest such that an increase of 2 ^{o}C increased energy required per day by 56 %. A 0.1 reduction of the proportion of egg covered by the incubating owl increased energy demand by 15 % and a decrease in attentiveness from 1.0 - 0.8 produced a 20 % increase due to the cost of rewarming the eggs.

The biophysical model for incubating white crowned sparrows (*Zonotrichia leucophyrys*) used by Walsberg and King (1978b) was modified to estimate the thermostatic costs of a female barn owl in the nest box. Heat flow was described using electrical analogues for three areas of the body surface: (i) the dorsal area which exchanges heat by convection and radiation with nest box air and radiative temperature of nest box surroundings, (ii) the ventral portion of the bird (which exchanges heat as above) and (iii) the area of brood patch which is in direct contact with eggs. Sensible heat loss from the barn owl during incubation H_{incub} was therefore calculated from the sum of these components:

$$H_{incub} = H_{dorsal} + H_{ventral} + H_{broodpatch} \qquad (5.21)$$

where H_{dorsal}, $H_{ventral}$ and $H_{broodpatch}$ are the heat loss from the dorsal, ventral and brood patch regions of an incubating barn owl, respectively. The latent heat loss from the barn owl was estimated from the evaporative loss of barn owls in nest boxes (Hamilton, 1985c) given in Section 5.2.3.1.

Heat exchange form the dorsal region was calculated as:

$$H_{dorsal} = \frac{A_{dor}}{A_{tot}} . \frac{\rho Cp(T_b - T_e)}{r_s + r_c + r_e} \qquad (5.22)$$

with the ratio of dorsal A_{dor} (0.018 m^2) to total area A_{tot} (0.046 m^2); r_s and r_c are tissue and coat resistances estimated to be 100 and 400 sm^{-1}; r_e is the boundary layer and radiative resistance in parallel, where r_a was estimated from the relationship derived for free convection from a sphere where $Nu = 2 + 0.54Gr^{0.25}$; T_b is core body temperature, which was reported to be 40.2 °C in the incubating barn owl (Howell, 1964) and T_e is the equivalent blackbody temperature for the owl in the nest.
Heat loss from the ventral area was estimated as above, such that:

$$H_{ventral} = \frac{A_{ven}}{A_{tot}} . \frac{\rho Cp(T_b - T_e)}{r_s + r_c + r_e} \qquad (5.23)$$

where A_{ven} is the ventral area excluding the area of brood patch (0.016 m^2).

Heat loss from the brood patch region occurs by conduction across the skin, eggs and nest according to:

$$H_{broodpatch} = \frac{A_{bptch}}{A_{tot}} . \frac{\rho Cp(T_b - T_{nest})}{r_s + r_{egg} + r_{nest}} \qquad (5.24)$$

where A_{bptch} is the area of brood patch (0.012 m^2) which was reported to represent approximately 25 % of total surface area in a barn owls (Hamilton, 1983), r_s (40 sm^{-1}) is the tissue resistance which was estimated to be equivalent to the resistance of fully dilated tissue. The thermal resistance of eggs, r_{egg} (72 sm^{-1}) was estimated from the mean dimensions of barn owl eggs (42.1 x 31.8 mm, Taylor, in press) and using the thermal conductivity of eggs, 0.57 $Wm^{-1o}C^{-1}$ (from Henderson in Walsberg and King, 1978b). The resistance of the nest material to heat transfer r_{nest} was provided by approximately 5 cm depth of accumulated pellets in a simple nest scrape. Skowron and Kern (1980) reported the thermal conductivity of bird's nests to be intermediate between that of animal fur and wood (0.052 - 0.239 $Wm^{-1o}C^{-1}$). The resistance to heat transfer through the nest was therefore calculated from the mean conductivity of 0.146 Wm^{-1} $^oC^{-1}$ to give a thermal resistance of 440 sm^{-1}. As heat loss is dominated by conduction across the brood patch area, the temperature gradient $T_b - T_{nest}$ was calculated where T_{nest} is the mean surface temperature of the nest box.

This model was relatively insensitive to changes in thermal resistances. Reductions of 20 % in radiative and boundary layer resistances together, produced only an increase in total heat loss of 1.5 % from dorsal and ventral regions, but combined with a 20 % reduction in body resistance (coat + tissue), heat loss increased by 11 % for each of the surfaces. By decreasing nest, egg and tissue resistance individually by 20 %, heat loss increased by 5 %, less than 1 % and less than 1 % from the brood patch, respectively. Together, heat loss from the brood patch increased by 25 %. Total heat loss for each of the surfaces was sensitive to estimates of surface area, however, the contribution to the total was small because of similar total thermal resistances of each region. An increase of 20 % in total surface area of the owl by development of a brood patch produced only a 5 % increase in total heat loss.

5.3 RESULTS

5.3.1 Microclimate of Roost

5.3.1.1 Temperature

Air temperature within the roost was correlated with seasonal changes in outside air temperature (Figure 5.4). The mean monthly temperature ranged from 15.4 °C in July 1991 to 2.4 °C in January and February 1991. Extreme values ranged from an hourly maximum of 31.4 °C in September 1991 to a minimum of -7.5 °C in January 1992. During the night the temperature inside the building was 0.3 - 1.9 °C greater than outside temperature during the winter and early spring months of December 1990 to March 1991 and October 1991 to March 1992 (paired t test $p > 0.02$). No significant differences occurred in April 1991 ($p = 0.16$) but roost temperature was 0.3 - 0.6 °C less than outside air temperature during May to September 1991 ($p > 0.01$). Roost temperature during the daytime was 0.6 - 3 °C above outside air temperature during all months of the year ($p > 0.01$), (Figure 5.5).

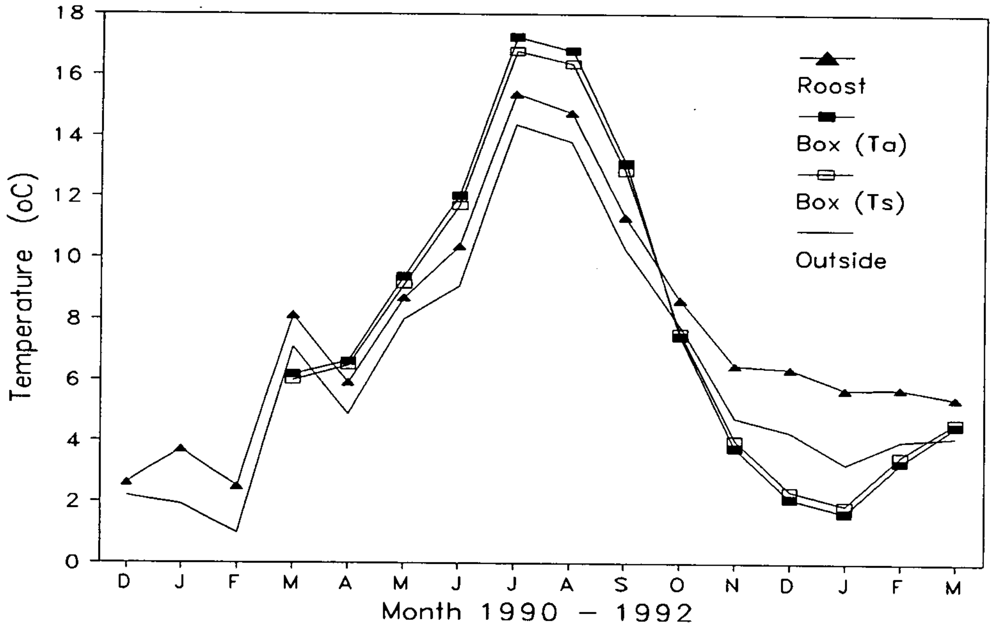


Figure 5.4. Monthly means of roost air temperature (Roost), nest box air temperature (Ta), nest box surface temperature (Ts) and outside air temperature (Outside) from December 1990 to March 1992.

The air temperature within the nest box was correlated with roost air temperature and outside air temperature with monthly means ranging from 17.2 °C in

July 1991 to 1.6 °C in January 1992 (Figure 5.4). There was considerable variation in hourly temperature, from a maximum of 37.6 °C in September 1991 to a minimum of -10.8 °C in January 1992. During the night, air temperature within the box was 0.5 - 1.3 °C greater than outside air temperature from May to September 1991 but was 0.4 - 2.4 °C less than outside temperature from October 1991 to March 1992 ($p > 0.01$) and during April 1991 temperatures were not significantly different ($p = 0.19$).

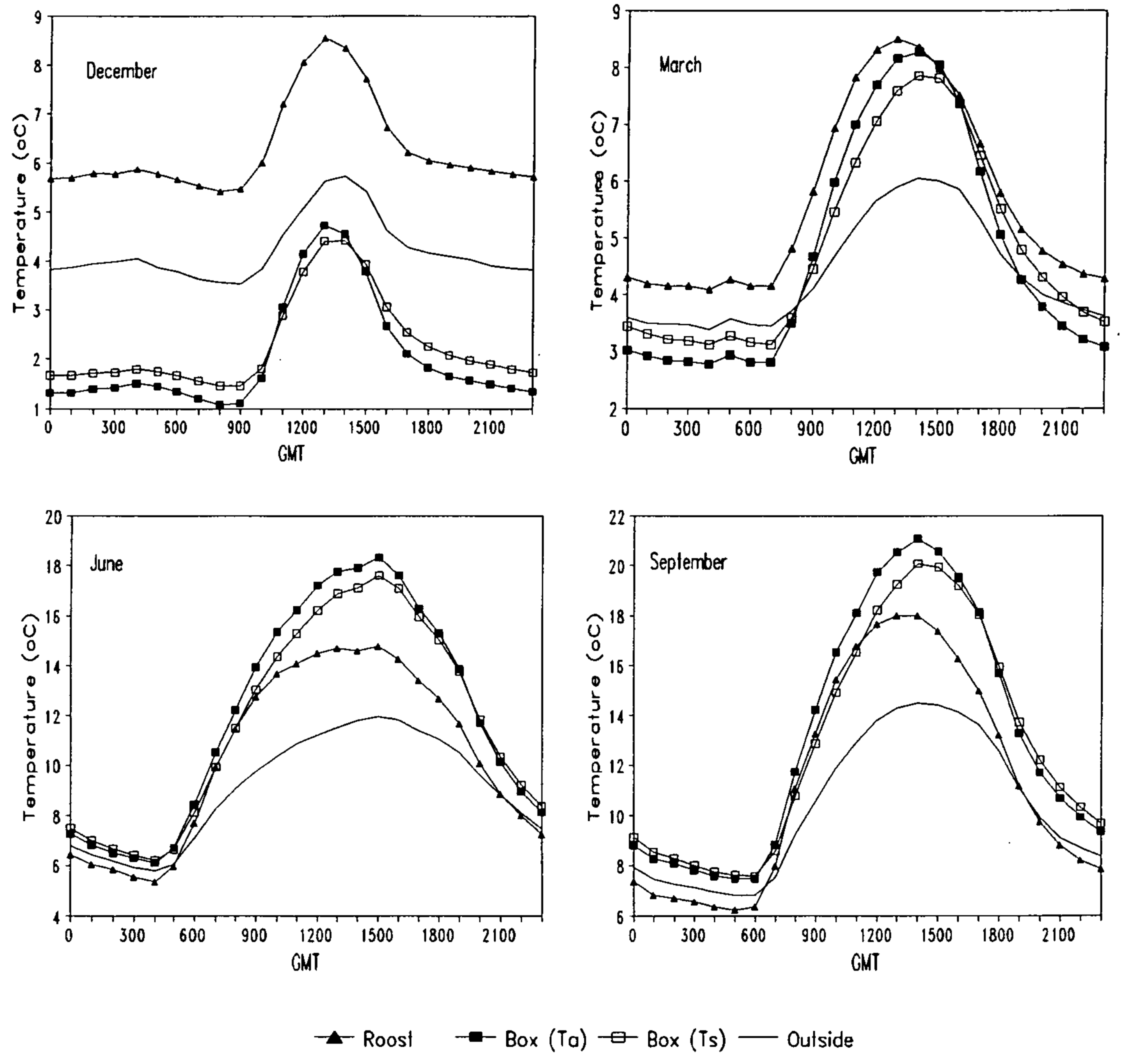


Figure 5.5. Daily means during March, June, September and December of roost air temperature (Roost), nest box air temperature (T_a), nest box surface temperature (T_s) and outside air temperature.

During the daytime, nest box air temperature was 0.5 - 3.9 °C greater than outside air temperature from April to September 1991 ($p > 0.01$) and in the months of October 1991 ($p > 0.03$) and March 1992 ($p > 0.01$). Daytime temperatures were 0.5 - 1.6 °C less than outside temperatures from December 1991 to February 1992 and not significantly different during November 1991 ($p = 0.06$), (Figure 5.5).

The inside surface temperature of the nest box was close to air temperature within the nest box and ranged from a monthly mean of 16.8 °C in July 1991 to 1.9 °C in January 1992 (Figure 5.4). The minimum hourly temperature was -9.7 °C in January 1992 and a maximum of 35.7 °C was recorded in September 1991.

The number of hours when the air temperature was recorded within the barn owl's thermo-neutral zone of metabolism (23 - 33 °C) was 11 hours outside the roost, 136 hours inside the roost and 304 hours inside the nest box. There were a total of 25 hours when the temperature in the nest box was recorded above 33 °C (Table 5.3).

	Number of hours air temperature was within TNZ			
Month	**Outside**	**Roost**	**Nest Box**	
	23 - 33 °C	23 - 33 °C	23 - 33 °C	33 - 40 °C
March	0	1	0	0
April	0	4	3	0
May	0	1	3	0
June	0	2	39	0
July	8	54	115	2
August	3	32	87	6
September	0	42	57	17
Total	11	136	304	25

Table 5.3. The number of hours recorded from December 1990 to March 1992 when the air temperature outside, inside the roost and in the nest box were within the thermo-neutral zone of metabolism reported to be 23 - 33 °C and exceeded this zone, from 33 - 40 °C. Months outside the period March - September had temperatures less than 23 °C at all times.

The effect of metabolic heating by barn owls on nest box temperature was investigated by calculating the difference in air temperature between the inside and outside of the nest box and was determined using mean night temperatures to exclude solar heating effects. This analysis indicated that changes in nest box temperature were related to the unusual and extended breeding season (Figure 5.6). Before incubation there were several periods when the nest box temperature was higher than the air temperature in the building. This was associated with records of barn owls in the nest box. Immediately before incubation, the nest box temperature increased relative to roost temperature over several days. During incubation, air temperature remained above the air temperature outside the box but fluctuated according to changes in ambient conditions. Following hatching of the chicks the nest box temperature increased significantly but decreased rapidly when three chicks were known to have died.

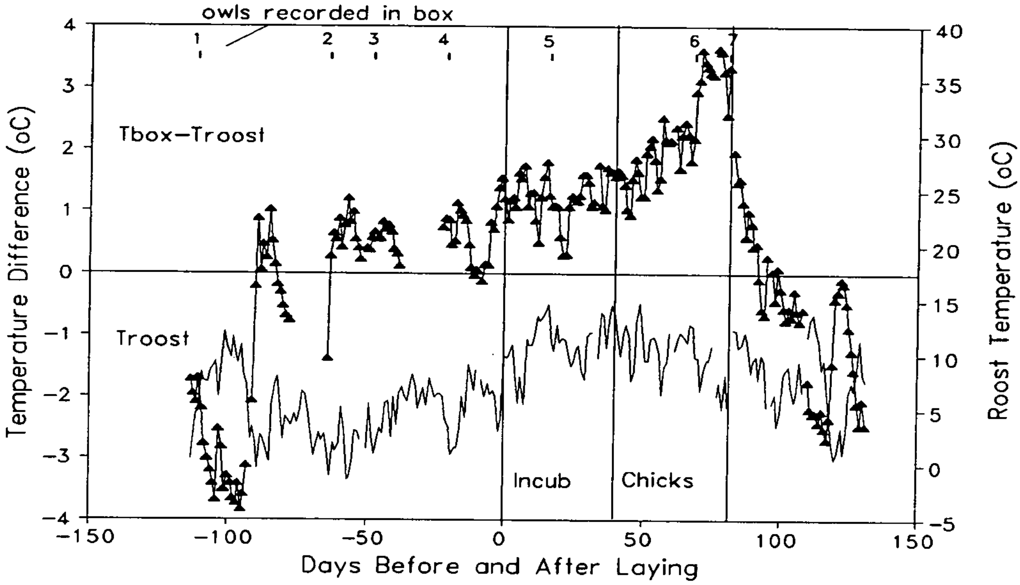


Figure 5.6. The difference in mean night temperature between the nest box air temperature and the air temperature in the roost building (Tbox - Troost) before and after the nesting period. Vertical lines represent incubation and period chicks were in the nest. Numbers correspond to days on which owls were seen in the nest box during the daytime: (1) male and female together in box at 1700 GMT, (2) male and female together at 1100 GMT, (3) male and female together at 1000 GMT (4) female in box, 900 GMT, brood patch developing, (5) male and female together at 1200 GMT, female on eggs, (6) 3 chicks in nest at 900 GMT and (7) last record of 3 chicks in nest at 1000 GMT.

The surface temperature of the building showed marked seasonal and diurnal changes matching the patterns of both air temperature and solar radiation. The temperature of the building surface ranged from a mean of 15.9 °C in July 1991 to 1.6 °C in January 1992 and extremes ranged from an hourly maximum of 37. 8 °C in September 1991 to a minimum of -10.7 °C in January 1992 (Figure 5.7).

At night, the surface temperature of the building cooled below air temperature but during the day became considerably warmer than air temperature (Figure 5.8). At night, the temperature of the roost surface was 0.5 - 2.6 °C colder than the outside air temperature in all months (paired t test $p > 0.01$), except during May when no significant differences were found ($p = 0.21$). Daytime surface temperatures, in comparison, were 1 - 3.7 °C warmer than outside air temperature from March 1991 to October 1991 ($p > 0.01$). Surface temperatures were not significantly different in November 1991 ($p = 0.31$) and February 1992 ($p = 0.33$) but 0.7 - 1.4 °C colder from December 1991 - January 1992 ($p > 0.01$).

Variation in temperature of the building surfaces was related to the aspect of the building, such that the roof and southerly facing wall reached the highest temperatures (Figure 5.8). This resulted in large differences in temperature between the roof, walls and floor. For example, during September 1991 the right wall, roof and back wall reached maximum temperatures of 49.2, 47.1 and 43.7 °C while the left wall and floor reached maxima of only 28.8 and 20.1 °C, respectively. Differences between surfaces were not as extreme at night, such that the minimum temperatures were -13.5 °C for the roof, -12.5 °C for the left wall, -11.8 °C for the back and -11.5 °C for the right wall in January 1992, but at this time the floor was -4.2 °C.

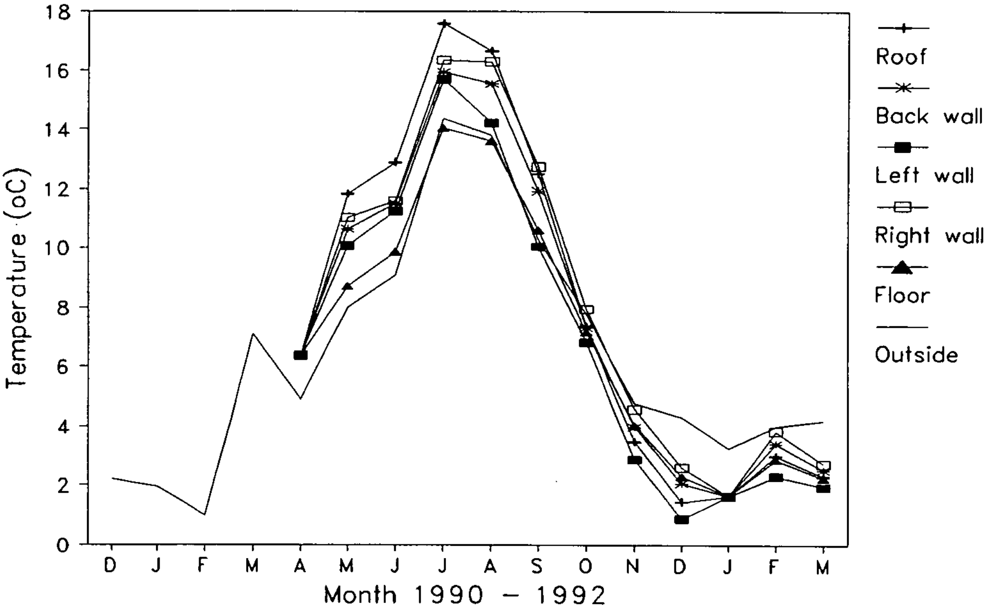


Figure 5.7. The mean monthly temperature of the roost surfaces from December 1990 to March 1992, together with the mean air temperature outside the roost.

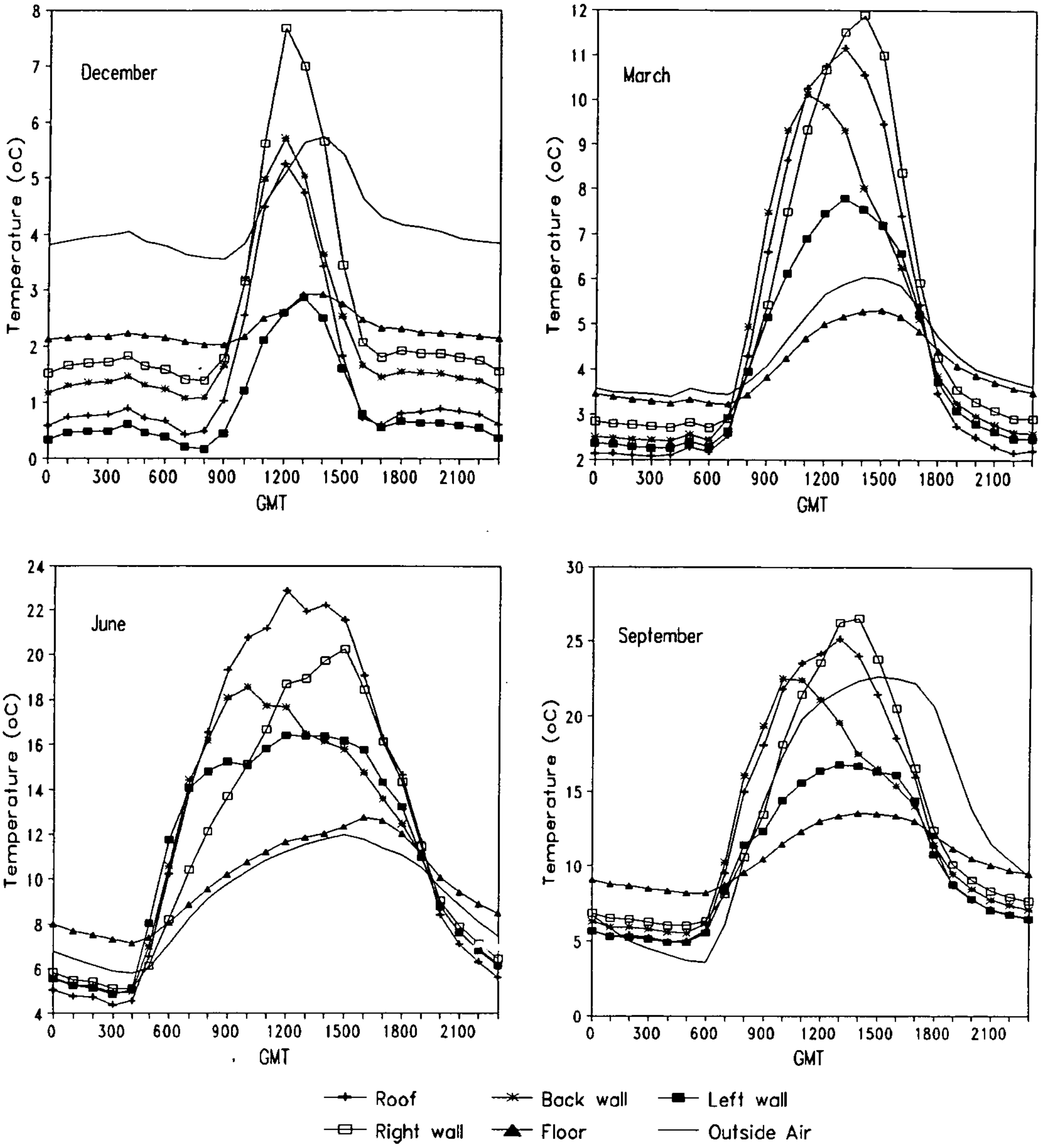
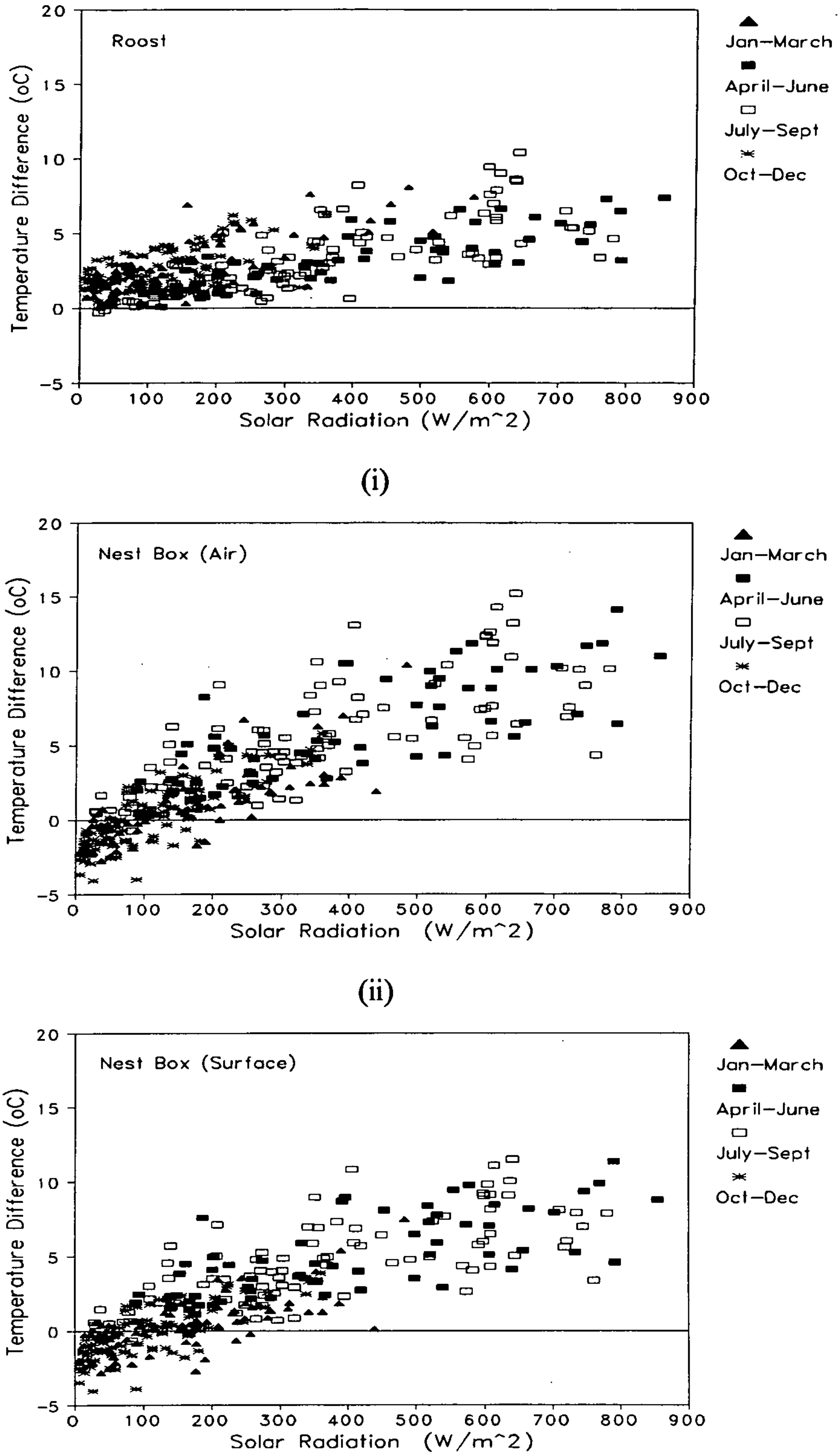


Figure 5.8. Mean daily surface temperature of the roost building from measurements on the inside roof, back wall, left and right sides and floor during December, March, June and September.

5.3.1.2 Correlation With Solar Radiation

The difference between roost temperature and outside air temperature was related to daily solar radiation. To remove the seasonal and daily correlation between temperature and solar radiation, the heating effect of the sun was calculated from the difference between roost temperature and outside air temperature at 1200 GMT for the months: January to March, April to June, July to September and October to December. This analysis indicated that there was good correlation between this temperature difference and solar radiation throughout the year (Figure 5.9).



(i)

(ii)

(iii)

Figure 5.9. Correlation of the temperature difference between roost temperature and outside air temperature with solar radiation for (i) roost air temperature, (ii) nest box air temperature and (iii) nest box surface temperature.

Roost temperature was found to be as much as 10.4 °C above outside air temperature (21.0 °C) when the mean hourly solar radiation was 642 Wm^{-2} at 1200 GMT. This analysis was also carried out for nest box temperatures and indicated that at this time, the temperature difference between air temperature in the nest box and outside air temperature was 15.2 °C and the surface temperature of the nest box reached as much as 11.5 °C above outside air temperature. Nest box temperature during the winter months remained below air temperature at midday and showed the poorest correlation with solar radiation (Figure 5.9).

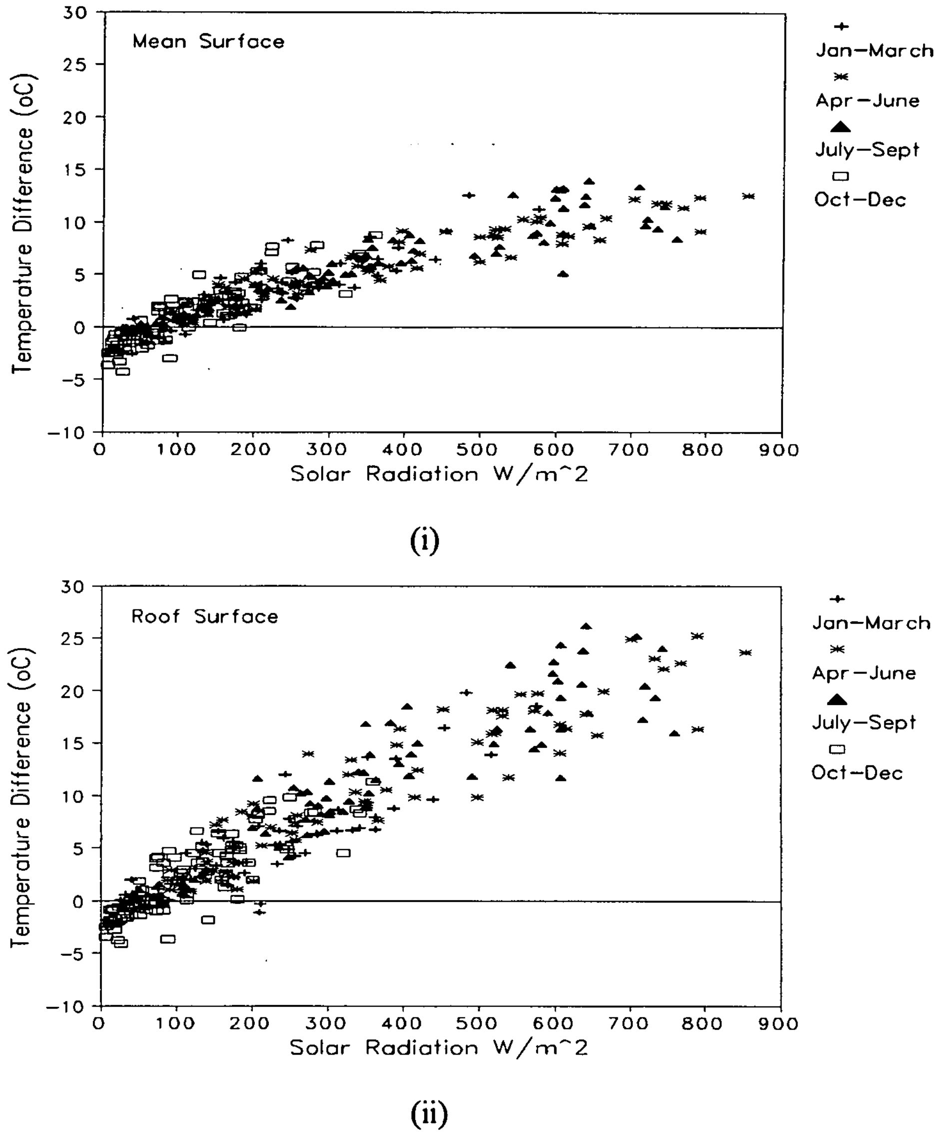
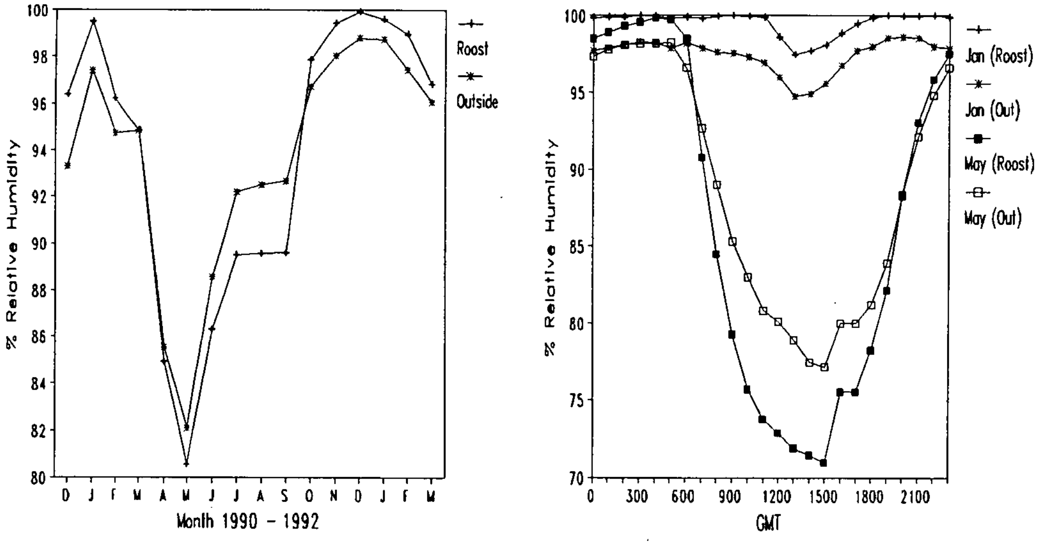


Figure 5.10. Correlation of (i) the difference in temperature between the mean surface temperature of the roost building and outside air temperature and (ii) the difference in temperature between the roof surface temperature and outside air temperature with solar radiation at 1200 GMT.

The surface temperature of the roost building were most strongly correlated with solar radiation (Figure 5.10). At 1200 GMT during September 1991, the surface temperature of the roof was 47.2 °C, right wall was 45.4 °C and back wall was 38.8 °C which were 26.2, 24.4 and 17.8 °C above air temperature when solar radiation was 642 Wm^{-2}. Two hours later, at 1400 GMT, a maximum temperature of 49.2 °C was recorded on the roof and right wall and on the back wall, a maximum temperature of 43.7 °C was measured at 1000 GMT.

5.3.1.3 Relative Humidity of the Roost

The roost building had mean relative humidities ranging from 99 % during December 1991 and January 1992 to 82 % in May 1991. The changes in relative humidity matched the seasonal and diurnal trends outside the roost (Figure 5.11) and indicated that in winter the relative humidity was marginally higher in the roost and during summer, marginally lower (paired t test of hourly values $p > 0.01$). The differences between inside and outside the roost were, however, within the measurement errors of the instrument, taking into account problems of over-ranging of the instrument when condensation on the sensor was thought to occur.



(i) (ii)

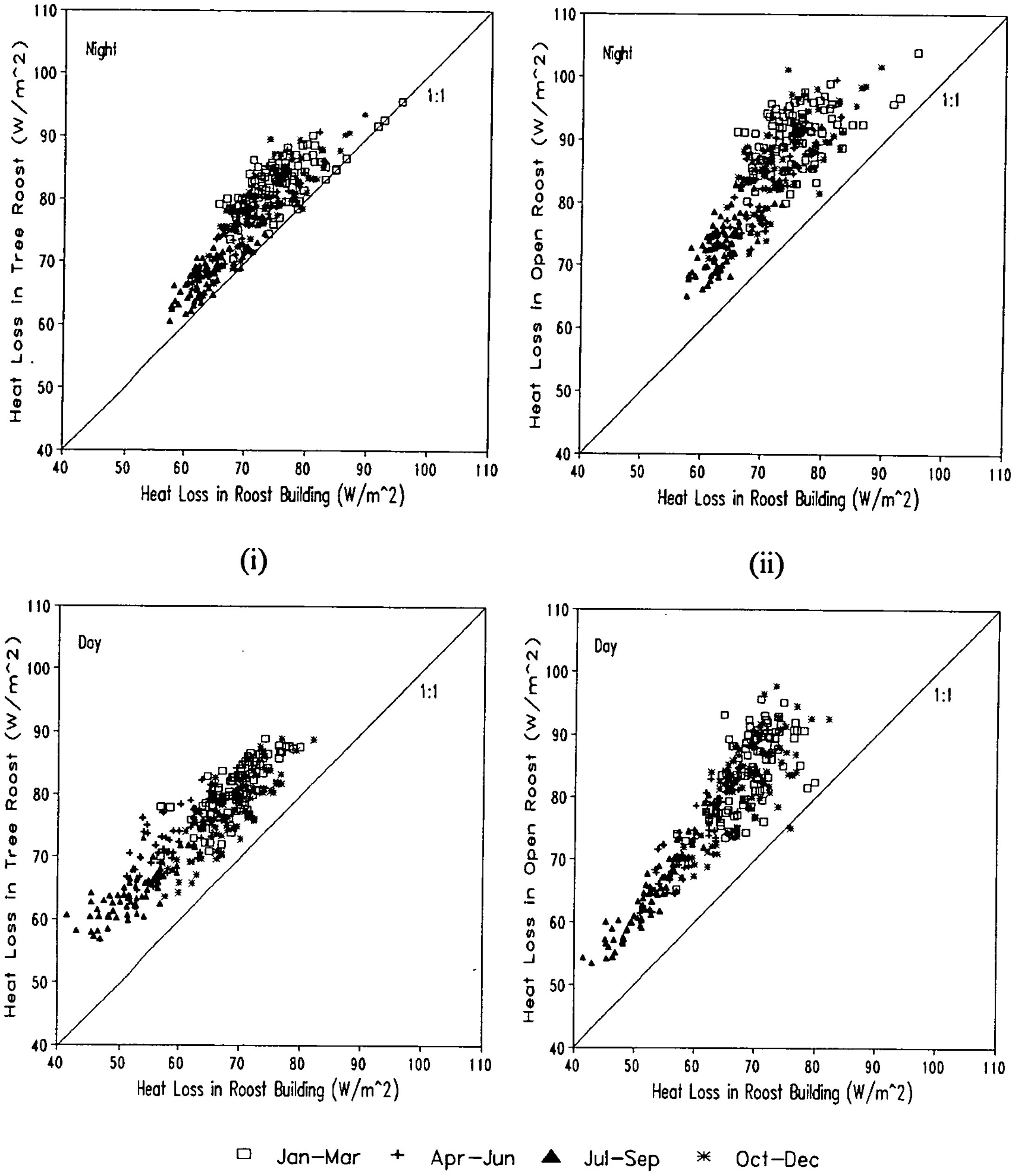
Figure 5.11. (i) The seasonal and (ii) the diurnal trends in relative humidity throughout the study period from December 1990 to March 1992.

5.3.2 Biophysical Estimates of Heat Loss from the Barn Owl

5.3.2.1 Comparison Between Roost Building, Tree and Open Sites

Rates of heat loss for a barn owl in the study site were determined for a total of 299 days from March 1991 to March 1992, during which continuous data was available of roost microclimate and ambient weather conditions. Based on calculations for dry conditions, the biophysical model estimated that heat loss for an owl in the roost building was significantly less than in tree and open sites at night (paired t test $p > 0.01$). The mean rate of heat loss in the roost was 71.3 Wm^{-2} (SE = 2.6), which compared with 77.2 Wm^{-2} (SE = 3.1) in the tree site and 84.2 Wm^{-2} (SE = 4.1) in the open site, (Figure 5.12). During the daytime, rates of heat loss in the roost were also significantly less than in tree and open sites ($p > 0.01$) with a mean rate of heat loss ranging from 63.4 Wm^{-2} (SE = 4.1) in the roost, 74.6 Wm^{-2} (SE = 3.5) in the tree site and 76.9 Wm^{-2} (SE = 4.4) in the open site. On average the roost building provided estimated savings of 18 % compared to the open and 8 % compared to a tree roost at night. During the day, the roost building gave savings of 21 % compared to the open and 18 % compared to a tree roost.

Heat loss for an owl was estimated to be greatest during the months January to March and least during July to September in the building, tree and open sites (Figure 5.13). At night, rates of heat loss in all three sites were significantly greater than during the day during all periods of the year (two sample t test, $p > 0.01$) with the exception of the tree site during October - December, when there was little difference in heat loss between night and day ($p = 0.06$). Differences in heat loss between night and day varied according to season such that at night, heat loss for an owl in the roost was greater than during the day by 4.1 Wm^{-2} (6%) in July - September but increased to 12.2 Wm^{-2} (20 %) in January - March. In the tree site night / day differences were smaller and ranged from 1.4 Wm^{-2} (2%) in July - September to 4.2 Wm^{-2} (6 %) in January - March and in open sites ranged from 4.0 Wm^{-2} (5%) in July - September to 11.0 Wm^{-2} (15 %) in January - March.

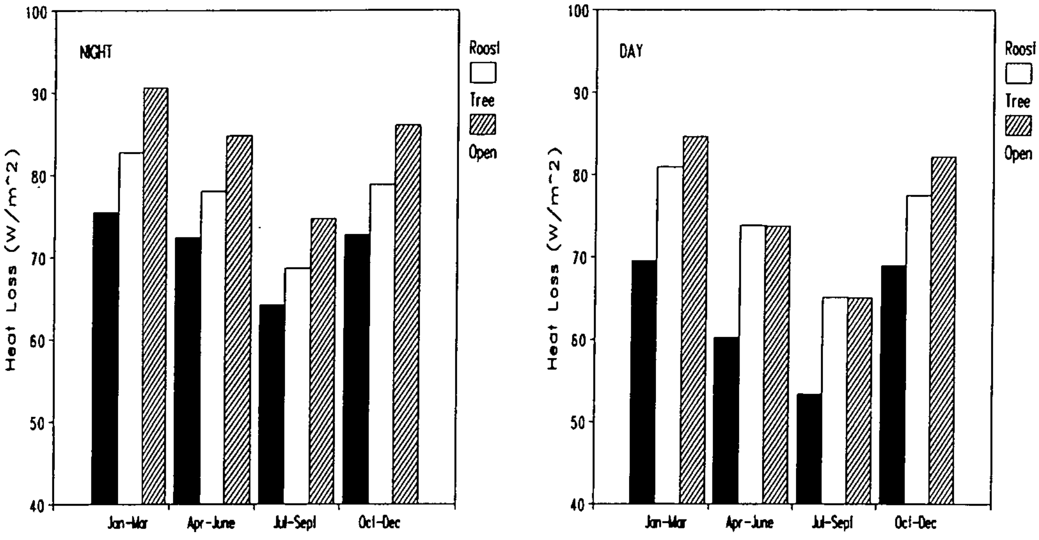


(i) (ii)

(iii) (iv)

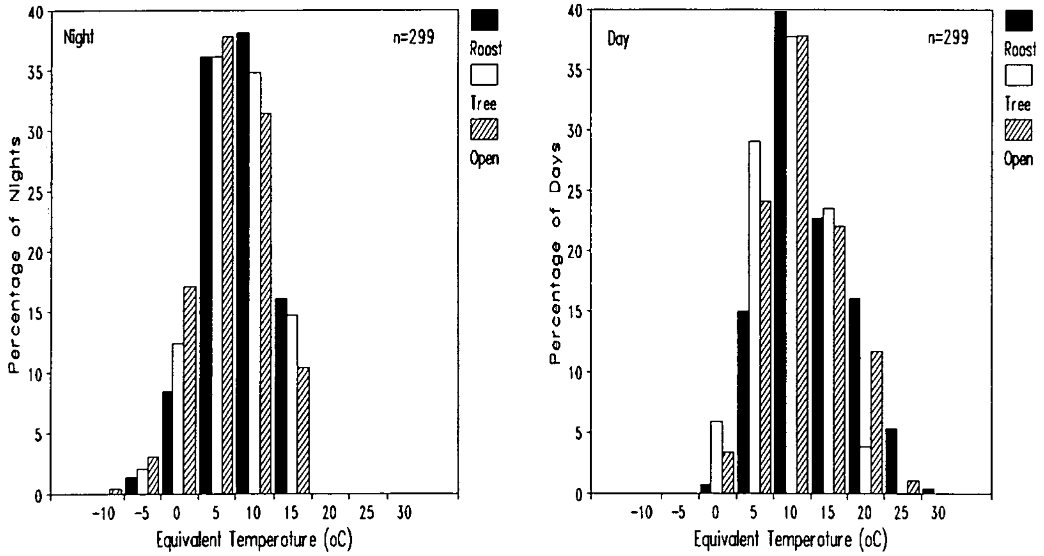
Figure 5.12. Estimation of the total heat loss of a barn owl in tree and open sites with respect to heat loss in the roost building during the night (i and ii) and day (iii and iv).

The distribution of equivalent blackbody temperatures in the three sites was similar (Figure 5.14) which reflected the diurnal and seasonal patterns of temperature in all sites. Equivalent temperatures in the roost were significantly greater than in tree and open sites with mean night values of 5.4 °C (SE = 0.24), 4.8 °C (SE = 0.30) and 4.0 °C (SE = 0.27) (paired t test $p > 0.01$) and mean daytime temperatures of 10.3 °C (SE = 0.32), 7.1 °C (SE = 0.26) and 8.5 °C (SE =0.29), ($p > 0.01$), respectively.



(i) (ii)

Figure 5.13. The mean heat loss estimated for a barn owl (i) at night and (ii) during the daytime in the roost building, tree and open during the periods January - March, April - June, July - September and October - December.

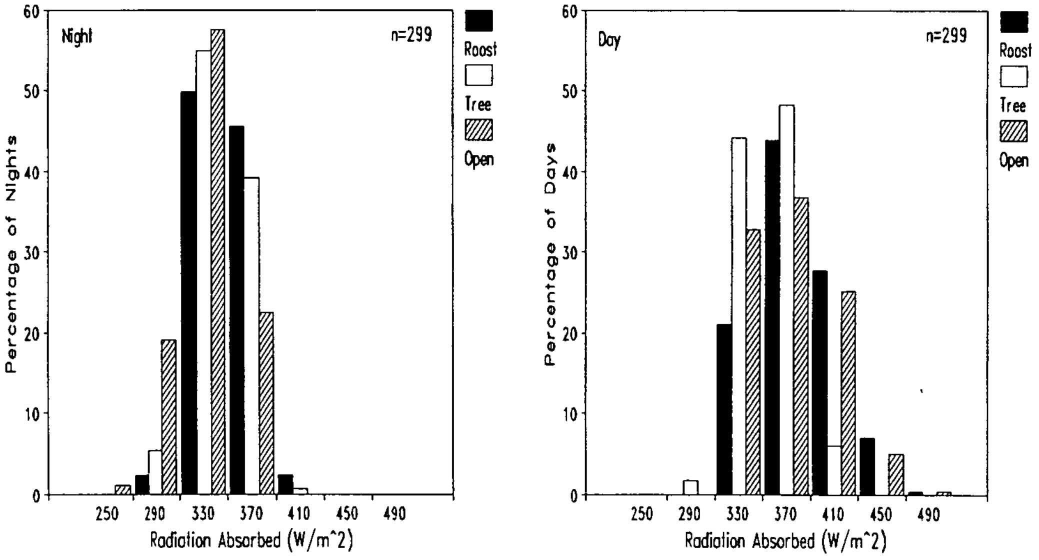


(i) (ii)

Figure 5.14. Frequency of equivalent blackbody temperatures for a barn owl in roost building, tree and open sites from March 1991 - March 1992, during (i) nights and (ii) days.

Radiation absorbed by an owl in the roost was estimated to be significantly higher than for a barn owl in tree or open sites throughout the year (paired t test $p > 0.01$) with night-time means of 330 Wm^{-2} (SE = 26.4), 324 Wm^{-2} (SE = 27.7) and 311 Wm^{-2} (SE = 32.0), respectively, which represented differences, relative to the roost site, of 2 % in the tree and 6 % in the open sites. During the day, radiation absorbed at the roost site, tree and open sites had overall means of 360 Wm^{-2} (SE = 62.6), 335 Wm^{-2} (SE = 29.6) and 352 Wm^{-2} (SE = 61.1), respectively, which represented differences relative to the roost site of 7 % in the tree site but only 2 % in the open, due to the contribution of solar radiation (Figure 5.15).

Estimated latent heat losses accounted for 1.8 to 12.8 Wm^{-2} (mean = 4.9 Wm-2 SE = 0.1) in the roost and 1.6 to 10.3 Wm^{-2} (mean = 4.4 SE = 0.1) in tree and open sites (assuming equal air temperature in tree and open sites), (Figure 5.16). There was estimated to be a small seasonal increase in latent heat loss in the roost associated with higher summer temperatures from a mean of 3.9 Wm^{-2} (SE = 0.1) in January - March to 6.8 Wm^{-2} (SE = 0.2) in July - September. Outside the roost building, latent heat loss was estimated to increase from 3.4 Wm^{-2} (SE = 0.1) in January - March to 6.4 Wm^{-2} (SE = 0.1) in July - September. The overall contribution of latent heat loss represented on average 7 % inside the roost building and 5% outside the roost.



(i) (ii)

Figure 5.15. Estimated radiation absorbed by a barn owl in the roost building, tree and open sites throughout period from March 1991 to March 1992 during (i) nights and (2) days.

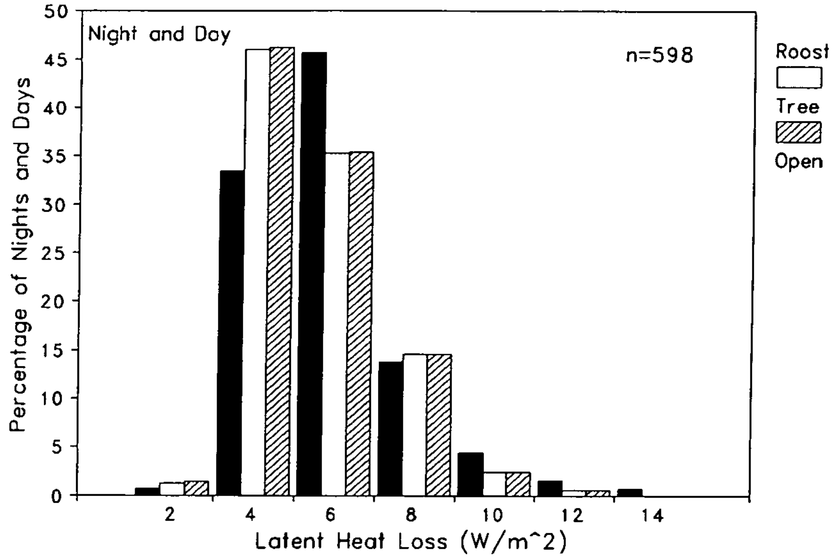


Figure 5.16. The estimated latent heat loss for a barn owl in the roost, tree and open sites from March 1991 - March 1992.

Differences in rates of heat loss for a roosting barn owl during the night and day were also estimated from diurnal patterns of temperature, wind speed and solar radiation (assuming cloudy conditions). These calculations indicated large reductions in heat loss for a barn owl in the roost building, tree and open sites throughout the year. A reduction in heat loss associated with significant increases in radiation absorbed were found and was most marked in the building and open sites (Figure 5.17).

5.3.2.2 Cloudy and Clear Conditions

Differences in the rate of heat loss of a barn owl during cloudy and clear conditions were examined (Table 5.4). Heat loss on clear nights was estimated to be significantly greater (two sample t test $p > 0.01$) in the roost building by: 4.0 - 6.9 Wm^{-2} (6 - 9 %); 4.2 - 7.6 Wm^{-2} (6 - 10%) in the tree site; and 4.7 - 9.3 Wm^{-2} (5 - 11 %) in the open. In the roost building during the day, heat loss on clear days was significantly less by: 3.3 - 5.0 Wm^{-2} (5 - 10 %) during April - June ($p = 0.03$) and July - September ($p = 0.01$), but not significantly different from cloudy days in other months ($p = 0.11 - 0.33$). In the tree site, heat loss increased on clear days by 3.2 - 4.6 Wm^{-2} (4 - 6 %) in April - June ($p > 0.01$) and during October - December ($p = 0.02$) but was not significantly different in other months ($p = 0.1 - 0.8$). In open sites, heat loss decreased on clear days by 4.2 Wm^{-2} (5 %), only during January - March ($p = 0.03$) but rates of heat loss were not significantly different from cloudy days in other months ($p = 0.1 - 0.36$).

Comparison of heat losses in the roost building with alternative roosts in tree or open sites allowed an estimate to be made of the energy savings associated with selection of roost sites by barn owls. The metabolic savings for a barn owl in the roost on cloudy nights was found to be 4.4 - 7.7 Wm^{-2} (8 - 10 %) compared with a tree roost and 12.5 - 15.6 Wm^{-2} (16 - 21%) compared with roosting in the open. Savings on clear nights were similar and were 4.6 - 7.0 Wm^{-2} (7 - 9 %) and 13.8 - 16.1 Wm^{-2} (18 - 21 %) compared with tree and open sites, respectively. During the day, savings from roosting in the building were greater. On cloudy days, savings accounted for 8.1 - 12.9 Wm^{-2} (12 - 21 %) and 11.4 - 15.3 Wm^{-2} (20 - 22 %) in comparison to tree and open roosts and increased on clear days to 11.9 - 19.4 Wm^{-2} (17 - 34 %) and 13.6 - 18.4 Wm^{-2} (17 - 32 %), respectively (Table 5.4).

The energy savings for a barn owl roosting in the building were associated with small radiative gains (Table 5.5). Radiation absorbed by an owl in the roost on cloudy nights was 2.7 Wm^{-2} (1 - 2 %) greater than in a tree roost (paired t test $p > 0.01$, Oct - Dec $p = 0.03$) and 3 - 18 Wm^{-2} (4 - 6 %) greater than in open sites ($p > 0.01$). On clear nights, radiation absorbed in the roost was estimated to be 10 - 15 Wm^{-2} (3 - 5 %) greater than in a tree roost and 29 - 34 Wm^{-2} (10 - 12 %) greater than in the open ($p > 0.01$).

On cloudy days, radiation absorbed in the building was estimated to be significantly greater ($p > 0.01$) than in the tree roost by 9 - 33 Wm^{-2} (2 - 7 %). On cloudy days, absorbed radiation in the roost building was significantly greater than the in the open ($p > 0.01$), but only by 2 - 9 Wm^{-2} (1 - 3 %) and on clear days was 6 - 27 Wm^{-2} (2 -7 %) greater than in the open ($p > 0.01$) with the exception of January - March when there was no difference between the building and the open ($p = 0.09$). In comparison, for an owl roosting in trees on clear days it was estimated that radiation absorbed was significantly less than in the roost building by 36 - 61 Wm^{-2} (8 - 18 %), ($p > 0.01$) .

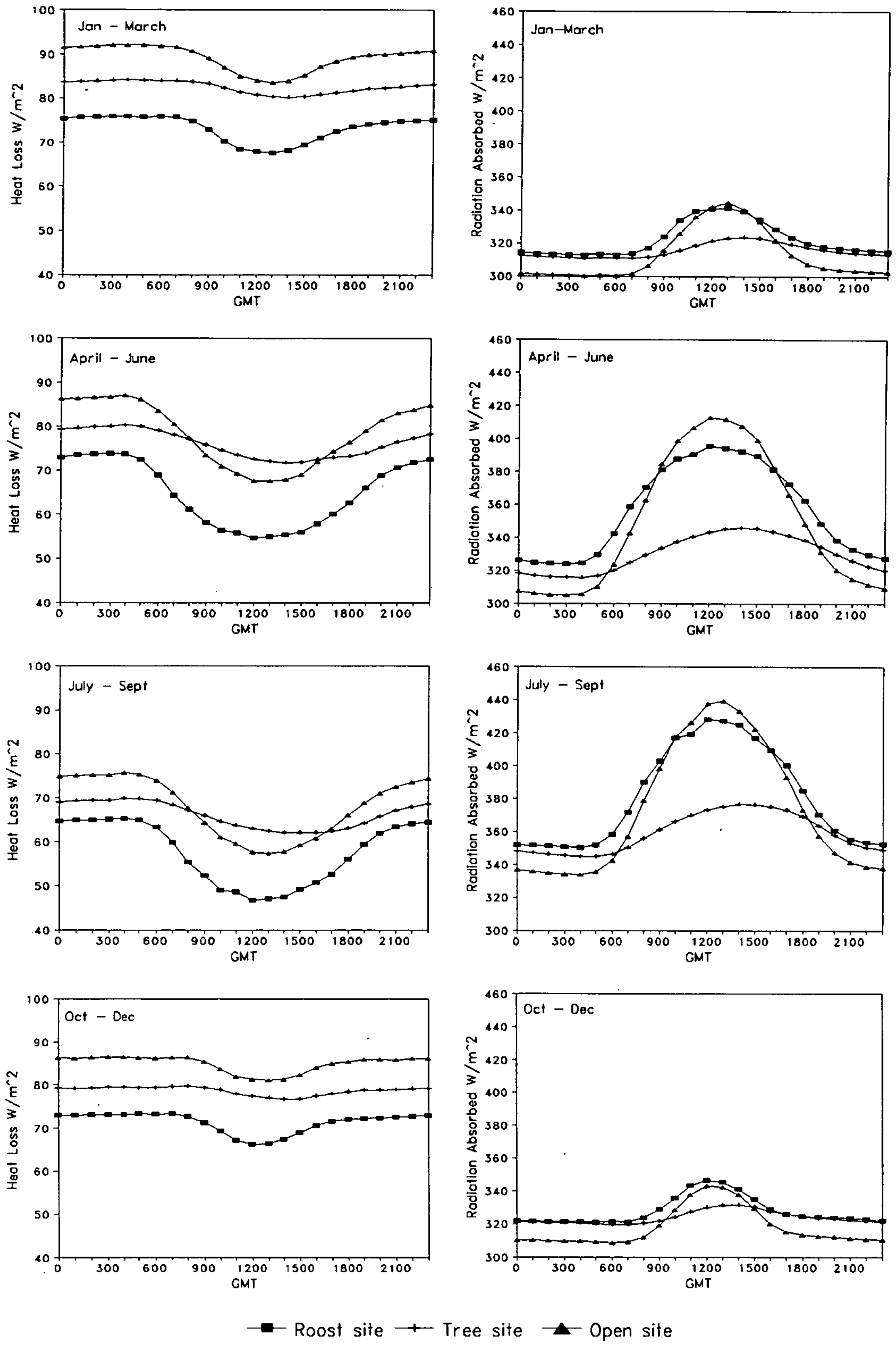


Figure 5.17. The diurnal pattern of heat loss and radiation absorbed for a barn owl roosting in the building, tree and open for periods January - March, April - June, July - September and October - December (assuming cloudy conditions).

		Heat Loss from Barn Owl (Wm^{-2})			**% Savings**	
		Roost	**Tree**	**Open**	***Tree***	***Open***
Cloudy Nights						
Jan - Mar	61	73.8 (0.5)	81.5 (0.5)	89.4 (0.6)	10	21
Apr - Jun	42	70.7 (0.6)	76.0 (0.8)	82.4 (0.9)	7	16
Jul - Sep	58	63.3 (0.4)	67.7 (0.5)	73.4 (0.6)	7	16
Oct - Dec	64	71.3 (0.6)	77.0 (0.7)	83.8 (0.8)	8	12
Clear Nights						
Jan - Mar	21	80.6 (1.5)	86.5 (0.9)	94.4 (0.9)	7	17
Apr - Jun	17	76.7 (1.0)	82.8 (1.0)	90.5 (1.1)	8	18
Jul - Sep	16	67.3 (1.1)	71.9 (1.0)	78.9 (1.1)	7	17
Oct - Dec	20	77.6 (1.4)	84.6 (1.1)	93.7 (1.1)	9	21
Cloudy Days						
Jan - Mar	75	69.6 (0.5)	80.8 (0.5)	84.9 (0.7)	16	22
Apr - Jun	53	60.5 (0.7)	73.4 (0.7)	73.3 (1.0)	21	21
Jul - Sep	62	54.1 (0.6)	65.1 (0.6)	65.5 (0.9)	21	21
Oct - Dec	73	68.6 (0.6)	76.7 (0.6)	82.0 (0.8)	12	20
Clear Days						
Jan - Mar	7	69.2 (3.1)	82.4 (1.9)	80.7 (1.9)	19	17
Apr - Jun	6	57.2 (1.3)	76.6 (0.8)	75.6 (1.7)	34	32
Jul - Sep	12	49.1 (1.8)	65.3 (1.7)	62.6 (2.2)	33	27
Oct - Dec	11	69.4 (1.8)	81.3 (1.8)	83.0 (2.3)	17	20

Table 5.4. The estimated total heat loss for a barn owl in roost building, tree and open sites during cloudy and clear nights and cloudy and clear days. The percentage savings from roosting in the building relative to tree and open roost sites are also indicated. Values in the brackets are standard errors of measurements.

The difference between tree and open sites during the day was due to the contribution of solar radiation. On cloudy days, absorbed solar radiation by a barn owl in the open was estimated to be 25 .8 Wm^{-2} (SE = 1.2) which represented, on average, 7 % of the total radiation absorbed by an owl. Solar radiation absorbed on clear days was significantly greater (two sample t test, $p > 0.01$) and was estimated to be 50.9 Wm^{-2} (SE = 2.4) which represented on average 14 % of the total radiation absorbed by an owl in this location (Figure 5.18).

Cloudy nights were significantly warmer than clear nights throughout the year (two sample t test $p > 0.01$) but there was no difference in wind speed except during the period January - March ($p > 0.01$) when the mean wind speed was two times greater on cloudy compared with clear nights (Table 5.6). In these months, the heat loss for a barn owl on a clear night was only 6 % greater than on a cloudy night compared with differences of 7 - 12 % during other months, when no differences in wind speed were recorded. This demonstrated that high wind speeds may reduce the thermal benefits for owls on cloudy nights.

		Total Radiation Absorbed by Barn Owl (Wm^{-2})						**% Savings**	
		Roost		**Tree**		**Open**		***Tree***	***Open***
Cloudy Nights									
Jan - Mar	61	320	(1.6)	318	(1.6)	307	(1.6)	2	3
Apr - Jun	42	333	(2.0)	326	(2.0)	315	(2.0)	7	18
Jul - Sep	58	357	(1.6)	352	(1.4)	340	(1.6)	5	17
Oct - Dec	64	328	(1.9)	326	(2.0)	315	(1.9)	2	13
Clear Nights									
Jan - Mar	21	306	(3.5)	292	(3.0)	273	(2.9)	14	33
Apr - Jun	17	315	(3.0)	300	(2.6)	281	(2.5)	15	34
Jul - Sep	16	343	(3.7)	331	(3.1)	310	(3.0)	12	33
Oct - Dec	20	309	(3.9)	299	(4.5)	280	(3.7)	10	29
Cloudy Days									
Jan - Mar	75	336	(1.8)	319	(1.5)	330	(2.0)	17	6
Apr - Jun	53	371	(2.7)	338	(1.6)	369	(3.1)	33	2
Jul - Sep	62	396	(2.7)	364	(1.6)	389	(3.1)	32	7
Oct - Dec	73	338	(2.0)	329	(1.8)	329	(1.9)	9	9
Clear Days									
Jan - Mar	7	339	(11.3)	303	(6.9)	333	(8.8)	36	6
Apr - Jun	6	385	(5.2)	326	(2.1)	368	(4.0)	59	17
Jul - Sep	12	418	(7.5)	357	(4.3)	391	(4.8)	61	27
Oct - Dec	11	336	(6.7)	310	(4.7)	327	(4.7)	26	9

Table 5.5. The total radiation absorbed by a barn owl in the roost building, tree and open sites during cloudy and clear nights (long wave) and during cloudy and clear days (long wave and short wave). The percentage radiative savings from roosting in the building relative to tree and open sites are indicated. Values in brackets are standard errors of measurements.

Clear days were found to be significantly colder in January - March ($p > 0.05$) and October - December ($p > 0.01$) but not in the summer months ($p = 0.30$). Wind speed on cloudy days was greater than on clear days during the periods January - March ($p > 0.02$) and July - September ($p>0.02$) but not significantly during other months (Table 5.6). The implication of this was that the estimated rate of heat loss for a barn owl in the open site on clear days was less than on cloudy days only when wind speed was significantly lower and therefore, thermal benefits from solar radiation only occurred during such periods as January - March when solar radiation in combination with low wind speeds compensated for cold air temperatures.

	Cloud Night		Clear Night		Cloudy Day		Clear Day	
Temperature °C								
Jan - Mar	4.2	(0.3)	0.6	(0.7)	5.0	(0.3)	2.9	(1.6)
Apr - Jun	6.1	(0.4)	2.5	(0.6)	8.6	(0.3)	8.0	(0.4)
Jul - Sep	11.4	(0.3)	9.2	(0.6)	13.8	(0.3)	14.3	(0.9)
Oct - Dec	6.1	(0.4)	2.2	(0.9)	6.6	(0.4)	4.6	(1.0)
Wind speed ms^{-1}								
Jan - Mar	1.4	(0.1)	0.7	(0.1)	1.4	(0.1)	0.7	(0.2)
Apr - Jun	0.8	(0.1)	0.7	(0.1)	1.2	(0.1)	1.2	(0.1)
Jul - Sep	0.9	(0.1)	0.7	(0.1)	1.2	(0.1)	0.9	(0.1)
Oct - Dec	1.1	(0.1)	1.0	(0.2)	1.3	(0.1)	1.0	(0.1)

Table 5.6. Air temperature and wind speed (at 1m) on cloudy and clear nights, and cloudy and clear days recorded at the study site from March 1991 to March 1992.

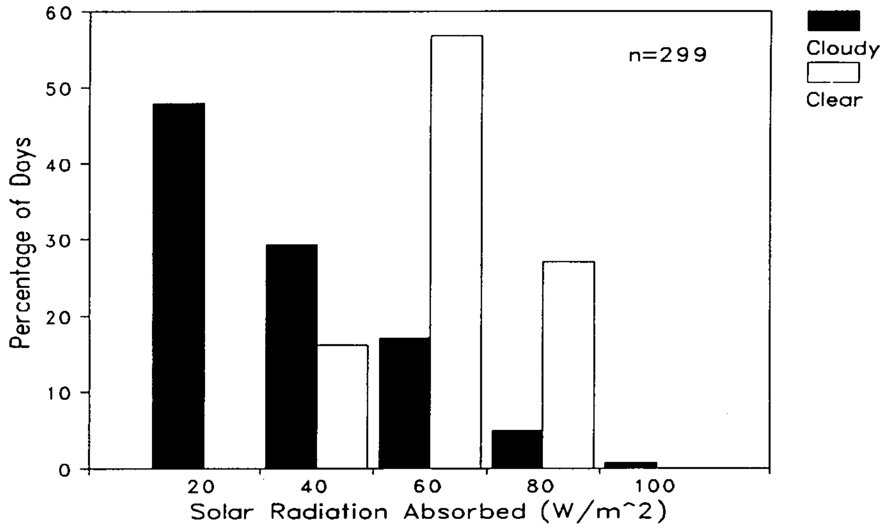


Figure 5.18. The estimated solar radiation absorbed by a barn owl in the open, on clear and cloudy days from March 1991 - March 1992.

The importance of solar radiation on the energy balance of barn owls that are active during the day may have been underestimated using values of solar radiation averaged over all daylight hours and therefore the energy balance of a barn owl in the open was also determined using mean hourly values of solar radiation at 1200 GMT on days of maximum and minimum solar radiation. This analysis indicated that on cloudy days (minimum solar), diffuse solar radiation absorbed by an owl amounted to 1.5 - 29.9 Wm^{-2} and on clear days (maximum solar) both beam and diffuse absorbed ranged from 60.8 - 106.8 Wm^{-2} throughout the year. Solar radiation represented 3 % (SE = 0.8) of the total radiation absorbed by an owl at 1200 GMT on cloudy days but as much as 21 % (SE = 0.6) on clear days (Figure 5.19). By comparing the total heat loss of a barn owl at 1200 GMT on clear days with cloudy days, solar radiation was estimated to reduce total heat loss of a barn owl by, on average 14.9 Wm^{-2} (SE = 2.7) or 24.5 %, throughout the year. Energy savings associated with solar gains on clear and cloudy days, were however, dependent on wind speed such that during August there was no difference in total heat loss because wind speed was 1.9 ms^{-1} greater on clear than on cloudy days.

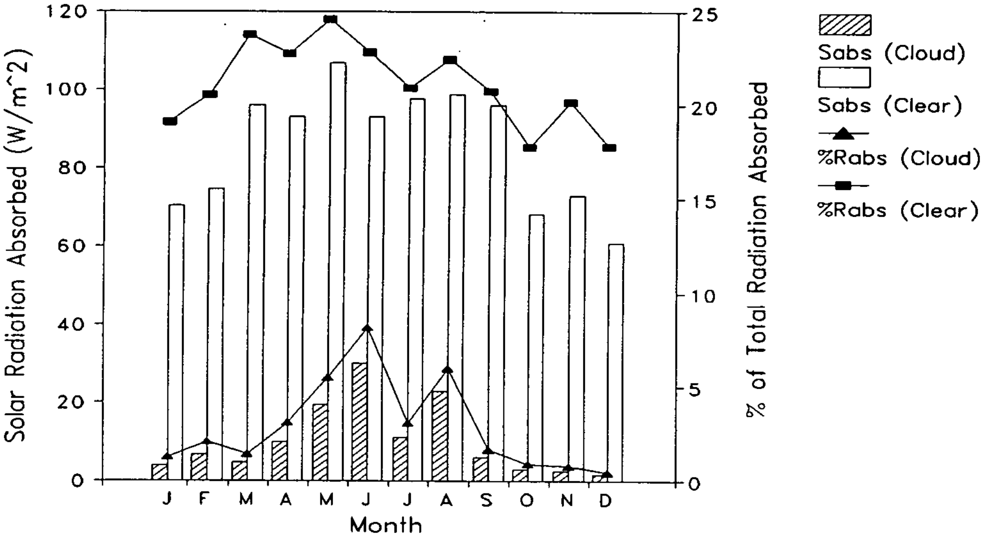


Figure 5.19. The estimated effect of cloud cover on solar radiation absorbed (Sabs) by a barn owl in the open at 1200 GMT on cloudy and on clear days during 1991. Solar radiation absorbed was also expressed as a percentage of total radiation absorbed (% Rabs) by an owl in this location.

5.3.2.3 Wet and Dry Conditions

Increases in heat loss from wetting during periods of rain were determined for wet and dry nights and days throughout the year. Wet periods were distinguished according to days on which more than 1 mm of rainfall occurred in 24 hours. In this way, there were a total of 148 wet and 151 dry days throughout the study period. Rainfall records were not checked to distinguish between night or daytime rainfall and therefore it was assumed that with this amount of rainfall, it rained at both times .

	Heat Loss of Barn Owl in the Open (Wm^{-2})							
	Wet Nights		**Dry Nights**		**Wet Days**		**Dry Days**	
Jan - Mar	96.7	(0.6)	89.9	(0.9)	92.0	(0.9)	83.9	(1.0)
Apr - Jun	88.1	(1.4)	85.7	(1.2)	80.9	(1.5)	71.3	(1.1)
Jul - Sep	79.7	(1.0)	73.8	(0.7)	72.8	(1.4)	62.1	(0.9)
Oct - Dec	90.7	(1.1)	86.4	(1.3)	88.3	(1.2)	80.7	(1.0)
	Heat Loss of Barn Owl in Roost Building (Wm^{-2})							
Jan - Mar	73.7	(0.6)	76.8	(1.1)	69.6	(0.5)	71.3	(0.8)
Apr - Jun	70.3	(0.8)	74.2	(0.8)	62.5	(1.0)	58.3	(0.8)
Jul - Sep	64.0	(0.6)	64.3	(0.6)	56.6	(0.9)	50.9	(0.7)
Oct - Dec	70.7	(0.6)	75.5	(1.1)	68.0	(0.7)	69.6	(0.9)

Table 5.7. Estimated heat loss of barn owl in the open and in the roost building during wet and dry nights and days. Numbers in brackets are standard errors of estimated heat loss.

The heat loss of a barn owl when in the open on wet nights was estimated to range from 79.7 Wm^{-2} on a wet night in July - September to 96.7 Wm^{-2} during the period January - March and during wet days, from 72.8 Wm^{-2} to 92.0 Wm^{-2} in the same months. Comparison between rates of heat loss on wet and dry nights indicated that heat loss was 4.4 - 6.8 Wm^{-2} (6 - 8 %) greater on wet nights in all periods (two sample t test $p > 0.01$) with the exception of the period April - June when no significant differences were found ($p = 0.1$). Heat loss on all wet days was significantly greater by 7.6 - 10.7 Wm^{-2} (9 - 17 %) than on dry days ($p > 0.01$), (Table 5.7).

Wet nights in January - March, April - June and October - December were warmer than dry nights ($p > 0.01$) but in July - September no significant difference was found ($p = 0.5$). Wind speeds on wet nights were significantly greater than dry nights. ($p > 0.01$). In contrast, daytime temperatures on wet days during January-March and April - June were not significantly different from dry days ($p=0.1$, $p=0.4$) but during July- September wet days were colder ($p > 0.01$) and during October - December wet days were warmer ($p > 0.01$). Wind speed during wet days was also greater than dry days for all periods ($p > 0.01$), (Table 5.8).

The difference in estimated heat loss between wet and dry nights was smaller than expected, relative to the difference during the day. Although wetting effects obviously did not occur on dry nights, heat loss was estimated to increase because of lower air temperatures. This effect did not often occur during the day, as differences in air temperature between wet and dry conditions were not as pronounced.

	Weather Conditions							
	Wet Nights		**Dry Nights**		**Wet Days**		**Dry Days**	
Temperature °C								
Jan - Mar	4.3	(0.4)	2.1	(0.6)	5.2	(0.4)	4.3	(0.5)
Apr - Jun	6.3	(0.6)	4.0	(0.5)	8.6	(0.5)	8.4	(0.4)
Jul - Sep	10.9	(0.4)	10.9	(0.4)	12.7	(0.5)	14.8	(0.3)
Oct - Dec	6.5	(0.4)	3.5	(0.5)	7.2	(0.2)	5.2	(0.3)
Wind speed ms^{-1}								
Jan - Mar	1.6	(0.1)	0.8	(0.1)	1.7	(0.1)	0.9	(0.1)
Apr - Jun	1.0	(0.1)	0.6	(0.1)	1.4	(0.1)	1.0	(0.1)
Jul - Sep	1.0	(0.1)	0.7	(0.1)	1.3	(0.1)	1.0	(0.1)
Oct - Dec	1.4	(0.1)	0.7	(0.1)	1.6	(0.1)	0.8	(0.1)

Table 5.8. Temperature and wind speed (at 1m) on wet and dry nights and days recorded at study site from March 1991 to March 1992. Values in brackets are standard errors of measurements.

A barn owl roosting in the building during wet and dry periods was estimated to have significantly lower rates of heat loss than a barn owl outside the roost, throughout the year (paired t test $p > 0.01$), (Table 5.7) and it is indicated that on wet nights a barn owl inside the building had estimated savings of 17.8 - 23.0 Wm^{-2} (25 - 31 %) compared with 9.5 - 11.5 Wm^{-2} (14 - 17%) on dry nights. On wet days savings of 16.2 - 22.4 Wm^{-2} (29 -32 %) were estimated compared with 11.1 - 13.0 Wm^{-2} (16 - 22 %) on dry days. The greatest saving of 31 % on wet nights and greatest daytime saving of 32 % on wet days were estimated to occur during January - March.

The energy balance of a barn owl in the open was also determined on a total of 51 snow days when snow was recorded lying at 9 am (Figure 5.20). Heat loss during these snow periods was on average 93.8 Wm^{-2} (SE = 5.9) on cloudy nights and 97.3 Wm^{-2} (SE = 0.1) on clear nights. The mean temperature and wind speed on cloudy nights was 1.2 °C (SE = 0.3) and 1.1 ms^{-1} (SE = 0.1) and on clear nights was -1.5 °C (SE = 1.1) and 0.7 ms^{-1} (SE = 0.2), respectively . During the daytime, the estimated rate of heat loss on cloudy days was 92.7 Wm^{-2} (SE = 6.4) and on clear days was 81.3 Wm^{-2} (SE = 12.6). The mean solar irradiance on cloudy days was 60 Wm^{-2} (SE = 8.4) and on clear days was of 125 Wm^{-2} (SE = 17.3) Temperature and wind speed were 1.8 °C (SE = 0.3) and 1.4 ms^{-1} (SE = 0.1) on cloudy days and were 0.7 °C (SE = 0.6) and 0.6 ms^{-1} (SE = 0.2) on clear days.

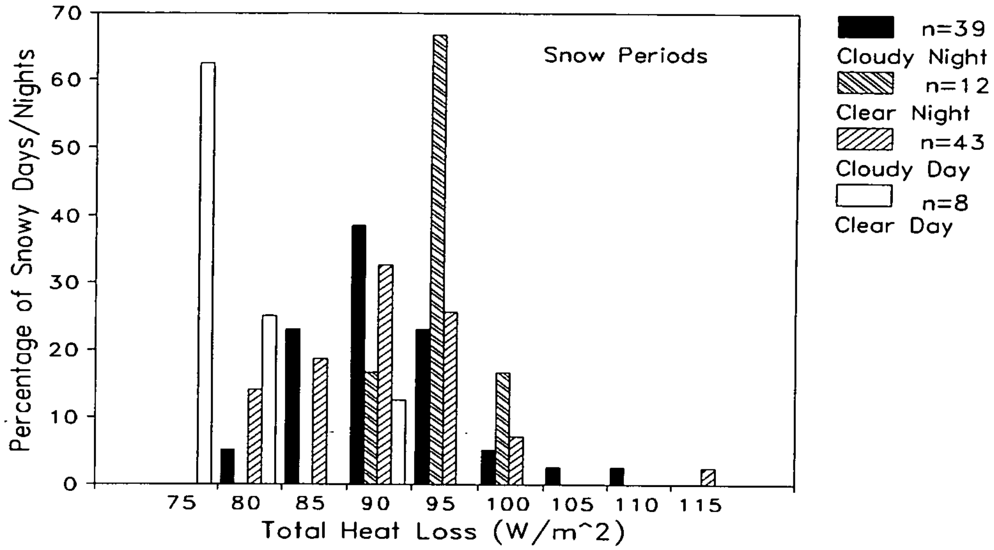


Figure 5.20. Estimated rates of heat loss for a barn owl on snowy days when snow was recorded lying at 9 am from December 1990 to March 1992. Data was divided into clear and cloudy periods from records of cloud cover at 0000 and 1200 GMT.

5.3.2.4 Combination of Weather Conditions

As demonstrated above, many of the factors leading to higher rates of heat loss occur together and therefore rates of heat loss were examined by dividing the data according to night and days which were wet or dry and had wind speed and air temperature, which were greater or less than mean monthly values. This analysis divided night and days into wet or dry which were windy - cold, calm - warm, windy - warm and calm - warm.

The heat loss of an owl in the open was estimated to increase according to the combination of weather conditions (Appendix 5). The maximum difference in heat loss occurred between wet windy - cold conditions and dry calm - warm conditions. Differences of 16.3 - 24.0 Wm^{-2} (13 - 32 %) were found for nights and 14.6 - 20.0 Wm^{-2} (18 - 33 %) for daytime estimates. The difference in heat loss for a barn owl was proportional to the difference in temperature between these two sets of weather conditions. There was no strong seasonal pattern but the smallest difference for nights occurred during the period July - September when the temperature of cold nights was on average only 1.2 °C colder than nights which were dry calm and relatively warm. This compared with mean temperature differences of 2.3 - 2.6 °C during other months with correspondingly greater differences in heat loss. Similarly, during the day, the smallest difference in heat loss between the two weather conditions was estimated to occur in October - December when wet windy cold days were only 1.1 °C colder and compared with mean differences of 2.5 - 4.3 °C in other months.

Weather Conditions	Rank	% Savings in Roost	Increments of Maintenance Roost	Increments of Maintenance Open
Wet wind cold day	1	31 - 37	1.6 - 1.9	2.1 - 2.5
Wet wind warm day	2	31 - 37	1.5 - 1.8	1.9 - 2.4
Wet wind warm night	3	28 - 35	1.6 - 1.9	2.1 - 2.5
Wet wind cold night	4	25 - 34	1.7 - 2.0	2.1 - 2.6
Wet calm cold day	5	24 - 27	1.4 - 1.9	1.8 - 2.4
Dry wind cold day	6	14 - 30	1.6 - 1.9	1.8 - 2.4
Wet calm cold night	7	20 - 26	1.8 - 2.0	2.1 - 2.6
Dry wind warm day	8	13 - 27	1.4 - 1.8	1.6 - 2.2
Wet calm warm day	9	21 - 26	1.3 - 1.8	1.6 - 2.1
Dry wind warm night	10	17 - 28	1.6 - 1.9	1.9 - 2.4
Wet calm warm night	11	19 - 27	1.6 - 1.9	1.9 - 2.4
Dry wind cold night	12	14 - 26	1.7 - 2.2	2.1 - 2.5
Dry calm warm day	13	12 - 17	1.3 - 1.8	1.6 - 2.1
Dry calm cold day	14	13 - 15	1.5 - 1.9	1.7 - 2.2
Dry calm cold night	15	12 - 15	1.8 - 2.1	2.0 - 2.4
Dry calm warm night	16	7 - 15	1.7 - 1.9	1.9 - 2.2

Table 5.9. The savings associated with the use of the roost building by the barn owl in different combinations of weather conditions during nights and days. The cost of thermoregulation in both locations was also given in increments of metabolic maintenance requirements (equivalent to a heat loss of 38 Wm^{-2}, Table 2.13) using estimated values of heat loss (Appendix 5).

The rate of heat loss for a barn owl in the roost building was also dependent on the combination of rain, wind speed and temperature (Appendix 5) and by dividing the data in this way, the savings associated with roosting behaviour could be examined according to a given set of weather conditions. On average, the savings from roosting in the building were 25 % during January - March, 23 % in April - June, 20 % in July - September and 22 % during October - December. Energy savings were, however, dependent on the combination of weather conditions and were determined by ranking each of these conditions within each period according to the highest percentage saving. This analysis indicated that a barn owl roosting in the building was estimated to make metabolic savings of 25 to 37 % on wet windy days and nights but only savings of 7 to 17 % on dry calm conditions (Table 5.9). The highest percentage savings for barn owls were estimated to occur by roosting in the building during the daytime.

5.3.3 Energetics of Incubation

Air temperature of the nest box throughout incubation ranged from 12.6 to 22.5 ^{o}C with a daily mean of 16.1 ^{o}C (SE = 0.4). Surface temperature of the nest box was similar and ranged from 12.4 to 21.7 ^{o}C with a mean of 15.7 ^{o}C (SE = 0.4). Based on chick weights (Taylor, in press), it was calculated that the first egg was laid on 22 June 1991 and a total of six eggs were laid of which five were known to have hatched. The energy requirement of maintaining eggs at constant temperature was estimated to range from 25.5 to 37.9 kJday^{-1} with a mean of 33.5 kJday^{-1} (SE = 0.5) for the entire incubation period (Figure 5.21). Variation in energy demands was due to a significant increase in temperature of the nest box over a 5 day period in the middle of the incubation period which reduced heating requirements.

The total energy balance of the incubating female ranged from 54.2 to 66.6 Wm^{-2} with a mean of 61.7 Wm^{-2} (SE = 0.6). This represented a daily thermostatic cost of 262 to 213 kJday^{-1} with a mean of 243 kJday^{-1} (SE = 2.2), (Figure 5.22). The heat flux from dorsal, ventral and brood patch regions were estimated to be similar, with contributions of 15.4 to 23.1 Wm^{-2} (mean = 20.4 Wm^{-2}, SE = 0.3) from the dorsal surface, 13.4 to 20.2 Wm^{-2} (mean = 17.8 Wm^{-2}, SE = 0.3) from the ventral surface and 11.1 to 16.6 Wm^{-2} (mean = 14.6 Wm^{-2}, SE = 0.2) from the brood patch. Evaporation was estimated to range from 6.7 to 14.2 Wm^{-2} (mean = 8.9 Wm^{-2}, SE = 0.3) throughout the incubation period. In percentage terms, total heat loss from the incubating barn owl was due to 33.0 % from the dorsal surface, 28.8 % from the ventral surface, 23.6 % from the brood patch and 14.6 % through cutaneous and respiratory evaporation.

The estimated rate of heat loss for an incubating barn owl was similar to estimates for a barn owl outside the roost. Ten days before incubation, heat loss for a barn owl outside the roost ranged from 54.0 - 74.4 Wm^{-2}, with a mean of 65.6 Wm^{-2} (SE = 1.9) for a female of the same body size and discounting increased heat loss from plumage overlying the brood patch. During incubation heat loss for a barn owl outside the roost ranged from 47.1 - 74.7 Wm^{-2}, with a mean of 60.1 Wm^{-2} (SE = 1.0).

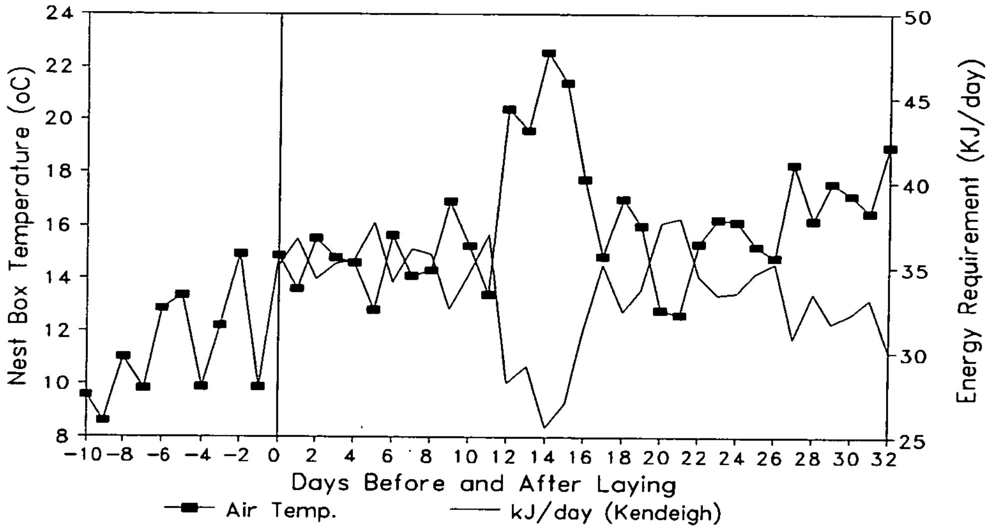


Figure 5.21. The correlation between the mean daily temperature of the nest box and the estimated energy required to maintain eggs at uniform temperature calculated according to Kendeigh (1963).

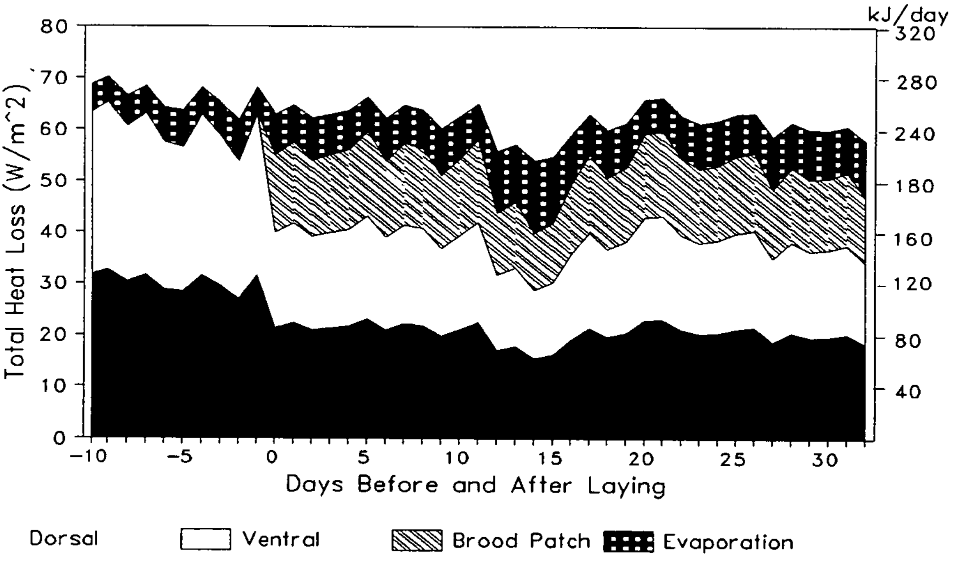


Figure 5.22. The cost of thermoregulation during incubation as calculated using the energy balance method of Walsberg and King (1978b). Heat loss was calculated for dorsal, ventral and brood patch surfaces and evaporation during incubation based on measurements for barn owls in nest boxes by Hamilton (1983, 1985c). The thermostatic energy requirement for a 420 g female was also expressed in kJday^{-1}.

5.4 DISCUSSION

5.4.1 Microclimates and Heat Loss

Local meteorological measurements throughout the study period together with long term records from Eskdalemuir Observatory indicated that the study area was situated in an area of relatively low temperature, high rainfall, with a considerable number of snow days, low levels of sunshine and relatively high wind speeds (Appendix 3 - 4). The seasonal and diurnal weather patterns and corresponding changes in the microclimate of the roost site were therefore estimated to alter the demands for heat production of barn owls within the study area.

Measurements indicated that barn owls experienced temperatures which were most often below the thermo-neutral zone of metabolism (TNZ), reported to be from 23 - 33 °C (Johnson, 1974, Edwards, 1987 and Hamilton, 1983, 1985c). There were only 11 hours in the 16 month measurement period when the air temperature was recorded within the TNZ and in the roost building, only 136 hours. A total of 304 hours were recorded in the nest box but this still represented a small proportion of the entire measurement period. There were, however, a total of 25 hours when nest box temperatures were above the upper critical temperature and on these occasions chicks may have become heat stressed for short periods. In adult barn owls, evaporative cooling by rapid ventilation of the respiratory tract (gullar flutter) provides a mechanism of losing heat at temperatures exceeding 35 °C (Bartholomew *et al*, 1968, Weathers, 1972 and Johnson, 1974) while barn owl chicks have been shown to be heat stressed and exhibit a rapid rise in body temperature at an air temperature of 45 °C (Howell, 1964).

It was therefore clear that barn owls in the study area were frequently faced with metabolic demands for high heat production. Selection of suitable roost sites was seen to be a mechanism for minimising these demands, as barn owls were estimated to reduce heat loss on average by 18 % when sheltering in the roost building at night and by 8 % when roosting in the nearby plantation. These savings were found to be typical for similar nocturnal roosts of birds with similar body sizes (Table 5.10). At night, estimated reductions in heat loss were largely from reduced exposure to wind and to a lesser extent, from small but not insignificant radiative gains. Overhead cover increased long wave radiation absorbed by an owl in the roost building by 6 % compared to the open and increased radiation absorbed in a tree roost by 2 %. The thermal significance of the roost was predominantly associated with the reduction of convective heat losses, as reported for the nocturnal roosts of the Phainopepla (Walsberg, 1986) and as indicated in many previous studies (Table 5.10).

At night, barn owls gained thermal benefits only during the winter months from higher temperatures of 0.3 - 1.9 °C in the roost building. Higher temperatures were associated with time lag effects from the cooling rate of the building relative to outside conditions. Barn owls were known to roost on the roofing beams in the centre of the roost building and therefore did not often benefit from any local heating effects, such as was found in the nest box during the breeding season. Local heating effects may, however, be important for barn owls roosting in tree cavities or in chimneys, as has been found elsewhere in SW Scotland and thereby reduce the temperature gradient between body temperature and surroundings, as reported in nest boxes and small tree cavities of small birds (Kendeigh, 1961 and Andreev in Reinersten, 1988). It therefore remains uncertain whether or not selection of well insulated sites in other disused buildings may allow barn owls to heat enclosed spaces to high temperatures, such as have been measured in the well insulated snow burrows of tetraonids (Marjakangas *et al*, 1984).

Heat loss for a barn owl roosting in the sitka spruce plantation was estimated by assuming that air temperatures were similar to air temperature measured above the plantation. Temperature differences between nocturnal tree roosts and open areas have been associated with short term temperature lags (Francis, 1976) and variation of roosting position by birds have been related to horizontal and vertical gradients in trees at night (Swingland, 1973, 1977 and Kelty and Lustick, 1977). This suggests that the diurnal pattern of heat loss for barn owls roosting in the building may differ from the pattern predicted by the change in temperature in the open but averaged over the course of the night or day, any decrease in heat loss due to small temperature differences between tree and open sites will be small.

The thermal benefits for a barn owl roosting in the building during the day were greater relative to nightime roosting. Daytime roosting for a barn owl was estimated to reduce heat loss on average by 21 % compared to the open and by 18 % compared to a tree roost. Barn owls were estimated to reduce heat loss significantly by sheltering from the higher wind speeds during the day and also from considerable long wave radiative gains and reduced free convective heat loss from increases in surface and air temperature of the roost building as a result of passive solar heating of the roost surfaces.

Species	Location	Temp (°C)	Rad (%)	Wind (%)	Savings (%)	Author
Lagopus lagopus	Snow burrow	-	-	-	50	Korhonen (1989)
Cinclus cinclus	Bridge	2.9	-	100	50	Shaw (1979)
Fringilla montifringilla	Conifers	1.5	-	40	47	Jenni (1991)
Bonasa umbellus	Snow burrow	1	-	-	33	Thompson & Fritzell (1988)
Corvus monedula	Town centre	2.5	-	-	30	Gyllin *et al* (1977)
Sturnus vulgaris	Pine woods	0	-	84	25	Kelty & Lustick (1977)
Sturnus vulgaris	Ficus grove	6.8	-	-	21	Yom - Tov *et al* (1977)
Phainopepla nitens	Small tree	0	20	24	20	Walsberg (1986)
Bonasa	Cedar tree	-	-	25	19	Thompson & Fritzell (1988)
umbellus	Cedar ground	-	-	25	18	Thompson & Fritzell (1988)
Carduelis tristis	Spruce wood	1.1	-	92	17	Buttemer (1985)
Junco hyemalis	Cedar / Yew	0.4	-	81	14	Webb & Rogers (1988)
Passer domesticus	Nest box	3.8	-	-	12	Kendeigh (1961)
Haliaeetus (1984)	Conifers	1.5	13	88	12	Stalmaster & Gessaman
leucocephalus	Pine trees	0.8	-	64	8	Keister *et al* (1985)
Corvus frugilegus	Decid. tree	1.3	-	40	8	Swingland (1973)
Bonasa umbellus	Decid. tree	-	-	50	6	Thompson & Fritzell (1988)
Turdus migratorius	Fir grove	< 0.1	16	28	4	Walsberg & King (1980)
Haliaeetus (1984) *leucocephalus*	Decid. trees	0	5	48	3	Stalmaster & Gessaman
Quiscalus quiscula	Pine wood	1.6	-	100	-	Francis (1976)
Emberiza schoeniclus	Reed bed	0.3	-	87	-	Warrilow *et al* (1978)
Parus spp.	Tree cavities	9	-	-	-	Andreev (Reinersten, 1988)
Tetrao urogallus	Snow burrow	22	-	-	-	Marjakangas *et al* (1984)

Table 5.10. The microclimate and energy savings associated with avian nocturnal roosts which include the mean difference between roost and outside temperature (°C), savings in downward long wave radiation (%), reduction in wind speed (%) and estimates of overall metabolic savings (%).

The estimated rate of heat loss from a barn owl in a tree roost was on average, only 3 % greater than heat loss in the open during the day, due to the contribution of solar radiation to the energy balance of a barn owl in the open. This suggested that tree roosting during the day provided only small energy savings compared with buildings for barn owls. Stalmaster and Gessaman (1984) found that the riparian deciduous trees used as daytime perches by bald eagles in winter were 0.2 - 1.7 °C colder than open feeding areas and net long wave radiation exchange was equal to or less by around 2 %, than in open areas. The selection of roost sites in the dense canopy of mixed evergreen forest by spotted owls allowed this species to avoid heat stress in summer, but in winter-time, roost sites were south-facing and owls were seen to select locations in trees which were in the sun (Barrows, 1981). The selection of tree roosts by barn owls may occur when building roosts are unavailable and although energy savings are estimated to be small compared with roost buildings, barn owls avoid disturbance, predation and mobbing from other birds during the day.

Many studies to date have considered the effects of temperature or wind speed as separate variables, but the metabolic rate of birds responds to conditions produced by the simultaneous interaction of temperature, wind, radiation and rainfall. As there was a general correlation between cloudy wet conditions with relatively warm, windy conditions in this study, it was more meaningful in an ecological context, to estimate the metabolic response of barn owls to combinations of weather conditions and as Walsberg (1983) has remarked, by considering more fully the consequences of rainfall on the selection of favourable microclimates. These factors were addressed in this study by estimating heat losses from barn owls in cloudy and clear conditions, in wet and dry weather and in further detail, by examining extreme conditions.

Rates of heat loss in the roost building, tree and open sites were estimated to be greater on clear nights by between 5 and 11 % compared to cloudy conditions. This difference was attributed to lower air temperatures on clear nights and the change in radiative temperature of the clear night sky. Compared with the open, the roost building provided a 10 - 12 % difference in radiation absorbed and metabolic savings of 18 - 21 % for a barn owl on clear nights. Although radiative savings were less on cloudy nights (4 - 6 % compared with the open), the reduction in heat loss was similar (16 - 21 %). Walsberg and King (1980) showed that fir trees used as roosts by American robins provided greater protection on clear nights, as the downward long wave flux was greater than in open areas by 26 % on clear nights, 9 % on cloudy and 6 % on totally overcast nights. Stalmaster and Gessaman (1984) were also able to show that radiative savings in coniferous roosts were 20 % greater on clear nights than on overcast nights, but on cloudy nights, the greater value of conifers as roost sites was due to reduction in wind speed. This evidence together with findings in this study indicate that nocturnal roost sites function to reduce radiation losses in clear conditions for birds, but on cloudy nights provide greater savings from reduced wind effects.

On cloudy days, energy savings from roosting in the building were 20 - 22 % compared with the open but on clear days the thermal gain in the building was as high as 17 - 32 %. The value of the roost building increased because solar heating of the building provided significant long wave radiant fluxes for the roosting owl. During January - March, however, when solar heating of the roost was minimal, radiative conditions were not significantly different between the roost and the open. Assessment of the contribution of solar radiation to the energy balance of barn owls is important as it was shown that barn owls on several occasions left the roost during the day (Section 6.3.1). It was estimated that barn owls active at times of maximum solar radiation had rates of heat loss which were 24.5 % lower than during periods of minimum solar irradiance. This finding compared closely with reductions in oxygen metabolism of long eared owls of 21 and 13 % in a metabolism chamber with a light source giving 61 Wm^{-2} of short wave radiation immediately above the bird at air temperatures of 1 and 10 ^{o}C respectively (Wijnandts, 1984).

Barn owl plumage was shown to have short wave reflectivities of 54 - 87 % on dorsal and ventral plumage samples from a female and 56 - 90 % on samples of a male (Appendix 2). These measurements compare with reflectivities of 32 - 52 % in dorsal and ventral samples in four species of North American owls (Gates, 1980). The remarkably high reflectivity associated with pale colouration of barn owl plumage may suggest that barn owls are unable to acquire high solar loads unlike species with darker colouration. This would be suggested from early studies which assumed that solar gain by birds was related to short wave absorptivity and hence, plumage colouration (e.g. Hamilton and Hepner, 1967 and Lustick, 1969). Recently, however, it has been suggested that solar heat gained by birds is determined by a complex set of micro-structural and micro-optical properties of plumage that determine the depth to which solar radiation penetrates the coat (Walsberg, 1988b). Walsberg *et al* (1978) showed that radiation penetrated deeper into white than black pigeon plumages. The consequence of this was that although black plumages gave much greater heat loads at low wind speeds, the heat loads of black and white plumages converged as wind speed increased. This implies that barn owls in the wild may gain similar solar heat loads to other owl species which have darker plumages of low reflectivity. This remains speculative, without further knowledge of the structural properties of barn owl plumage, but the importance of absorbed solar radiation for barn owls active during the day should not be discounted. In this study, solar radiation was estimated to provide significant thermal gains for barn owls active during the day. However, the energy balance of a barn owl indicated that the rate of heat loss in the roost always remained less than that of a barn owl in the open, even at times of maximum solar radiation.

The highest rates of heat loss for barn owls, at around 3 times the basal metabolic rate, were estimated to occur during wet conditions when coat resistance was reduced by wetting and during snow periods when low temperatures increased the temperature gradient between body core and environment. The rate of heat loss was found to be 6 - 8 % greater on wet nights than on dry nights and 9 - 17 % greater on wet than dry days. The small differences at night were associated with colder temperatures on dry nights which compensated for the greater resistance of dry plumage and indicated the interaction between temperature and wetting on the energy balance of owls. The highest rates of heat loss occurred when wet conditions were combined with high wind speeds and low air temperatures. These conditions increased heat loss by as much as 30 % compared with dry, calm, warm nights. Barn owls were, however, predicted to reduce heat loss by more than 30 % by roosting in the building during these severe conditions and it was indicated that the thermal value of roosting behaviour changed according to the severity of environmental conditions.

Calculations based on mean hourly data indicated that the daytime heating of the roost brought about large diurnal reductions in heat loss for owls. These occurred in response to increases in temperature; however, studies of oxygen consumption of owls in captivity have found diurnal reductions in metabolism and body temperature which are independent of temperature (Graber, 1962; Gatehouse and Markham, 1970; Siegfreid *et al* 1975; Chaplin *et al*, 1984 and Wijnandts, 1984). These circadian patterns are related to the normal activity patterns of owls which are the reverse of diurnal species. Wijnandts (1984) found that the oxygen consumption of long eared owls was 8.2 % lower and body temperatures were on average 0.5 °C lower when owls were inactive during the daytime. Controlled hypothermy during the day may therefore be seen as a mechanism for reducing energy demands when inactive and although not included in the model, a decrease of core temperature of only 0.5 °C could account for small but significant reductions of at least 1.5 % of total heat production in barn owls. Greater energy savings of 4.7 % of total heat production have also been estimated for 1.5 °C body temperature changes in the bald eagle (Stalmaster and Gessaman, 1984). Further reductions in thermostatic costs of inactive barn owls may be attributed to the heat increment of feeding, otherwise known as the specific dynamic action (SDA) of feeding. This contribution to temperature regulation from the digestion of high protein diets has been estimated as 14 % of metabolisable energy in long eared owls (Wijnandts, 1984). The heating effect has also been reported to continue for 20 hours after a single meal in kestrels (*Falco tinnunculus*) and represented 17 % of the metabolisable energy of each meal (Masman *et al*, 1988). The selection of sheltered microclimates of roost buildings by barn owls, combined with the controlled reduction in body temperature when inactive and the heat increment of feeding may therefore be seen as effective mechanisms for reducing the high thermostatic costs of barn owls in SW Scotland.

5.4.2 Nest Microclimate and Incubation

Energetics of incubation have been reviewed by Drent (1975) and more recently by Walsberg (1983) who pointed out that controversy surrounding the energetics of incubation have arisen by asking three different questions:

(i) 'How much heat does the adult supply to the eggs ?' This deals solely with heat flow to the eggs and does not consider other avenues of heat exchange for the adult.

(ii) 'What is the energy balance of the adult associated with the specific act of incubation?' This includes both the heat flow to the eggs as in (i) and the heat loss to the environment from other surfaces.

(iii) 'What changes occur in the adults energy budget during this phase of the annual life cycle?' This includes (i) and (ii) as well as the energy and nutrient demands of egg production and changes in the activity pattern of the adult during this period.

There is a natural progression in these questions and therefore in this study I attempted to answer questions (i) by calculating the energy required to maintain eggs at uniform temperature and (ii) by estimating the energy balance of the female during incubation inside the nest box using a biophysical model of heat loss. These calculations provided a framework to consider further factors affecting the energetics of the female barn owl during incubation.

The formula of Kendeigh (1963) predicted that 33.5 kJday^{-1} was required to maintain eggs at uniform temperature throughout incubation in the barn owl. Temperature of barn owl eggs during incubation were reported to be 34.2 °C, which was similar to egg temperatures in other species, such as the burrowing owl (*Speotyto cunicularia*) of 35.5 °C (Howell, 1964) and the long eared owl of 34.9 °C (Wijnandts, 1984). The energy balance of the barn owl in the nest box during incubation was estimated to be 61.7 Wm^{-2} or 243 kJday^{-1} at temperatures from 12.4 - 21.7 °C. These results agree with measurements of the metabolic rate of incubating barn owls in nest boxes in the field of 177 to 278 kJday^{-1} at 5 - 25 °C (Hamilton, 1983) and were similar to Hamilton's estimates using the model of Walsberg and King (1978b), (Table 5.11). The contribution of embryonic metabolic heat production to the heating costs of incubating owls was shown by Hamilton (1983) to represent a small but not insignificant proportion of the total heat required. The respiration rates of 8 eggs at the 1 - 10 day stage were equivalent to 0.7 - 1.3 kJday^{-1} and at the 15 - 27 day stage 6.2 - 6.4 kJday^{-1}.

	Kendeigh	**Thermal Model**		**Measurement**	
Temp °C	**kJday^{-1}**	**Wm^{-2}**	**kJday^{-1}**	**kJday^{-1}**	
5	52.5	76.4	286	266 - 278	Hamilton (1983)
15	42.0	57.5	215	222 - 238	Hamilton (1983)
25	19.5	41.2	154	177 - 199	Hamilton (1983)
12.4 - 21.7	33.5	61.7	243		This study

Table 5.11. The energy cost of incubation for a female barn owl estimated as the energy required to warm eggs using the formula of Kendeigh (1963), as the total energy balance of the female in the nest based on the biophysical model by Walsberg and King (1978b) and from gas exchange measurements in nest boxes in the field (Hamilton, 1983).

The biophysical model demonstrated that heat loss from the brood patch area supplied heat to the eggs at a rate equivalent to 61 kJday^{-1} which would easily meet the requirements of maintaining eggs at a constant temperature. Based on crude approximations of surface areas, the heat lost from each of the body regions was estimated to be similar. Heat loss from the skin surface of the brood patch is considerably greater than from other body regions due to the increased blood supply and lack of feathering (Drent, 1975) but while a bird is sitting on eggs the high thermal conductivity of this region was seen to be compensated by additional thermal resistance provided by the eggs and the insulating material of the nest. The thermal resistance across the brood patch skin surface, eggs and nest material was 513 sm^{-1} which was not considerably different from the total thermal resistance of dorsal and ventral feathered regions (630 sm^{-1}) when it is considered that the tissue resistance of dilated skin on the brood patch is around 40 sm^{-1}. The barn owl nest consists of a shallow scrape amongst accumulated pellets within the nest box which results in a substantial depth of insulating material from the fur of small mammals and largely accounts for the high thermal resistance below the brood patch when incubating.

Comparison between the energy balance of an incubating barn owl with the energy balance of a female barn owl outside the nest box indicated that the thermostatic cost of heat production for a female was not significantly increased during the incubation period. This agreed with Hamilton (1983) who found that the metabolic rates of 5 female barn owls during incubation were not significantly different from the metabolic rate of 6 post incubating females in nest boxes (4 birds were the same individuals). The biophysical model in this study, however, did not account for increases in heat loss associated with moult during the incubation period which would further increase thermal benefits from the sheltered microclimate of the nest box. The metabolic rate of birds has been reported to be significantly higher during the period of moult (Walsberg, 1983) and 18 % increases of standard metabolic rate have been measured in the long eared owl (Wijnandts, 1984). Increased peripheral blood supply and feather loss may contribute to substantial increases in heat loss but high metabolic demands associated with growth of new feathers are also increased at this time.

By selecting the sheltered microclimate of nest boxes, barn owls appear to have no additional thermostatic demands during incubation associated with warming eggs. The inactivity of females at this time considerably reduces a female's energy expenditure; however, the cost of ovary development, egg synthesis and moult during egg laying and incubation have been reported to result in the highest yearly energy requirements in kestrels (Masman *et al*, 1988 and Dijkstra *et al*, 1988) and long eared owls (Wijnandts, 1984) and are reflected in the large increase in body mass of barn owls during laying (Taylor, in press). Following hatching, the metabolic heat production of chicks increased nest box temperature by 1 - 4 ^oC until the chicks were last known to occupy the nest. Increases in nest box temperature of 1.5 - 6.2 ^oC have been reported inside a nest box used as a winter roost of house sparrows (Kendeigh, 1961) and maximum differences of 4.6 ^oC were recorded when monk parakeets occupied nests (Caccamise and Weathers, 1977). Newly hatched chicks are unable to thermoregulate and require brooding by the parent. Howell (1964) reported that barn owl chicks were brooded by the female at 36 - 39 ^oC but showed dramatic declines in body temperatures when removed, such that the body temperature reached an ambient temperature of 22 °C in an hour. The heat required to brood chicks was estimated to represent 76 % and 66 % of basal metabolic rate of long eared owls at 1 and 2 weeks after hatching (Wijnandts, 1984) and therefore, brooding in barn owls is expected to be easily covered by normal levels of metabolic heat production. The measurements of Howell (1964) indicate that approximately 10 days after hatching, chicks become at least partially homeothermic and are able to regulate body temperature to around 31 - 32 °C. The value of asynchronous hatching in barn owls therefore allows young chicks to benefit from shared metabolic heating and the greater insulation of the thick downy mesoptile plumage of older chicks.

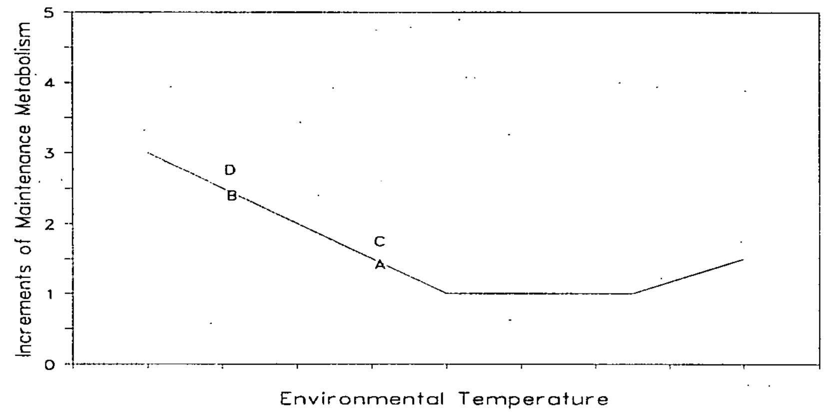


Figure 5.2.3. Schematic metabolic diagram for the barn owl, indicating the range in metabolic rate (increments of maintenance) throughout the year for an owl in the roost (A and B) and for an owl outside the roost (C and D).

The maintenance requirement of a barn owl within the thermo-neutral zone in still air has been shown to be equivalent to a heat loss of approximately 38 Wm^{-2} (Table 2.13). Based on average rates of heat loss for a barn owl in different weather conditions (Appendix 5) it was found that the cost of thermoregulation for barn owls in the roost building ranged between 1.3 and 2.2 times the resting maintenance metabolism in the periods July - September and October - December, respectively (Table 5.9). The effects of wind speed and wetting outside the roost was found to increase the metabolic cost of thermoregulation to 1.6 to 2.6 times maintenance metabolism in the periods July - September and January - March, respectively. This can be considered in the context of a metabolic diagram for the barn owl (Figure 5.2.3). Drawn schematically, this indicates that despite roosting, the metabolic rate of barn owls remains below the thermo-neutral zone of metabolism throughout the year. When outside the roost the metabolic rate rises to a level in winter which approaches the summit metabolism of 3 times maintenance, typical of the thermoregulatory scope of many animals.

5.5 SUMMARY

1. Energy savings from selection of favourable microclimates by barn owls were estimated by measuring the microclimate / nest site, together with local meteorological conditions. Measurements were used in a biophysical model to determine the heat loss from a barn owl in the roost building, in tree and in open sites.

2. In 16 months there were a total of 11 hours when ambient temperature was within a barn owl's TNZ. Air temperature in the roost was within the TNZ for 136 hours and for 304 hours inside the nest box. Roost temperatures were correlated with seasonal and diurnal changes in ambient temperature. At night, air temperature was 0.3 - 1.9 ^{o}C higher than outside temperature only during the winter, but was 0.6 - 3 ^{o}C greater during the day throughout the year. The temperature of the roost was correlated with solar radiation and building surfaces reached a maximum of 47.2 ^{o}C above an air temperature of 21 ^{o}C with mean solar radiation at 1200 GMT of 642 Wm^{-2}.

3. The biophysical model indicated that at night barn owls reduced heat loss by 18 % when roosting in the building and by 8 % when roosting in the nearby plantation. These estimates were similar to previous studies on nocturnal avian roosts and demonstrated that energy savings were associated with reductions in convective heat loss and small radiative savings. The thermal benefit from the building during the day was greater, with savings of 21 % compared to the open but in the tree site, heat loss was reduced by only 3 % due to the contribution of solar radiation in the open.

4. Rates of heat loss for barn owls were 5 - 11% greater on clear than on cloudy conditions in all locations. Energy savings were similar as the roost building reduced radiative exchange on clear nights but on cloudy nights it provided greater savings from wind effects. During the day, the passive solar heating of the building was estimated to reduce heat loss by 17 - 32 % compared to the open. Highest heat losses for barn owls were 3 x BMR in wet conditions and during snow periods. Wet, cold and windy conditions gave highest losses but on these occasions roosting in the building compensated for heat losses with energy savings of more than 30 %.

5. The incubating barn owl required 33.5 $kJday^{-1}$ to maintain eggs at uniform temperature. Total heat loss from the female at this time was 61.7 Wm^{-2} or 243 $kJday^{-1}$. Comparison with the heat loss of a barn owl outside the nest box showed that there was no additional thermostatic cost associated with incubation.

CHAPTER 6

ROOSTING BEHAVIOUR OF BARN OWLS

6.1 INTRODUCTION

Measurements of the microclimate of the roost / nest site in this study, combined with biophysical estimates of heat loss, indicated that by remaining in the building, barn owls may reduce thermostatic costs from 7 to 37 %, depending on weather conditions. This suggested that the roosting behaviour of barn owls is an adaptation to reduce energy expenditure and therefore it was necessary to examine this hypothesis by measuring the roosting behaviour of barn owls at different times and according to different weather conditions.

Activity and behaviour of barn owls in the field have been examined using a variety of techniques including visual observations, radio-telemetry and detection of nest visits using automatic recording equipment. In the study area in SW Scotland, Taylor (in press) found that barn owls were active both at night and during the day in summer and winter. When feeding chicks, barn owls usually started hunting between 1900 and 2000 hours, resulting in 3 - 4 hours of daylight foraging.

One of the first studies to examine activity patterns of barn owls was by Bussmann (1935) who used a weighing device to register the movements of adults when feeding 4 chicks at a nest site in Germany during May and June. Arrivals at the nest commenced between 2050 and 2325 hours and ended between 0025 and 415 hours. Bussmann (1937) again recorded nest visits in a nest with 4 chicks during August and September and determined that adults made an average of 11.3 feeding visits per night with a total hunting period of 5.6 hours. Ritter and Gorner (1977) studied the feeding activity at another German nest site containing five young (only 1 fledged) from June to September. The mean number of daily visits during incubation was 3.3, and 4.1 in the remainder of the breeding season. In this study, the circadian rhythm exhibited two main peaks of activity during the night. Hunting commenced shortly after sunset and the first peak of activity occurred an hour later, from 2100 - 2200 hours; activity was less common around midnight and a second peak occurred between 0100 - 0200 hours. There were also a number of occasions when hunting continued after sunrise. In the Netherlands, however, de Jong (1991) used a video camera to show that adult barn owls fed chicks throughout the night.

Langford and Taylor (1992) recorded prey deliveries at 19 nests over 3 years using an infra red directional switch which was recorded on a logger and which operated a camera to take photographs of the owl with prey on entry to the nest. Prey delivery rates during incubation were high, averaging 16.4 items per 24 hours and fell to around 8 - 11 items during incubation. Feeding rates increased from the date of hatching to reach a peak of 14 - 16 items per 24 hours, approximately 30 days following hatching. Mean brood size of the nests studied was 3.6 so that at maximum feeding rates, each chick received on average about 4 items per 24 hours.

Less information on the activity of barn owls outside the breeding season is available. Bunn *et al* (1982) made anecdotal summaries from visual observations of 9 barn owls hunting in forestry plantations. Eight of these (5 males and 3 females) were found to regularly hunt during daytime and were noted to start foraging during late afternoon in winter and an hour or more before sunset in summer. Observations at dawn during December also indicated that owls commenced foraging 22 - 68 minutes before sunrise and were still active more than 2 hours following sunrise. The occurrence of daytime foraging in British barn owls has previously been noted by Dunlop (1911), Smalley (1911), Hailman (1960), Bunn (1972) and Dickson (1972) and for barn owls in Surinam by Haverschmidt (1970). In a review of the literature, Taylor (in press) suggested that throughout most of its range barn owls are mainly nocturnal and daytime activity may be more common in northern European barn owls than in other areas.

Any effects of weather on the behaviour of barn owls has not convincingly been examined. Bunn *et al* (1982) stated that during continuous rain barn owls remained in roosts and during showery conditions would take refuge until the rain stopped. In contrast Dickson (1972) reported an individual foraging in rain 40 minutes before sunset in SW Scotland. However, comparable information from radio-telemetry of foraging long eared owls (*Asio otus*) showed that flight was inhibited during precipitation and in particular, long eared owls almost completely avoided flying during sleet (Wijnandts, 1984).

It was the aim of this study to quantify the amount of time that barn owls occupied the roost site, especially during winter when energy savings may be critical and examine the use made of the roost according to different weather conditions.

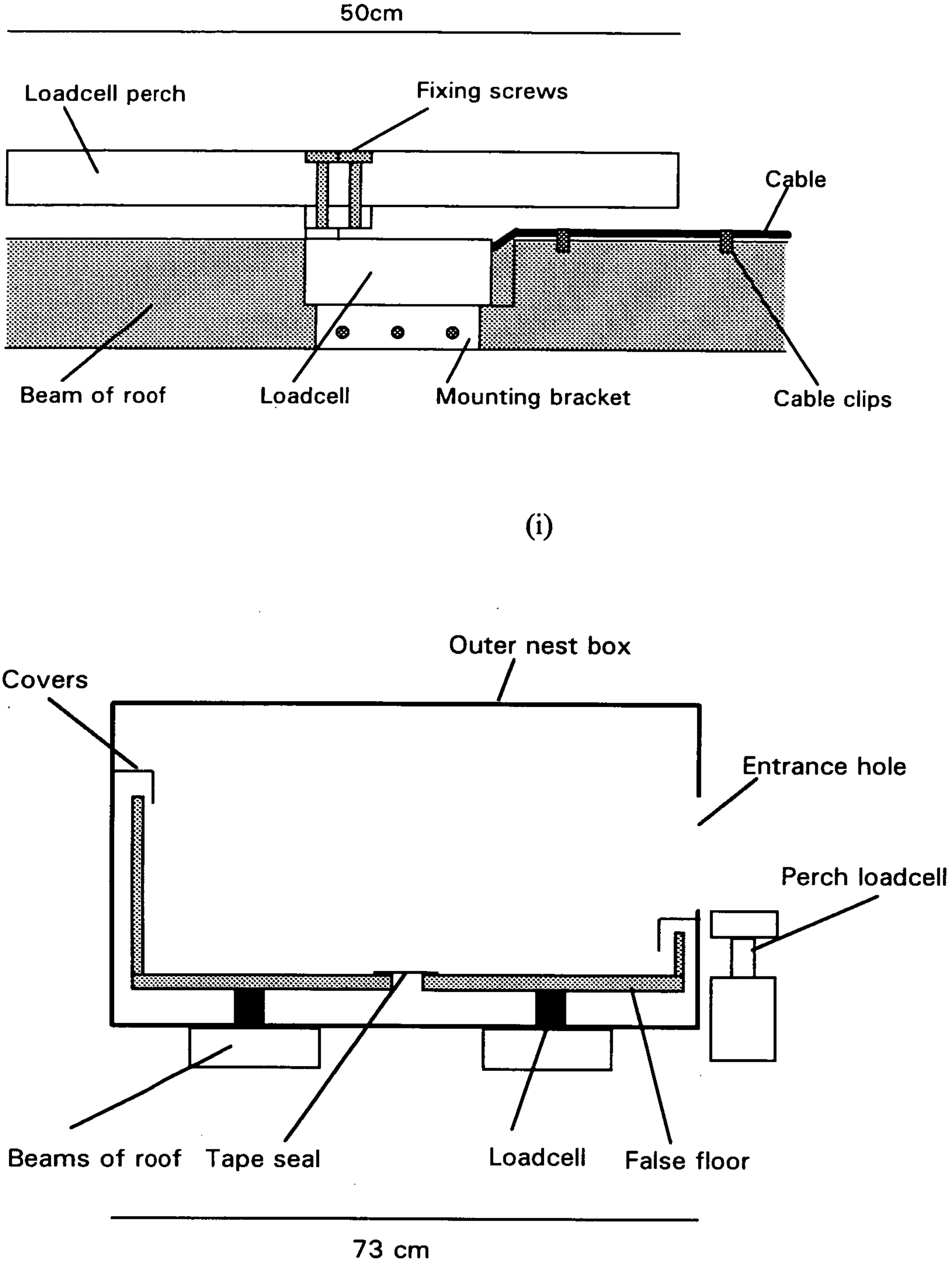
6.2 MATERIALS AND METHODS

6.2.1. The Monitoring System

An automatic recording system was designed to determine the timing of visits to the roost and nest site and the length of time that the roost was occupied. This system consisted of a series of electronic weighing devices (loadcells) which recorded the presence of barn owls when roosting on the roof beams of the building and the presence of owls when inside the nest box. Suitable perching places in the roost building were limited to beams below the roof of the building and the most frequently used roosting sites were apparent from large quantities of pellets, excreta and moulted feathers on the floor of the building. Several months prior to installation of the recording system, the owls were encouraged to roost on the centre (approximately 50 - 70 cm) of three commonly used beams. Owls were deterred from landing on other sites by securing strips of wood containing small upward facing nails.

Commercially available loadcells were fitted with wooden perches (50 x 4 x 3 cm) to the working platform. These were then secured to the 3 roosting positions with a metal bracket. The fourth loadcell was fitted with a similar perch and mounted at the entrance to the nest box (Figure 6.1). A specially designed nest box was constructed which incorporated two loadcells in the base of the nest platform. The nest box consisted of an external plywood box (73 x 52 x 43 cm) with an entrance hole of 15 x 15 cm. The box was fitted with a false floor which was made from two 38.5 x 38.5 cm bases, under which were mounted the centrally placed loadcells. The floor of the box was fitted with sides to prevent nest material obstructing movement of the floor and the box also incorporated thermocouples to measure air and surface temperature, as described in Section 5.2.1.

All loadcells were fitted with extension cables which were secured to the sides of the building and led to a weatherproof box which contained power supplies and loggers, approximately 15 m outside the roost building. The voltage output from each of the loadcells was averaged over 10 minute intervals by a Campbell Scientific 21X logger and during the period when chicks were present in the nest, the averaging period was 5 minutes for the loadcell at the entrance to the nest box. When chicks were in the nest, averaging was performed over one minute intervals for several days and indicated that the mass recorded at the entrance to the nest was less than obtained with 5 minute averaging but the number of arrivals were not underestimated. Records of arrival and exit of barn owls on each loadcell were typical of that in Figure 6.2.



(i)

(ii)

Figure 6.1. The design of the monitoring system: (i) perch loadcells and (ii) nest box incorporating two loadcells on false floor and perch loadcell at the front of the entrance hole.

The supply voltage to the loadcells was also monitored and recorded by the logger and indicated that fluctuations of no more than +/- 3 mV occurred throughout each measurement period. The system allowed continuous operation over a 2 week period, after which data was retrieved from the logger using a Toshiba T1200 Portable computer. The loadcells were calibrated on the day of installation and rechecked on 1 June.

The monitoring system was installed in the roost building during January 1991 and gave continuous records for 85 days from 30 January to 31 May 1991, excluding periods of equipment malfunction, over-run of the logger memory and excluding days when the roost was entered for nest inspection. The accumulation of pellets and the chicks' preference for roosting in the back corner of the box, however, gave unreliable records of occupation of the nest box and therefore timing of visits to the nest box were only determined from the arrival times of barn owls on the loadcell at the entrance to the nest box. This gave continuous records of arrival times for 101 days from 1 June to 30 September excluding data as described above. The monitoring system was continued throughout the winter of 1991 - 1992 but there was no evidence that barn owls were using the roost site during this time.

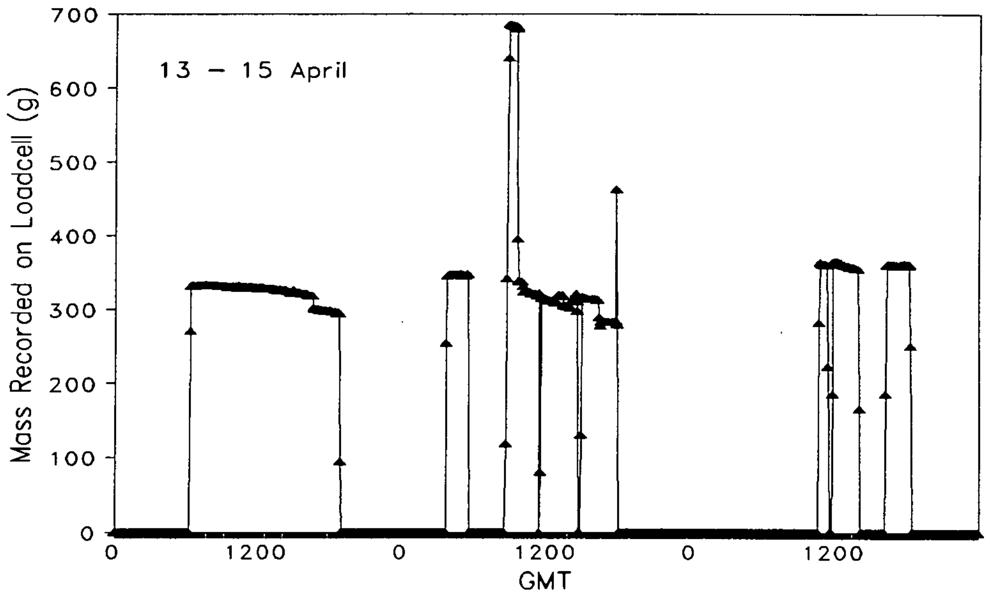


Figure 6.2. An example of a record from a loadcell in the roost building over 3 days (13 - 15 April 1991) with 10 minute averaging of mass indicating the entry and exit of barn owls and showing the presence of 2 birds on the roost perch at one time.

The data was examined and the drift in output from the loadcells was corrected. The arrival and exit times were calculated by taking the arrival time as the first period when a barn owl was present in the roost and exit time as the period immediately following last record of a barn owl in the roost. In this way occupation of the roost was described by the presence and absence of barn owls.

6.2.2 Specification of Loadcells and Calibration Tests

The monitoring system used loadcells (RS Ltd) with maximum capacity of 2 kg on the 4 perches and two with a maximum capacity of 20 kg in the base of the nest box. A set of two loadcells was powered from a 12V 24 Ah lead acid battery (Yuasa NP24-12B) and the voltage was regulated (+ 0 - 5 V) to amplifier circuits. Voltage regulators and amplifier circuits were housed within tight-fitting plastic boxes containing small sachets of desiccant.

A series of calibration tests on the loadcells and circuitry was carried out before field operation. The output from the loadcells was found to be linear by placing brass weights (1 - 1000 g) on the centre of the working platform. The 2 kg loadcells gave a typical voltage output of 4 mVg^{-1} and the amplifier circuit allowed the offset to be controlled. The 20 kg loadcells on the base of the nest box had smaller outputs of 0.1 - 0.2 mVg^{-1}.

The effect of temperature on the output from the loadcells was determined by placing a 2 kg loadcell, amplifier and voltage regulator in a cooled incubator (Gallenkamp Ltd). The output from the loadcell was monitored with a 200 g load over the temperature range -8 to 18 ^{o}C and was found to increase linearly over the temperature range with a temperature coefficient of 0.2 $mV^{o}C^{-1}$ and indicated that it was relatively insensitive to temperature changes.

The loadcells were modified to fit under perches by securing a wooden beam to the working platform of the loadcell. The effect of landing position on the output from the loadcell was examined by fixing a 80 cm wooden beam to the platform and loading the perch with a 200g brass weight at different distances from the centre point. This experiment indicated that the mass was overestimated when the load was on the left side and underestimated when on the right. Finally, the 4 loadcells modified as perches were tested in an outdoor aviary with a captive female barn owl in which the owl was able to fly from one perch to another. This test confirmed that barn owls could be detected arriving and leaving perches and that over 5 days, the mass of the 355 - 360 g owl was recorded as having a mean mass of 370 - 376 g. Following these tests, the length of the perches was reduced and the method of attachment modified for use in the field.

6.3 RESULTS

6.3.1 Timing of Visits to Roost

The use of the roost site from 30 January 1991 to 31 May 1991 was dominated by frequent entry and exit to the roost building according to the time of sunrise and sunset (Figure 6.3). In all months there were several entries and exits from the roost during daylight hours but were most common in the months January - February and May.

	Number of Events		Percentage of Period		
	Entry	Exit	Present	Absent	n
Calendar Day					
Jan-Feb	3.7 (0.3)	3.7 (0.3)	57.7 (3.6)	42.3 (3.6)	21
March	2.5 (0.3)	2.5 (0.3)	68.1 (2.6)	31.9 (2.6)	15
April	2.8 (0.3)	2.8 (0.3)	77.8 (2.9)	22.2 (2.9)	21
May	3.2 (0.3)	3.1 (0.3)	68.5 (2.2)	31.5 (2.2)	28
Daytime					
Jan-Feb	0.76 (0.20)	0.81 (0.21)	83.0 (5.4)	17.0 (5.4)	21
March	0.07 (0.07)	0.13 (0.09)	98.0 (1.9)	2.0 (1.9)	15
April	0.05 (0.05)	0.05 (0.05)	97.3 (2.7)	2.7 (2.7)	21
May	0.93 (0.16)	1.0 (0.17)	81.1 (4.7)	18.9 (4.7)	28
Nightime					
Jan-Feb	3.0 (0.2)	2.8 (0.3)	47.5 (5.2)	52.5 (5.2)	21
March	2.4 (0.4)	2.3 (0.4)	45.2 (4.4)	54.8 (4.4)	15
April	2.8 (0.3)	2.8 (0.3)	50.8 (4.8)	49.2 (4.8)	21
May	2.1 (0.2)	2.0 (0.2)	49.1 (4.3)	50.9 (4.3)	28

Table 6.1. The mean number of entries and exits from the roost site and percentage of time barn owls were present and absent from the roost from 30 January to 31 May 1991. The data was based on continuous records and excluding days when visits to the roost were made. Values in brackets are standard errors of measurements.

The number of entries and exits from the roost per calendar day remained relatively constant throughout this period. The number of entries per day were greatest during January - February, with 3.7 (SE = 0.3) and dropped to 2.5 (SE = 0.3) and 2.8 (SE = 0.3) in March and April, followed by an increase to 3.2 (SE = 0.3) in May. The number of exits followed a similar pattern, ranging between 3.7 in January - February to 2.5 (SE = 0.3) and 2.8 (SE = 0.3) in March and April and 3.1 (SE = 0.3) during May.

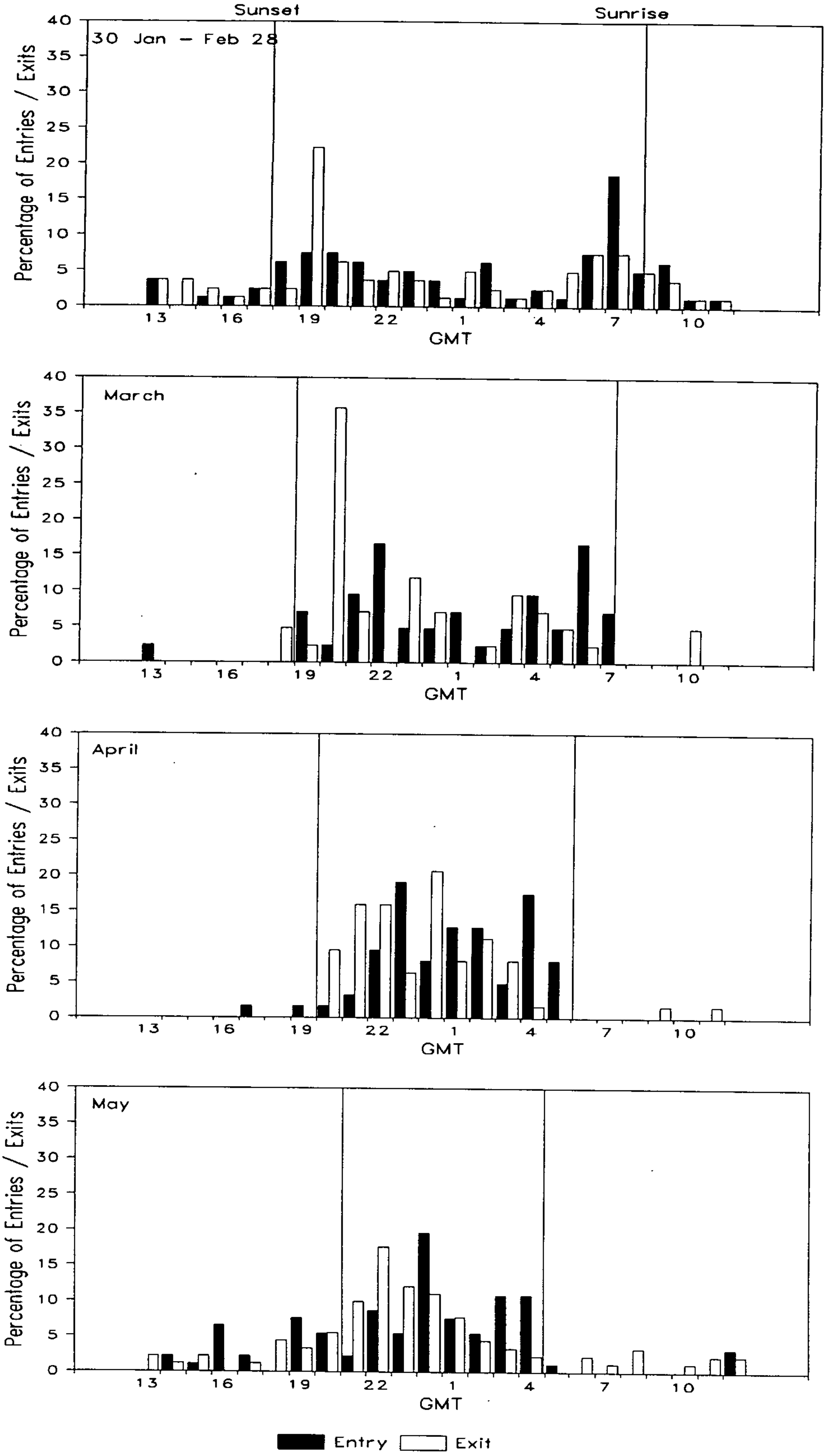


Figure 6.3. The entry and exit times of barn owls from the roost building, from 30 January - 31 May 1991, expressed as a percentage of the total number of events each month.

Differences in the number of exits and entries between months were due to a larger number of events during the daytime, which decreased from a mean of 0.76 entries during daytime (SE = 0.2) in January - February to essentially no entries during the day, with means of 0.07 (SE = 0.07) in March, 0.05 (SE = 0.05) in April but a larger number of entries in May of 0.93 (SE = 0.16) entries during daytime. The number of exits during daytime were similar with 0.81 (SE = 0.21) in January - February, 0.13 (SE = 0.09) in March, 0.05 (SE = 0.05) in April and 1.0 (SE = 0.17) in May. During the night, the number of entries and exits from the roost remained relatively constant throughout the period with 2.1 - 3.0 entries and 2 - 2.8 exits (Table 6.1).

The length of time that owls were present or absent from the roost was highly skewed towards entry and exit lengths of 0 - 2 hours (Figure 6.4). The length of time the roost was occupied was dependent on the time at which the roost building was entered such that the length of stay increased as sunrise was approached and decreased throughout the day (with the exception of two days when the roost was occupied from early afternoon to the evening of the following day), (Figure 6.5). The length of time during which the roost was occupied following entry was not significantly different between months (two sample t test on log transformed data, p = 0.08 - 0.58) and averaged 4.1 to 5.5 hours (Table 6.2).

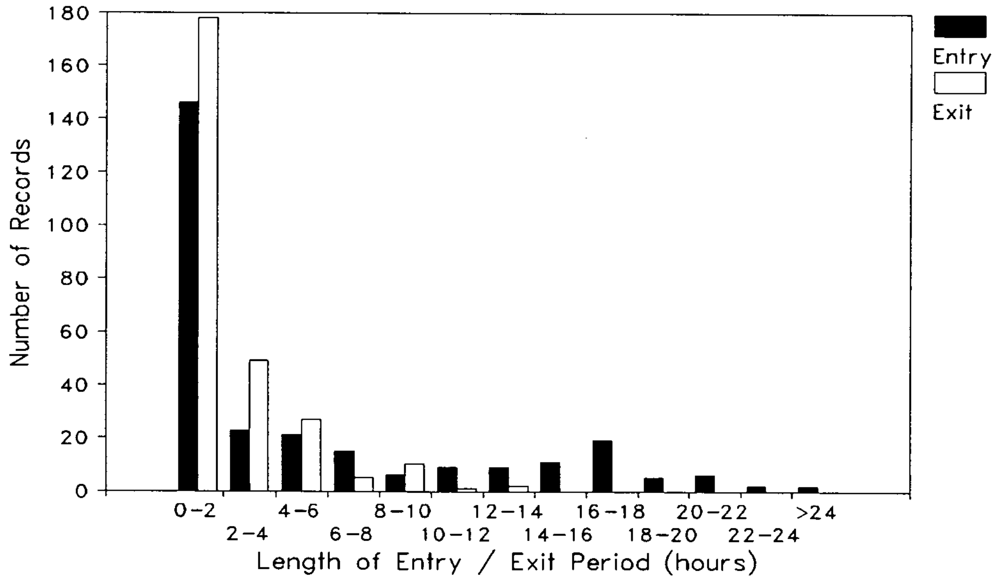


Figure 6.4. Summary of the length of occupation of the roost site following entry (n = 274) and the length of period following exit of barn owls during which the roost building was not occupied (n = 272). Data was from 30 January - 31 May 1991.

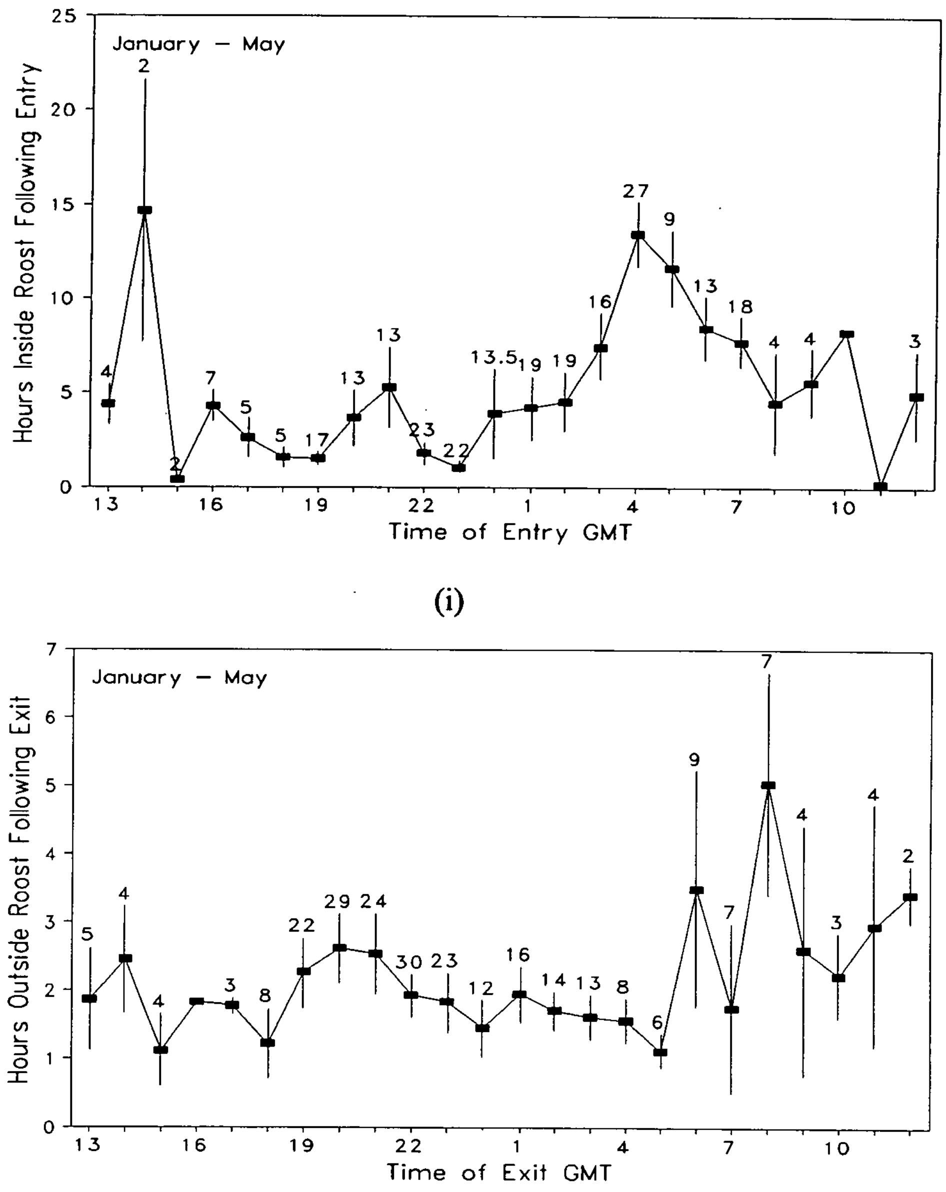
On average, the time between exit and next entry was relatively constant and lasted between 1.8 and 2.7 hours (Table 6.2). Analysis indicated that exit length was marginally longer in March than in other months (two sample t test on log transformed data, p = 0.02). The length of exit period was also dependent on timing of exit such that at night, length of exits from the roost were shorter than if the birds left during the morning (Figure 6.5).

	Length of Entry		**n**	**Length of Exit**		**n**
Jan-Feb	4.1	(0.5)	80	2.1	(0.3)	79
March	6.6	(1.0)	40	2.7	(0.4)	41
April	6.4	(1.0)	63	1.8	(0.3)	61
May	5.5	(0.9)	91	2.1	(0.3)	91

Table 6.2. The mean length of entry and exit periods from the roost site from 30 January to 31 May 1991. Values in brackets are standard errors of measurements.

During the period January - February, the roost was on average occupied for a total of 13.9 (SE = 0.9) hours representing 58 % of the day. Occupancy increased to 16.3 (SE = 0.6) hours (68%) and 18.7 (SE = 0.7) hours (78%) in March and April and then decreased to 16.4 (SE = 0.8) hours (68 %) during May (Table 6.1). The percentage occupancy of the roost per calendar day was significantly different (two sample t test p = 0.01 - 0.03) with the exception of March and May which were not significantly different (p = 0.07). The increase in occupancy from January - April was in part due to the increase in daylength. Analysis of occupancy of the roost for hours of daylight, however, indicated that there was also an increase in the percentage of daylight hours occupied, from 83 % in January - February to 98 % in March, 97.3 % in April but a decline during May to 81.1 %. This difference was due to a change in the relative proportion of days with daytime exits. Absence from the nest site during the day was infrequent and as a result the frequency of percentage occupancy was highly skewed towards 100 %. Differences in use of the roost site during hours of daylight were therefore examined by dividing the days during each month according to the percentage of days with and without daytime exits. This indicated that during March and April there were only 13 % and 5 % of days when owls were absent from the roost during the daytime, but in January - February and during May there were 57 % and 68 % of days with daytime exits (Figure 6.6).

There was a fall in the occupancy of the roost during hours of darkness from 6.9 (SE = 0.8) hours in the period January - February to 3.9 (SE = 0.3) during May. This was related to the shortening of the night, but as a total percentage of the night, occupancy of the roost remained constant at 45.2 to 50.8 % and was not significantly different for each of the months (two sample t test p = 0.2 - 0.5) (Table 6.1).



(i)

(ii)

Figure 6.5. (i) The length of time the roost was occupied by barn owls following entry to the roost and (ii) the length of time barn owls were not present in roost following exit, at hourly intervals for the period January - May 1991. Bars given are +/- standard errors.

The corresponding length of time when the roost was not occupied decreased from 10.1 (SE = 0.9) hours per calendar day, or 42 % of the time in January - February to 7.6 (SE = 0.6) hours per day in March (32 %), 5.3 (SE = 0.7) hours in April (22 %) but increased to 7.6 (SE = 0.8) hours during May (32 %), (Table 6.1). The percentage of the day when the roost was not occupied was significantly different during each month (two sample t test p = 0.01 - 0.03) with the exception of March and May which were not significantly different (p = 0.07). This was related to the increase in daylength but there was also a decrease in the percentage of daylight hours when owls were absent from the nest site from 17 % in January to February to 2.9 % in March, 2.7 % in April and 18.9 % in May, due to the increase in proportion of days when owls were absent from the roost during the hours of daylight (Figure 6.6).

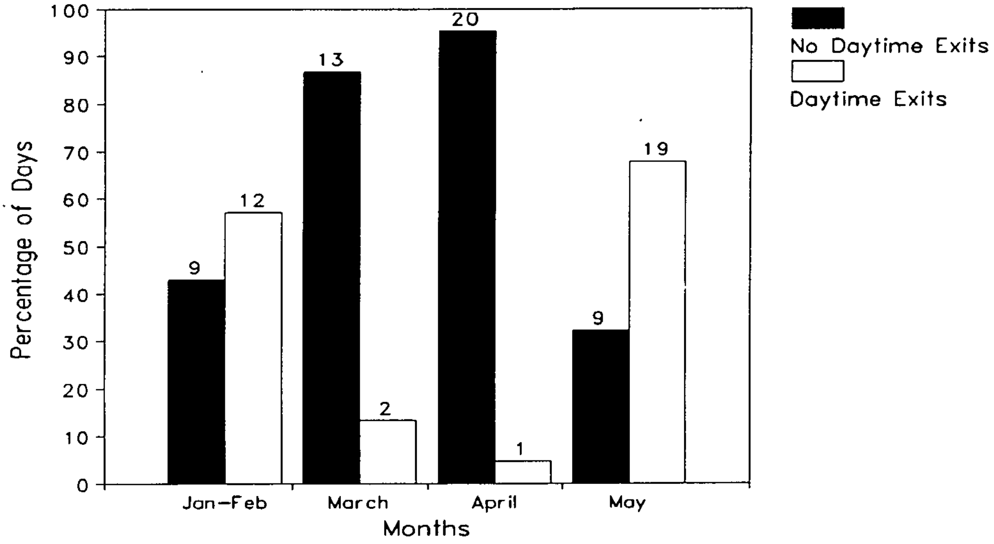


Figure 6.6. The percentage of days with and without daytime exits during each month, from 30 January and 31 May 1991.

There was a decrease in the time owls were absent from the roost during hours of darkness from 7.6 (SE = 0.8) hours in the period January - February to 4.1 (SE = 0.3) during May. This was related to the shortening of the night, but as a total percentage of the hours of darkness, owls were absent from the roost for 49.2 to 54.8 % of the time, which was not significantly different for each month (two sample t test p = 0.2 -0.5) (Table 6.1).

6.3.2 Timing of Arrivals During Nesting Period

The arrival of barn owls at the nest box was examined on a total of 101 days from June to September 1991 during the nesting period. The first egg was laid on 22 June with an estimated hatching date of the first egg on 24 July. A clutch of 6 was laid but only 5 chicks were present on the 9 August. There was further mortality between this nest inspection and the 29 August, when only 3 chicks were present. All 3 were present on 11 September but with low body weights. However, 2 chicks were found dead at the nest site on 25 September and the third was last recorded at the entrance to the nest box at 1440 GMT on 7 October. This chick was later found dead outside the roost on 9 October.

Timing of visits to the nest box most often occurred between sunset and sunrise but there were a large number of visits to the nest box during daylight hours in June (Figure 6.7). The number of visits to the nest box was summarised as a two day running mean (Figure 6.8). This indicated that visits to the nest site were highest just prior to and following the start of incubation. The number of visits fell during the middle of the incubation period but there was an indication that the number of visits increased after the hatching date.

	Arrivals	**SE**	**n**
Calendar Day			
Before Incubation	6.6	0.6	19
During Incubation	4.0	0.6	33
After Hatching	4.5	0.4	49
Daytime			
Before Incubation	4.2	0.4	19
During Incubation	2.1	0.4	33
After Hatching	1.6	0.2	49
Nightime			
Before Incubation	2.3	0.2	18
During Incubation	1.9	0.3	33
After Hatching	2.8	0.3	46

Table 6.3. The mean number of arrivals at the nest box, from 1 June - 30 September 1991, before incubation, during incubation and after hatching of the first egg.

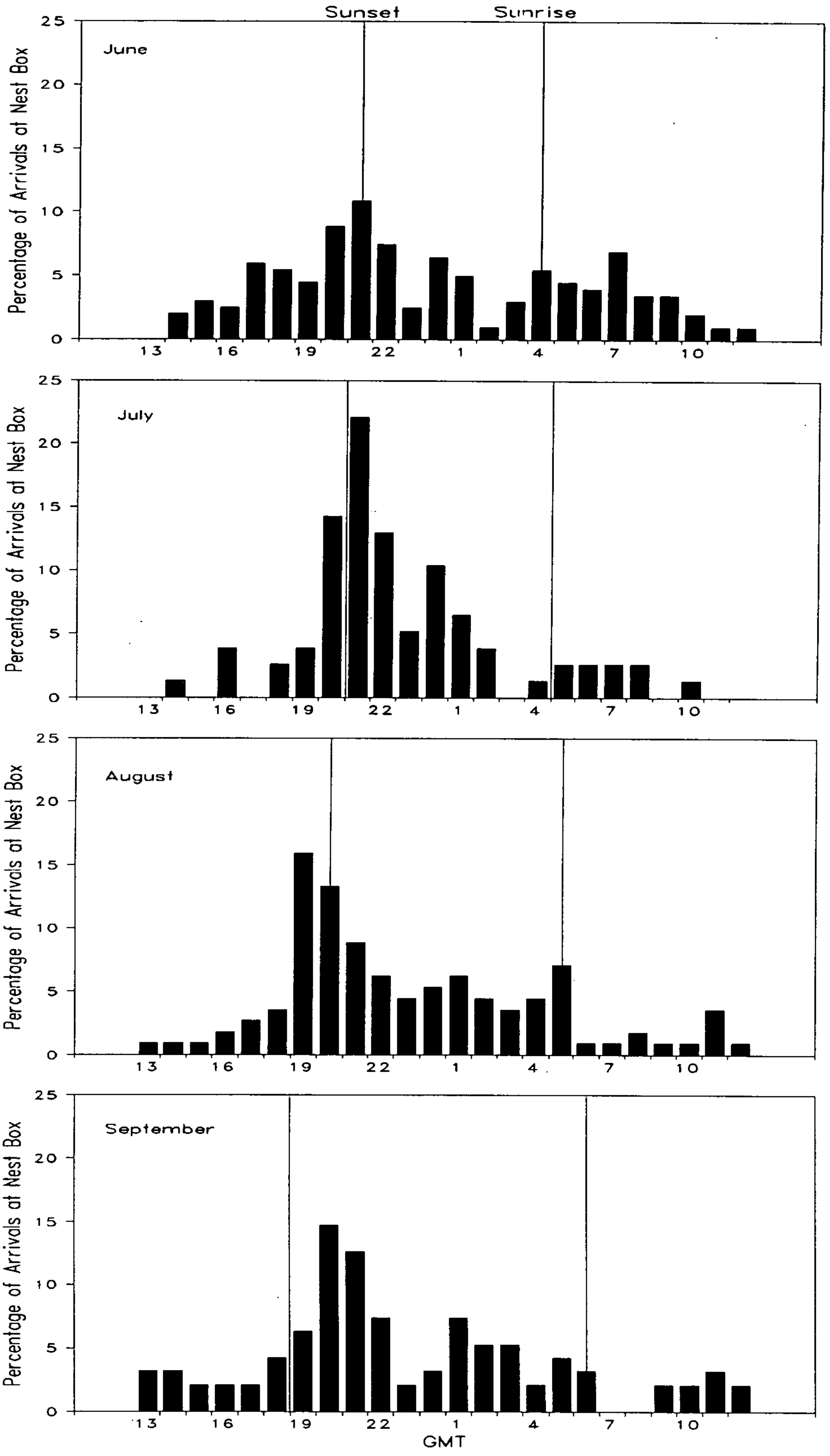


Figure 6.7. The timing of arrivals to the nest box from June to September 1991. Arrivals are expressed as percentage of monthly total. Times of sunset and sunrise are indicated.

Before incubation, there was an average of 6.6 (SE = 0.6) visits to the nest each day, which consisted of 4.2 (SE = 0.4) visits during daylight hours and 2.3 (SE = 0.2) at night. During the incubation period, there were 4.0 (SE = 0.6) each day, with on average 2.1 (SE = 0.4) during the daytime and 1.9 (SE = 0.3) at night. After hatching, the average number of visits was 4.5 (SE = 0.4) which consisted of 1.6 (SE = 0.2) during the day and 2.8 (SE = 0.3) at night (Table 6.3).

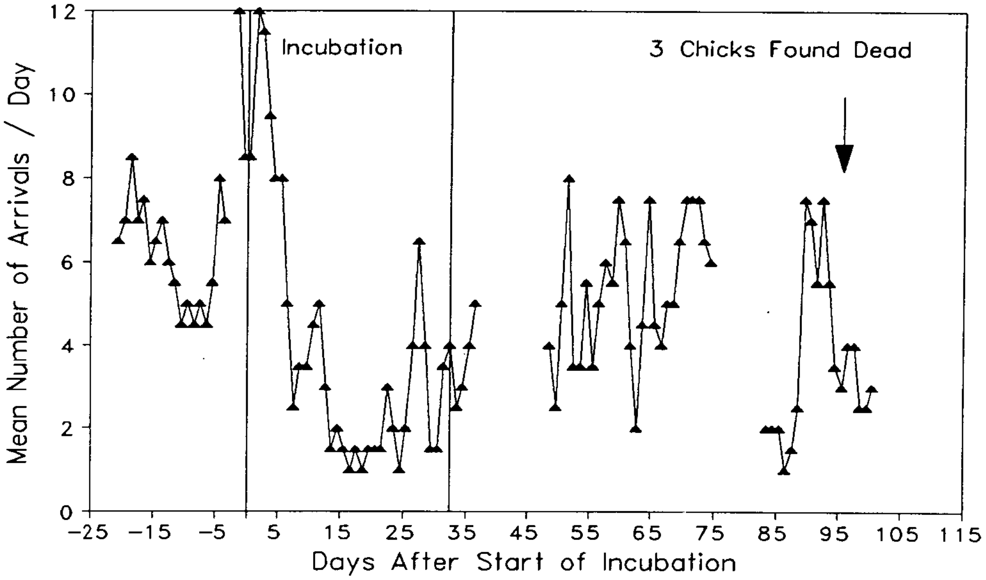
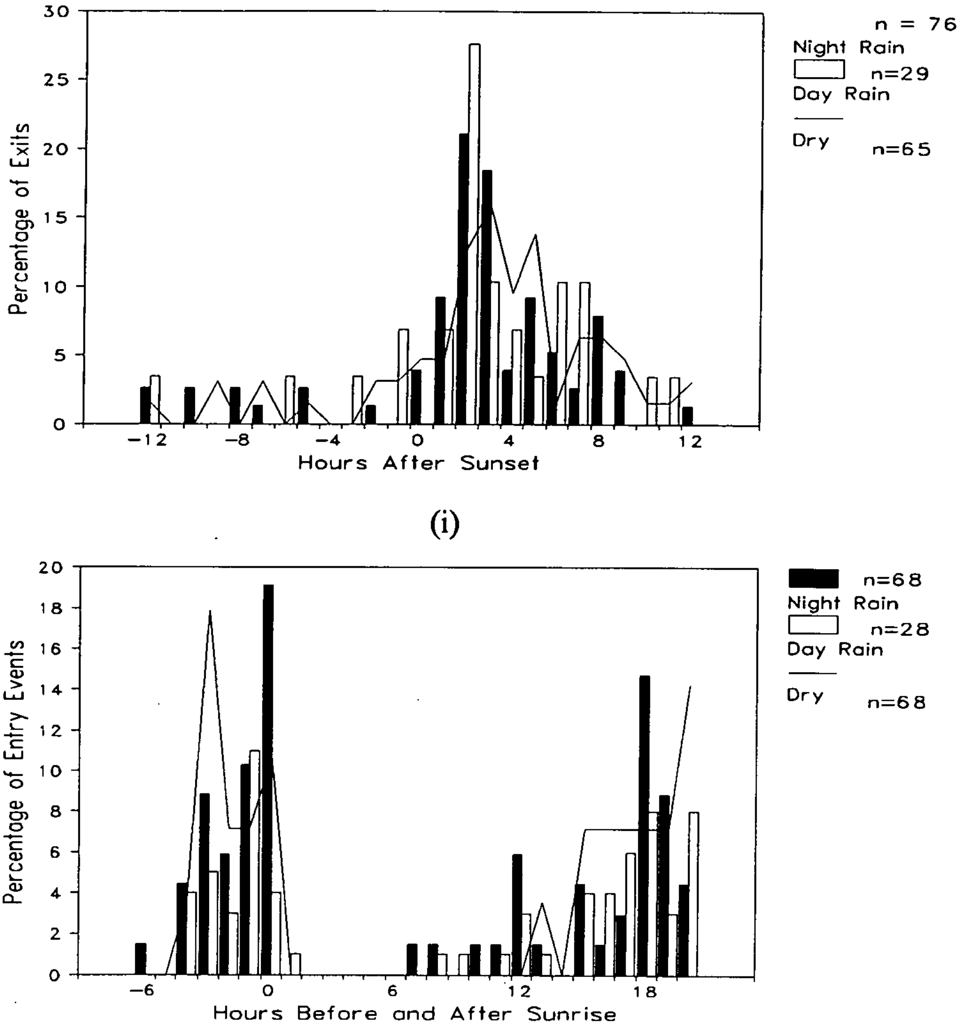


Figure 6.8. The two day running mean of the number of arrivals recorded at the nest box in relation to the start of incubation. Breaks in the data were due to equipment malfunction and when barn owls were disturbed during nest inspections.

6.3.3 The Effect of Weather Conditions on the Use of the Roost Site

6.3.3.1 Rainfall

There was found to be no significant difference in the number of entries and exits or in the percentage of 24 hours during which barn owls were present or absent from the roost between wet days with ≥0.2 mm of rain in 24 hours and on days with no recorded rainfall (Table 6.4). Due to rain gauge malfunction at the start of the study period, the timing of rainfall was only available for a total of 37 days from 2 March to 31 May when data on the use of the roost site was also available. The duration of rainfall was defined when ≥0.2 rainfall was recorded within a 30 min period. In this way, the length of rain on 37 wet days was equivalent to 128 hours of continuous rainfall.



(i)

(ii)

Figure 6.9. The timing of (i) exits and (ii) entries from the roost site with respect to sunrise and sunset for 27 days when rain started during the night (2100 - 900 GMT) and for 10 days when rain started during the day (900 - 2100 GMT), compared to 23 days which had no rain at any time.

Of a total of 98 entries to the roost site, 85 were made during dry periods and only 13 entries while it was raining. Ten of the 13 entries occurred within 30 minutes of the start of the rain event and the remaining 3 after greater than 1.5 hours. Of a total of 92 exits from the roost site, 81 occurred during dry periods and only 11 during rainfall. Five of these occurred within 30 minutes of the start of rainfall, 3 from 1 - 1.5 hours and 3 greater than 1.5 hours. Of the 630 hours when barn owls occupied the roost during these wet days, 70.5 hours of these were rain hours, which represented 11.2 % of the total time in the roost. Of the 210 hours when owls were absent from the roost site, 32.2 were wet, which represented 10.8 % of the time.

Records / day	Wet Days	Dry Days
Number of Entries	3.0 (0.2)	3.6 (0.4)
Number of Exits	2.9 (0.2)	3.4 (0.4)
% Time Present	67.0 (2.1)	70.5 (3.5)
% Time Absent	33.0 (2.1)	29.5 (3.5)

Table 6.4. The mean number of entries and exits and the percentage of time during which barn owls were present and absent from the roost site per calendar day on 58 wet days with >= 0.2 mm of rain and on 27 dry days with no recorded rainfall, from 30 January to 31 May 1991. Values in brackets are standard errors of measurements.

The data suggested that barn owls most often returned and left the roost site during dry periods, however, the frequency of entries and exits during rain was no different to the frequency of encountering rainfall. The effect of rainfall on the use of the roost was also examined according to the start of rainfall, both at night (2100 - 900 GMT) and during the day (900 - 2100 GMT), (Figure 6.9). This analysis suggested that on days when rain started during the night, the arrival of barn owls to the roost was later relative to sunrise, (the evidence for this was poor).

6.3.3.2 Snow Cover

Data on the use of the roost was available on 10 days during January and February when snow was recorded lying at 9 am. This data was compared with 10 days without snow during the same months. There was no difference in the number of entries and exits and in the percentage of time that owls were present or absent from the roost site per calendar day or during the night, between these two periods (two sample t test p = 0.2), (Table 6.5). On days of snow cover, the owls were absent from the roost site during the daytime on 8 of the days and there were only 2 days when no daytime exits were made. In comparison, on snow-free days, only 2 days had daytime exits and on the remaining 8, no exits were made. This result indicated that on days of snow cover, barn owls made 0 - 3 exits during daylight (mean = 1.4, SE = 0.30) which resulted in a total of 0 - 3.3 hours (mean = 1.5, SE = 0.37) away from the roost, or 15.7 % (SE = 3.9) of daylight hours. The timing of exits both on days with and without snow cover indicated that although exits from the roost were predominantly made after sunset and around sunrise, barn owls made a number of exits from the roost during the afternoon on days with snow while on snow-free days, afternoon exits were rare (Figure 6.10).

	Number of Events		**% of Period**	
	Entry	**Exit**	**Present**	**Absent**
Calendar Day				
Snow	4.2 (0.4)	4.1 (0.4)	55.8 (3.3)	44.2 (3.3)
No Snow	3.4 (0.4)	3.4 (0.3)	58.9 (7.0)	41.1 (7.0)
Daytime				
Snow	1.2 (0.4)	1.4 (0.3)	84.3 (3.9)	15.7 (3.9)
No Snow	0.4 (0.2)	0.3 (0.2)	80.0 (10.8)	20.0 (10.8)
Nightime				
Snow	2.9 (0.4)	2.6 (0.4)	41.0 (7.0)	59.0 (7.0)
No Snow	3.1 (0.4)	3.2 (0.4)	51.8 (8.0)	48.2 (8.0)

Table 6.5. The mean number of entries and exits and the percentage of time that the roost site was occupied during 10 days on which snow was recorded lying at 9 am, compared with 10 days without snow during the same period January - February 1991. Values in brackets are standard errors of measurements.

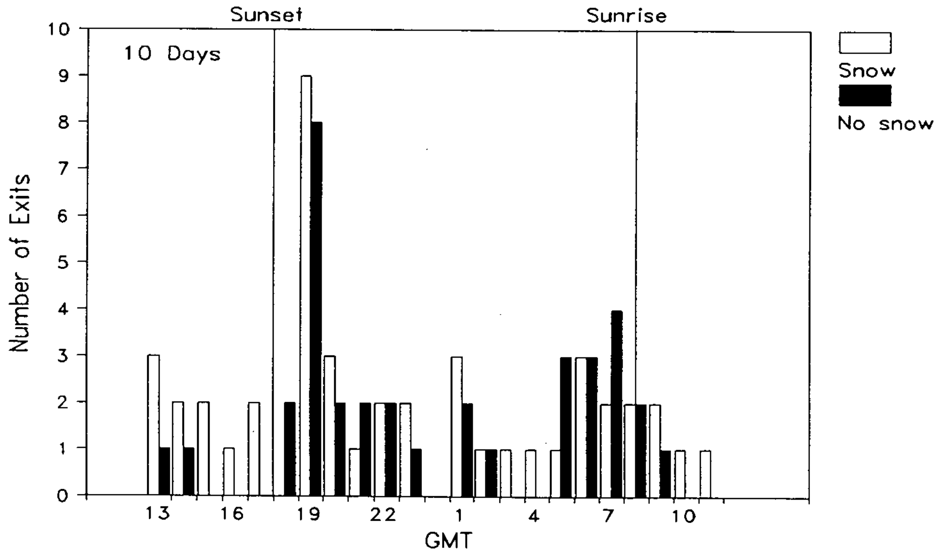


Figure 6.10. The exit times of barn owls from the roost on 10 days with snow cover (45 exits) and 10 days of no snow cover (35 exits) during January - February 1991. The time of sunset and sunrise are indicated.

6.3.3.3 Cloud Cover and Solar Radiation

The effect of cloud cover on the use of the roost building was examined according to clear conditions when cloud cover was ≤ 3 octas and on cloudy conditions when cloud cover was ≥ 4 octas. This analysis indicated that on 14 clear days the roost was occupied for an average of 78.7 % (SE = 4.1) of each calendar day, which was significantly greater than 66.0 % (SE = 1.9) for 71 cloudy days (two sample t test $p > 0.01$) (Table 6.6). There was a small difference in use of the roost site on clear and cloudy nights. On 20 clear nights, the roost was occupied for 56.1 % (SE = 4.6) of the night, which was significantly greater than 46.1 % (SE = 2.7) for cloudy nights (two sample t test $p = 0.04$) (Table 6.6). Differences in occupation of the roost were also examined during daylight hours for the period January - February and for May, when there were a greater number of days with daytime exits and entries. Combining the data for each of these periods indicated that on 20 clear days, 45 % had daytime exits. On 30 cloudy days, 67 % had daytime exits suggesting that barn owls more frequently left the roost during the hours of daylight on cloudy days (Figure 6.11).

	Number of Events		% of Period		
	Entry	**Exit**	**Present**	**Absent**	**n**
Calendar Day					
Cloud	3.2 (0.2)	3.0 (0.2)	66.0 (1.9)	34.0 (1.9)	71
Clear	2.8 (0.4)	3.1 (0.4)	78.7 (4.1)	21.3 (4.1)	14
Nightime					
Cloud	2.6 (0.2)	2.5 (0.2)	46.1 (2.7)	53.8 (2.7)	66
Clear	2.2 (0.4)	2.4 (0.3)	56.1 (4.6)	43.9 (4.6)	20
Daytime	**January - February and May Only**				
Cloud	0.9 (0.2)	1.0 (0.2)	75.3 (5.0)	24.7 (5.0)	30
Clear	0.8 (0.2)	0.8 (0.2)	91.7 (3.7)	8.3 (3.7)	20

Table 6.6. The mean number of entries and exits and the percentage of time that barn owls were present and absent from roost site on cloudy and clear conditions from 30 January to 31 May. Daytime analysis was made for January - February and May 1991 when there were a large number of daytime exits. Values in brackets are standard errors of measurements.

The effect of solar radiation on the use of the roost site during daytime was examined on days of high and low solar radiation during the periods January -

February and May. Days of low solar radiation were determined when the mean solar radiation at 1200 GMT was 50 % or less than the monthly maximum at 1200 GMT and classed as high sunshine when the mean was greater than or equal to 50 %. On 13 days of high solar radiation during this period, there was a similar number of days with and without daytime exits. On 20 days of low sunshine, however, 15 of the days had daytime exits and only 5 days had no such exits from the roost. This indicated that barn owls more often made daytime exits on days of low solar radiation (Figure 6.11, Table 6.7).

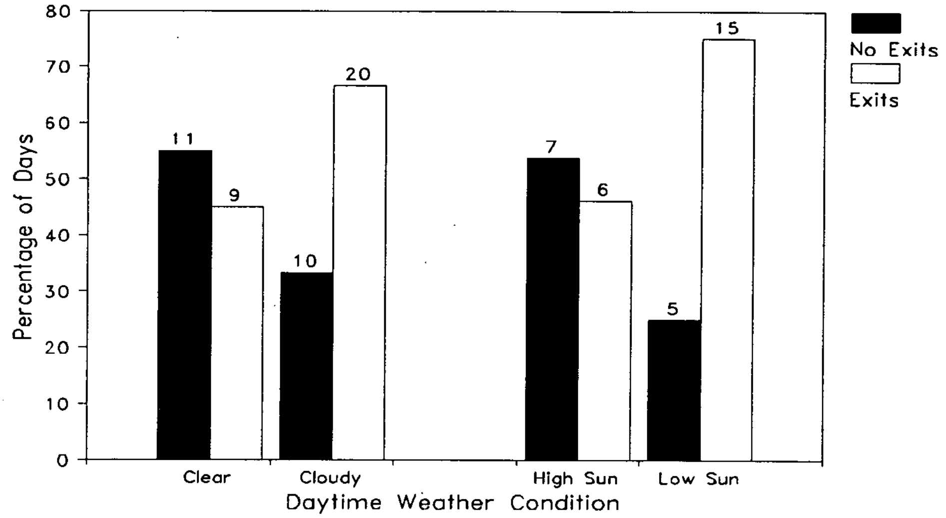


Figure 6.11. The percentage of clear and cloudy days and days of high and low solar radiation with and without daytime exits, during January-February and May 1991.

	Number of Events				% of Period				
	Entry		**Exit**		**Present**		**Absent**		**n**
Low Sun	1.0	(0.2)	1.2	(0.2)	70.4	(6.4)	29.6	(6.4)	20
High Sun	0.7	(0.2)	0.6	(0.2)	86.9	(5.5)	13.1	(5.5)	13

Table 6.7. The mean number of entries and exits and the percentage of time that barn owls were present and absent from the roost during daylight hours on days of weak (low sun) and bright (high sun) sunshine in January - February and May 1991. Values in brackets are standard errors of measurements.

6.3.3.4 Combination of Weather Conditions

The use of the roost was examined for cold and warm conditions, when the mean temperature was greater or less than the mean monthly temperature and for windy and calm conditions when the mean wind speed was greater or less than the monthly mean. This analysis indicated that in cold conditions the roost was occupied for 70.8 % of each day (SE = 2.3), which was significantly greater than 57.9 % (SE = 3.8) on warm days (two sample t test $p > 0.01$). There was a small, but significantly greater use of the roost on cold nights, with a mean of 51.5 % (SE = 4.0) compared with 41.0 % (SE = 3.4) on warm nights ($p = 0.03$) (Table 6.8). During the daytime there was on average 91.0 % (SE = 3.0) occupancy on cold days and 80.6 % (SE = 5.4) during warm days. However, infrequent exit from the roost site gave a highly skewed distribution of percentage occupation and indicated that on warm days (n = 28) barn owls made no daytime exits on 17 days. This was similar to the number of daytime exits on cold days (n = 32) when no daytime exits were made on 20 days.

There was no significant difference in the occupancy of the roost site on windy and calm days as a percentage of each calendar day (two sample t test $p = 0.1$). On windy nights, however, it was found that the roost was used for a shorter proportion of the night: 34.8 % (SE = 3.3) compared with 53.2 % (SE = 3.4) on calm nights (two sample t test $p > 0.01$) (Table 6.9). Of 34 calm days, 22 had no daytime exits while on the 26 windy days there were 15 on which no daytime exits were made, indicating that there was no preference for daytime exits according to wind speed.

	Number of Events				**% of Period**				
	Entry		**Exit**		**Present**		**Absent**		**n**
Calendar Day									
Warm	3.1	(0.2)	3.0	(0.2)	57.9	(3.8)	42.1	(3.8)	24
Cold	3.3	(0.3)	3.3	(0.3)	70.8	(2.3)	29.2	(2.3)	34
Daytime									
Warm	0.5	(0.1)	0.5	(0.1)	80.6	(5.4)	19.4	(5.4)	28
Cold	0.5	(0.1)	0.5	(0.1)	91.1	(3.0)	8.9	(3.0)	32
Nightime									
Warm	2.5	(0.2)	2.4	(0.2)	41.0	(3.4)	59.0	(3.4)	29
Cold	2.8	(0.3)	2.8	(0.3)	51.5	(4.0)	48.5	(4.0)	31

Table 6.8. The mean number of entry and exits and the percentage of time that barn owls were present and absent from the roost on warm and cold conditions from 31 January - 31 May 1991. Values in brackets are standard errors of measurements.

Use of the roost was examined for windy-cold, calm-cold, windy-warm and calm-warm conditions as in Section 5.3.2.4. These were not divided further into wet and dry conditions as sample sizes became small. Analysis of the data summarised for each calendar day indicated that the percentage occupation of the roost was significantly greater on calm-cold conditions than on calm-warm or windy-warm conditions, with an average occupation of the roost of 74.0 % (SE = 2.8) per calendar day, 60.0 % (SE = 4.2) and 54.4 % (SE = 7.6) respectively (two sample t test p >0.01). There were no significant differences between other sets of conditions (Table 6.10). On 18 calm-warm days there were 50 % with no daytime exits, 80 % on 10 windy-warm days, 81 % on 16 calm-cold days and 44 % on 16 windy-cold days. This suggested that on windy-warm and calm-cold conditions barn owls most often remained in the roost. On calm-warm and windy-cold daytime conditions there was no difference in the proportion of days when birds left the roost.

On cold-windy nights, barn owls occupied the roost for on average of 39.1 % (SE = 5.8) of the night, significantly less than 56.6 % (SE = 4.8) on calm-cold nights (p = 0.02). The use of the roost on windy-warm nights was 31.8 % (SE = 3.9), also significantly less than calm-cold nights (p > 0.01) and in these windy-warm conditions the use of the roost was significantly less than 48.5 % (SE = 4.5) occupation during calm-warm nights (p > 0.01) (Table 6.10).

	Number of Events				**% of Period**				
	Entry		**Exit**		**Present**		**Absent**		**n**
Calendar Day									
Calm	3.3	(0.2)	3.2	(0.2)	67.8	(2.7)	32.2	(2.7)	34
Windy	3.0	(0.3)	3.0	(0.3)	62.1	(3.8)	37.9	(3.8)	24
Daytime									
Calm	0.5	(0.1)	0.5	(0.1)	87.6	(3.5)	12.3	(3.5)	34
Windy	0.5	(0.2)	0.5	(0.1)	84.3	(5.3)	15.7	(5.3)	26
Nightime									
Calm	2.7	(0.2)	2.6	(0.2)	53.2	(3.4)	46.8	(3.4)	38
Windy	2.6	(0.3)	2.6	(0.3)	34.8	(3.3)	65.2	(3.3)	22

Table 6.9. The number of entries and exits and the percentage of time that barn owls were present and absent from roost site during calm and windy conditions from 30 January - 31 May 1991. Values in brackets are standard errors of measurements.

	Number of Events				**% of Period**					
	Entry		**Exit**		**Present**		**Absent**		**n**	
Calendar Day										
Windy-Cold	2.9	(0.5)	3.0	(0.4)	66.7	(3.6)	33.3	(3.6)	15	
Calm-Cold	3.6	(0.3)	3.5	(0.3)	74.0	(2.8)	26.0	(2.8)	19	ab
Windy-Warm	3.2	(0.4)	3.1	(0.4)	54.4	(7.6)	45.6	(7.6)	9	a
Calm-Warm	3.0	(0.3)	2.9	(0.3)	60.0	(4.2)	40.0	(4.2)	15	b
Daytime										
Windy-Cold	0.8	(0.2)	0.8	(0.2)	87.1	(5.3)	12.9	(5.3)	16	
Calm-Cold	0.3	(0.2)	0.3	(0.2)	95.0	(2.6)	5.0	(2.6)	16	
Windy-Warm	0.2	(0.1)	0.2	(0.1)	79.9	(11.1)	20.1	(11.1)	10	
Calm-Warm	0.6	(0.2)	0.7	(0.2)	81.1	(5.9)	18.9	(5.9)	18	
Nightime										
Windy-Cold	2.7	(0.6)	2.8	(0.5)	39.1	(5.8)	60.9	(5.8)	9	c
Calm-Cold	2.9	(0.3)	2.9	(0.3)	56.6	(4.8)	43.4	(4.8)	22	cd
Windy-Warm	2.5	(0.3)	2.5	(0.3)	31.8	(3.9)	68.2	(3.9)	13	de
Calm-Warm	2.5	(0.3)	2.3	(0.3)	48.5	(4.5)	51.5	(4.5)	6	e

Table 6.10. The mean number of entries and exits and the percentage of time barn owls were present and absent from the roost site on windy-cold, calm-cold, windy-warm and calm-warm conditions from 30 January to 31 May 1991. Values in brackets are standard errors of measurements and letters indicate when use of the roost was significantly different (two sample t test, $p > 0.05$).

6.4 DISCUSSION

6.4.1. Timing of Visits to the Roost And Nest Site

Records from the loadcell logging system from 30 January to 31 May indicated that barn owls predominantly occupied the roost building throughout the daytime and for around 50 % of the night. Exits from the roost building were common during the daytime during January - February when owls remained outside the roost until after sunrise and emerged on several occasions during the afternoon before sunset. In May, daytime exits from the roost also occurred during the morning, mainly returning during the afternoon and early evening. These findings agreed well with what is already known of the activity of British barn owls outside the breeding season, which report the barn owl to be mainly nocturnal but also active during the day (Section 6.1). The pattern of exits from the roost was timed to sunset and sunrise which is the reverse of activity in diurnal birds. There is some experimental evidence that the activity of barn owls reaches a maximum at low light levels (reviewed in Mikkola, 1983).

The length of time that barn owls remained in the roost building was dependent on the time of entry and indicated that occupation of the roost at sunrise was followed by a relatively long period of inactivity. There were, however, a few occasions when barn owls were absent from the roost throughout the day which suggested that the barn owl was roosting elsewhere. Observed exits of owls (when the nest was inspected), revealed that owls quickly took cover in the spruce plantation and it was known that the birds occasionally roosted in a nearby farm building.

Overall, the length of the exit period away from the roost was found to be between 1.8 and 2.7 hours. Assuming that the majority of exits from the roost represented foraging periods, the length of activity outside the roost suggested that activity was matched to the short term activity of field voles as discussed in Section 4.4.2. This would agree with the 2.3 hour periodicity in nocturnal activity of long eared owls measured using radio-telemetry (Wijnandts, 1984). Behavioural adaptation of predators to changes in the activity of voles have also been noted in diurnal raptors including kestrels (*Falco tinnunculus*), hen harriers (*Circus cyaneus*) and rough legged buzzards (*Buteo lagopus*) (Raptor Group RUG/RIJP, 1982). The regular exits of barn owls from the roost following sunset and to a lesser extent, around sunrise may also be a response to the increased activity of voles at these times and the daytime exits from the roost in winter may indicate adaptation to the increased diurnal activity of field voles during these months.

During the period of laying and early incubation in June, arrivals at the nest were recorded at all times of the day but reached a peak at sunset and had a lesser peak 2 - 3 hours following sunrise. Throughout incubation and hatching in July, the arrivals peaked at sunset and declined throughout the night. In both these months, the arrivals represented prey deliveries to the female as it has been established that prior to laying, during incubation and when brooding chicks to around 10 days following hatching, the male has the sole responsibility of food provision (de Jong, 1991, Taylor, in press). With 5 and then 3 chicks in the nest during August, feeding visits occurred throughout the night but again showed peaks around sunset and sunrise. Finally, during September, when there were 3 chicks and latterly only one chick, there were two main visits, the first 1 - 2 hours after sunset and the second between 0000 and 0400 GMT. Bussmann (1935) and Ritter and Görner (1977) also found two main peaks in visits when chicks were in the nest: the first following sunset and the second before sunrise. In contrast de Jong (1991) recorded no peaks in prey deliveries at a nest in the Netherlands.

In this study, the number of nest visits was found to reach a peak of 12 per day corresponding to the laying of the first egg, after which there was a decline during incubation followed by a small increase when chicks were in the nest. The pattern of nest visits in this study was similar to the pattern of prey delivery shown by Langford and Taylor (1992) to be high at laying, followed by a decline during incubation and reaching a maximum 30 days after the hatching of the first chick. The number of visits to the nest in this study was considerably lower than in the study by Langford and Taylor (1992). However, the breeding success was almost identical to that reported by Ritter and Gorner (1977), who measured visits to a nest site with a brood of 5 chicks but where only one chick fledged. Ritter and Gorner (1977) recorded 3.3 visits per 24 hours during incubation and 4.1 following hatching, similar to 6.6 before laying, 4.0 during incubation and 4.5 visits per 24 hours recorded in this study. Langford and Taylor (1992) recorded maximum feeding rates of 14 - 16 prey items per 24 hours at 19 nests with a mean brood size of 3.6. These previous studies and the measured arrivals in this study indicate that each chick requires at least 4 prey items per day to survive to fledging. This can be related to energy requirement from the energy content of prey and the assimilation efficiency of the chicks. The average field vole (*Microtus agrestis*) taken by barn owls in Britain is reported to be around 20 g (Bunn *et al*, 1982 and Taylor, in press). Hansson and Grodzinski (1970) found the energy content of the field vole to be 6.13 kJg^{-1} fresh weight and therefore the energy content of each prey is equivalent to 123 kJ. The assimilation efficiency of long eared owl chicks decreased from 92 % following hatching to 78.5 % at 4 weeks old (Wijnandts, 1984). Using a mean value of 85 % for chicks, four prey items were equivalent to an average metabolised energy of 418 kJday^{-1} which was almost identical to an estimated metabolised energy of 25 MJ over the 60 days (417 kJday^{-1}) of the nestling period for barn owls (de Jong, 1991).

The low feeding rates for an initial brood size of 5 resulted in the survival of only one chick to the point of fledging. The reason for the poor breeding success of the adults was undoubtedly due to inadequate food supply. Variations in the abundance of prey have marked effects on all aspects of breeding performance. Taylor (in press) found that over 12 years in SW Scotland the mean laying date of first clutches was from 9 April - 26 May and therefore, the laying date of 22 June in this study was exceptional. Analysis showed that laying dates were closely correlated with spring prey densities and air temperature immediately before breeding. Owls laid earliest when prey abundance and Spring temperatures were high and together, these factors alone accounted for 86 % of the annual variation in laying date (Taylor, in press). In this study prey abundance was low throughout the entire breeding season, no summer increase in abundance was noted (pers obs.) and spring temperatures were relatively cold (Appendix 3). The timing of laying was closer to that of second broods which typically produce fewer young and result in poor fledging success late in the year when weather conditions are deteriorating. A low body weight of the remaining chick was measured following 6 days of rain (2.6 - 18.4 mm) and on the last day the fledgling was recorded in the roost by the logging system, the daily rainfall was 29.4 mm. This suggested that rainfall prevented the adults from hunting and brought about rapid death of the remaining fledgling by starvation.

6.4.2 Weather Conditions and Roosting Behaviour

The roosting behaviour of barn owls is fundamentally different from that of diurnal birds, as roosting occurs principally during the hours of daylight when temperature and solar radiation are greatest. The thermal consequences of this, as outlined in Section 5.4, are that roosting owls derive considerable benefit from the high temperatures associated with the diurnal increase in air temperature and from passive solar heating of the roost building. At night, barn owls are thought to make use of waste heat generated by activity and by specific dynamic action (SDA) of digestion to compensate for cold nocturnal conditions. The severity of the cold night, however, imposes high metabolic costs during periods of inactivity, especially during the cold winter night. Barn owls consistently used the roost throughout the night and would often arrive and then leave the roost within only 10 - 30 minutes, presumably between foraging sessions. Barn owls may also have benefited from the nocturnal drop in wind speed which reduces heat loss, flight costs and possibly, reduces noise interference for the detection of prey.

It has been suggested that rainfall is one of the most important weather variables affecting the hunting activity of barn owls. Barn owls emerged and returned to the roost most often during dry spells, however this was consistent with the frequency of rainfall during wet days. It was noticeable that on the few occasions when barn owls entered or left the roost during rain, most occurred within 30 minutes of the start of rain. This suggested that there was some response to rainfall but a lack of strong evidence may have been due to the inaccurate estimation of the start of rain events associated with the design of the rain gauge, from the 30 minute rain event analysis or that the rain intensity was in some way important.

During periods of snow cover in January and February, there were a greater number of daytime exits from the roost than in a similar snow free period. There was no significant difference in percentage occupation of the roost according to snow cover and barn owls still continued to leave the roost around sunset and sunrise as on snow free days. This suggested that low temperatures and prey availability forced the owls to make more regular but shorter foraging exits. Taylor (in press) has reported that barn owls are able to catch prey through shallow snow but it is unlikely that they have the ability to penetrate deep frozen snow surfaces as in larger species, such as the great grey owl (*Strix nebulosa*), (Mikkola, 1983). At these times, barn owls may make use of wind-exposed snow-free areas to obtain prey but the combination of low temperature and snow cover leads to a severe reduction in prey availability.

Barn owls were found to show a 12.7 % increase in occupation of the roost over 24 hours on clear than on cloudy days and there was a 10.0 % increase in occupation on clear nights. This was in line with estimated increases in heat loss of 5 - 11 % in the open on clear than on cloudy nights (Section 5.3.2.2). On clear days during January - February and May when daytime activity was greatest, there were equal proportions of days with and without daytime exits. This contrasted with the results from cloudy days which indicated that there were a greater proportion of days with daytime exits and on days of low solar radiation, there were a greater proportion of days with daytime exits. Reasons for a greater proportion of daytime exits on cloudy conditions is unclear but may have been correlated with temperature, rainfall and wind speed.

Barn owls were found to occupy the roost for 12.9 % more each day (24 hours) on cold days and by 10.5 % more during cold than on warm nights. The energetic consequences of this are obvious and as the exit number per night was equal, it was apparent that barn owls spent less time per exit on relatively cold than on warm nights. At night, during periods of relatively high wind speed, the roost was used 18.4 % less often than on calm nights which correspondingly meant that barn owls spent a higher percentage of the night away from the roost on windy nights. Foraging in windy conditions may be less efficient due either to the difficulty of flight hunting or in the detection of prey and as the number of exits and entries from the roost remained constant in high and low wind speeds, there was no evidence that barn owls avoided hunting in high winds. Barn owls may adapt by seeking more sheltered areas to avoid difficulties of foraging in these situations.

The roosting behaviour of barn owls was only partially in response to maximum rates of heat loss. Based on the percentage occupation of the roost each calendar day, it was found that occupation was greater on calm-cold days than on calm-warm days. This was in line with predictions of energy savings. On windy-cold days, however, when maximum savings were expected, occupation was not significantly different from any other sets of conditions. Overall, the number of entry and exit events remained constant during all weather conditions suggesting that any effect of weather was either to increase / decrease the time absent from the roost or change the timing of exits rather than change the number of times barn owls left the roost over the course of a 24 hour period.

6.4.3 Estimated Energy Expenditure of Barn Owls

Despite the absence of strong correlations between weather and roosting behaviour, barn owls still made considerable energy savings because of the length of time they roosted in the building each day. During the period January - May, the roost was occupied on average for 57.7 - 77.8 % of 24 hours and even during the time of greatest activity, for 45.2 - 50.8 % of the night. From the amount of time barn owls were recorded in the roost, it was possible to estimate the energy expenditure of barn owls from January - May. The approach taken followed that of Wijnandts (1984) which assumed that during activity the heat generated from flight and SDA compensate for thermoregulation. In this way, when barn owls were absent from the roost, energy consumption was equal to the cost of flight and between flight activity, the energy consumption was equal to the basal metabolic rate. Flight was estimated to be similar to the total length of continuous flight of the long eared owl in winter. This was 165 minutes or 20 % of the active period, taken as lasting from the exit from the roost site following sunset to just before sunrise (Wijnandts, 1984). Barn owls were away from the roost each night for 174 minutes during January-February, 150 in March, 120 in April and 96 in May. As barn owls were recorded to spend approximately 50 % of time between sunset and sunrise in the roost, continuous flight was estimated to represent around 40 % of the time owls were absent from the roost (40 % of exit length was also used to estimate flight lengths during hours of daylight).

Activity	Energy Expenditure ($kJhr^{-1}$)	
Flight	69.0	Pennycuick (1989)
Roost (Night)	10.7 - 11.1	Section 5.3.2.1
Roost (Day)	8.9 - 10.2	Section 5.3.2.1
Basal	5.2	Section 2.4.8

Table 6.11. The estimated energy expenditure of a barn owl ($kJhr^{-1}$) during flight; while roosting in the building for the periods January - March (maximum value) and April - June (minimum value) and including the basal metabolic rate.

Barn owl energetics were therefore approximated using the energy costs of flight, basal rate when inactive between periods of flight and from biophysical estimates of heat loss while roosting (Table 6.11). Daily energy expenditures estimated in this way were 428 during January - February, 374 in March, 332 in April and 373 kJday^{-1} during May (Table 6.12).

	Jan - Feb		**March**		**April**		**May**	
	Hours	**kJ**	**Hours**	**kJ**	**Hours**	**kJ**	**Hours**	**kJ**
Night								
Flight	2.9	200	2.5	172	2.0	138	1.6	110
Inactive	4.7	24	4.3	22	2.9	15	2.5	13
Roosting	6.9	77	5.7	63	5.1	54	3.9	42
Day								
Flight	0.6	41	0	0	0	0	1.2	83
Inactive	1.0	5	0	0	0	0	1.8	9
Roosting	7.9	81	11.5	117	14	125	1.3	116
Total		428		374		332		373

Table 6.12. The estimated energy expenditure of a barn owl (kJday^{-1}) calculated from the energy expenditure in flight, at basal rate when inactive during foraging and when roosting in the building.

This was an approximation of daily energy expenditure but agreed closely with reported energy intake rates of free living barn owls. Taylor (in press) estimated from pellet contents, an average intake of 75.2g (fresh prey mass) for two wild males over 30 days in November (air temperature of 4.5 °C), which was equal to a metabolised energy of 428 kJday^{-1}. The reported intake rate of barn owls in captivity range between 42 - 117 gday^{-1}, depending on diet and conditions which represent an average intake of 16 % (SE = 1.8) of body mass (Table 6.13). In these studies, the assimilation efficiency was on average 76 % (SE = 1.9) and energy lost in pellets was 12 % (SE = 0.75) and in excreta was equal to 12 % (SE = 2.0). As described above, the typical energy content of prey was 123 kJ and therefore, using the mean assimilation efficiency, it was estimated that 3 to 4 field voles were required to meet energy expenditure during January - May. This corresponded closely to 2.5 - 3.7 exits each day from the roost, recorded using the monitoring system in this study and was close to an average of 4.2 prey items per pellet for barn owls feeding predominantly on common voles (*Microtus arvalis*) in the Netherlands (de Jong, 1991).

Body Mass (g)	**Intake** (g fresh day^{-1})	**ME** kJday^{-1}	**Efficiency** %	**Pellet** %	**Excreta** %	**Author**
603	60.5	-	-	-	-	Marti (1973)
561	77-117	386-588	78	12	10	Hamilton (1983, 85b)
524	74	361	68	14	8	Wallick & Barrett (1976)
470	54	229	79	-	21	Johnson (1974)
358	70	357	80	10	10	Appendix 2
280	67	358	76	14	10	Ceska (1980)
262	42	190	72	12	16	Kirkwood (1979)
Mean			76	12	12	

Table 6.13. The intake (g fresh food day^{-1}), metabolised energy (ME kJday^{-1}), assimilation efficiency (%), energy loss in pellets (%) and excreta (%) for barn owls in captivity.

6.5 SUMMARY

1. Roosting behaviour was examined using an automatic monitoring system which recorded the presence and absence of a pair of barn owls with loadcells on frequently used perches in the roost building and inside the nest box. Records of roost occupation were obtained for 85 days from January - May 1991 and visits to the nest box were obtained for 101 days from June to September 1991.

2. Records from January to May indicated that barn owls occupied the roost throughout the daytime and for around 50 % of the night. Daytime exits were also common in January, February and May and agreed with previous reports of daytime activity. Daytime exits, peaks in activity around sunset and sunrise and average exit lengths of 1.8 to 2.7 hours suggested that barn owls may have responded to the daytime activity of voles in winter and short term activity patterns of voles.

3. Visits to the nest during breeding reached a peak of 12 visits per day corresponding to laying. The number of visits was lower during incubation and nestling stages and indicated that at least 4 prey items per day were required by each chick. This was equivalent to an average metabolised energy of 418 $kJday^{-1}$ for a chick. The low feeding rates accounted for the poor breeding success recorded in this study and this in turn, was attributed to low vole abundance.

4. Barn owls left and returned to the roost most often, but not exclusively, during dry periods which was consistent with the frequency of rainfall. With snow cover, barn owls made a large number of afternoon exits from the roost, suggesting that low temperatures and reduced prey availability were involved. In line with predictions of heat loss, barn owls occupied the roost 10 % longer on clear than cloudy nights and 10.5 % longer on cold than warm nights. However, on windy nights, barn owls occupied the roost for 18.4 % less time than on calm nights which suggested that foraging was prolonged in high wind speeds.

6. Roosting behaviour was not in response to periods of maximum heat loss, despite this, barn owls were estimated to make considerable energy savings because of the long periods spent in the roost. Including flight costs, the energy expenditure of a barn owl was calculated to be 332 - 428 $kJday^{-1}$ from January to May. This was equivalent to an intake of 3 to 4 field voles each day which corresponded to 2.5 to 3.7 exits from the roost per day recorded in this study.

CHAPTER 7

FINAL DISCUSSION

7.1 Thermal Resistance of Barn Owls

For a species such as the barn owl, which has a thermo-neutral zone of metabolism from around 23 - 33 °C (Johnson, 1974; Hamilton, 1983; 1985a and Edwards, 1987), it is clear that the thermal resistance of plumage and factors responsible for changes in total thermal resistance, are important in determining overall energy expenditure in temperate environments such as those found in Scotland. Avian plumages are effective insulating materials and on average provide 50 % of the insulation of an equivalent depth of still air. Conduction, radiation and convection within the coat are important mechanisms of heat transfer and are influenced by plumage properties and environmental conditions. The insulation properties of barn owl plumage were examined in detail in this study and it was found that the thermal resistance per unit depth was similar to the plumage from other species of birds. There are two factors, however, which call into question the degree of insulation provided by barn owl plumage. The first concerns the depth and distribution of feathers on the body of barn owls. Plumage thickness was compared with single coats from the tawny owl (*Strix aluco*) and the short eared owl (*Asio flammeus*). On dorsal and ventral regions, barn owl plumage was thinner than that found on the tawny owl coat and thinner than plumage from ventral regions of the short eared owl. This in part accounted for the greater coat resistances of these two species. However, examination of the properties of plumage also suggested that tawny and short eared owls had a greater number of feather layers per unit area of coat.

The barn owl is one of the few European owls which does not posses a thick covering of feathers on tarsi and talons and this contrasts strongly with the plumage covering on tawny, short eared and long eared owls (*Asio otus*), all of which occur in similar British climates. The correlation between the degree of feathering of the body and climate has previously been remarked upon for owls. Species with bare tarsi and talons were generally found to be associated with humid warm environments of the tropics, subtropics and temperate zones, while species with densely feathered tarsi and talons were associated with colder less humid environments (Kelso and Kelso, 1936). Barrows (1981) also reported that the greater feather length on talons of North American boreal owls was an indication of adaptation to cold climates.

The second factor associated with the insulation of barn owl plumage is related to the ability of barn owl plumage to resist the penetration of wind and rain and is likely to be associated with the physical structure of feather layers. In comparison to tawny owl and short eared owl plumages, barn owl feathers are soft and are easily bent when handled. Although not quantified, microscopic observation indicated that barn owl contour feathers had a relatively thin rachis and the barbs and barbules are fine in structure. This suggested that the plumage is less able to withstand the mechanical forces of wind and forces associated with wetting. It is interesting to speculate that the elongation of barbules on owl feathers which have evolved as noise limiting structures may also increase its effectiveness as an insulating medium.

The thermal resistance of barn owl plumage was strongly reduced by wind speed. Changes in resistance were better described using conductance and it was found that there was a linear increase with increasing wind speed such that at a wind speed of 2 ms^{-1} (typical of barn owl habitat) conductance increased by 20 %, due to the penetration of wind to around 15 % of the total depth of plumage. Further comparisons need to be made to be able to confirm that wind did not reduce the resistance of short eared owl plumage to the same extent, but results from one sample suggested that this was so.

The physical structure of feathers and to a lesser extent, the oils provided by the preen gland mean that avian coats are remarkably resistant to the penetration of water. Wind tunnel studies indicated only a 10 % reduction in coat resistance with wetting for the barn owl, although it is difficult to be certain of the extent to which plumages become wet in natural conditions. This provides uncertainty regarding the wetting experiments in the laboratory, but from similar wetting regimes, it appears that the resistance of avian coats is not as greatly reduced by wetting as the resistance of mammalian fur. A 67 % reduction in the coat resistance of the field vole was measured in this study. This was a typical reduction when compared with previous wetting experiments on mammal coats.

Other factors which influence the total thermal resistance of owls include behaviour which increase the insulation value provided by the plumage or reduce the area of the body exchanging heat with the surroundings. Johnson (1974) noted that captive barn owls respond to low temperatures by fluffing up plumage and by crouching. These are mechanisms which increase the amount of still air trapped within the plumage. Ptiloerection has been found to increase thermal resistance by 56 % in pigeon plumages (Walsberg *et al*, 1978) and by adjusting posture, barn owls are able to minimise areas of heat exchange. The importance of posture in minimising heat loss was examined using the technique of IR thermography. In this way, the areas of highest surface temperature and hence areas of greatest heat loss were found to be on the head, noticeably around the eyes, on areas of main flight muscles and on the lower abdomen corresponding to the area of brood patch. High surface temperatures in these areas were also recorded on the great grey owl (*Strix nebulosa*) and on the snowy owl (*Nyctea scandiaca*) and have been shown to be similar in other species of birds. When active, barn owls are unlikely to be able to reduce energy exchange from around the head as orientation of the facial disk is essential for sound detection. Roosting barn owls, however, characteristically 'close up' the facial disk and thereby reduce heat loss. It is also noticeable that the plumage is thickest around the head of barn owls and this may be associated with minimising heat loss from this area.

A change in body posture was also seen as a method of increasing boundary layer resistance. Wind tunnel studies with the heat transfer model indicated that the physical nature of the plumage surface makes it difficult to be precise about boundary conditions, but the method of employing dimensionless numbers from engineering studies provided a good approximation of boundary layer resistances. As the process of free convection is proportional to the temperature difference between the surface and air, adjustments in body size which minimise areas of high surface temperature result in an increase in boundary layer resistance. Similarly, the turbulent nature of forced convection in natural environments is responsible for destroying boundary resistance and therefore, orientation and body shape are important in reducing this effect.

Heat exchange from the main flight muscles was considered to be an important mechanism for losing excess metabolic heat generated during flight. Plumage under the wings of barn owls and other raptors is thin and therefore this area is likely to act as a region of efficient heat exchange when barn owls fly. Published estimates indicate that during flight, energy expenditure may rise to as much as 3.4 to 22.6 times basal metabolic rate (Masman and Klaassen, 1987). Metabolic heat production associated with flight most probably compensates for thermostatic demands when barn owls are flying. The high cost of such activity may influence the amount of time barn owls spend flying when energy reserves or food supply is low. This could account for the increase in daylight perch hunting by barn owls from 54 % in summer to 87 % in winter reported by Taylor (in press) which was also observed in hunting kestrels (*Falco tinnunculus*), (Village, 1983). Although absolute costs of flight are responsible for this change in behaviour, barn owls reduce energy expenditure when inactive by covering up these areas of heat loss under the wings.

Thermal resistance to heat exchange in barn owls is a product of the physical properties, thickness and distribution of plumage; boundary layer resistance associated with body size and posture and is under physiological control from changes in blood circulation and tissue resistance. Seasonal changes in total thermal resistance were not examined in this study but are likely to occur during the period of moult from the increase in peripheral blood supply and loss of feathering. Rises in metabolic rate have been reported during moult for other species but as yet the heat loss attributed to changes in thermal resistance have not been quantified.

7.2 The Metabolic Rate of Barn Owls

Although the metabolic heat production of barn owls may be relatively high owing to poor feather covering, the metabolic rate of owls as a group (Strigiformes) has been reported to be low in comparison to other groups of birds. Ligon (1969), Johnson (1974) and Wijnandts (1984) summarised metabolic rates of owls and found that the standard metabolic rate per unit body mass was lower than that of other non-passerines. This may be a genuine adaptation, as low metabolic rates can be maintained by long periods of inactivity in sheltered roosts and at night, heat may be a by-product of activity. Many measurements were made during the day when owls display a drop in metabolism and therefore comparison of metabolic rates may only indicate differences between the inactive phase of owls and the active metabolic phase of diurnal species. Wijnandts (1984), however, found that the daily metabolised energy of caged owls was also consistently lower than that of other non-passerines including Falconiformes. General inactivity of owls in captivity could account for these differences and therefore there is a need to take into account measurement time and inactivity of different species in further studies.

The heat transfer model predicted reasonably accurately, the sensible heat loss of barn owls in the thermo-neutral zone when compared with traditional gas exchange techniques. Sensible heat loss was 37 Wm^{-2} which compared with standard metabolic rates (sensible and latent) of 36 - 43 Wm^{-2} for captive owls. The increase in heat loss with decreasing temperature was however, two times greater than the temperature coefficients calculated from reported measurements of metabolic rate below the lower critical temperature. This indicated the importance of physiological and behavioural mechanisms in reducing heat loss at low temperatures which are absent in simple physical models.

The increase in sensible heat loss from the model at wind speeds from 0 to 7 ms^{-1} was similar to metabolic increases which are either proportional to wind speed or to the square root of wind speed. At wind speeds of 2 ms^{-1}, the sensible heat loss was found to increase by 18 % which was in line with rises in the metabolic rate of the long eared owl (Wijnandts, 1984) and the snowy owl (Gessaman, 1972). The effect of wetting was to increase the total heat loss from the model by 34 % at all wind speeds. As noted above, this increase was due to a reduction in coat resistance and by evaporation from an incompletely saturated surface. This compares with studies on captive birds which have reported metabolic increases of up to 35 % with realistic levels of wetting. Evaporation will be less important at temperatures encountered by barn owls in SW Scotland and therefore the reduction in resistance was used to approximate the effect of rainfall on the energy exchange of barn owls in natural environments. There is however, an obvious need to improve our understanding of the effects of wetting on the metabolism of birds and as importantly, to quantify the degree to which birds become wet by rain in natural conditions.

7.3 Microclimate, Biophysical Models and Roosting Behaviour

The energetic consequences of a relatively poorly insulated species in which heat loss is strongly dependent on wind speed and wetting were obvious, when local meteorological conditions and roost microclimate were studied. Measurements at the altitudinal limit of the population indicated that barn owls encounter temperatures which are almost always well below the thermo-neutral zone of metabolism and are exposed to high wind speeds combined with periods of snow, sleet and rain throughout the year. This suggested that the characteristic roosting behaviour of barn owls was an adaptation to minimise the thermal stress imposed by climate.

Air temperature inside the roost / nest site in this study showed seasonal and diurnal increases matching the seasonal and diurnal changes in ambient temperature. Over the course of the year, the daytime temperature inside the roost was on average 0.6 - 3 °C higher than outside air temperature and at night, temperatures were 0.3 - 1.9 °C higher during the winter months. Passive solar heating was shown to bring about high surface temperatures of the roost building, to over 40 °C and when combined with the heat production of chicks, nest temperatures reached as much as 36.2 °C when outside temperature was only 21 °C. The roost was sheltered from the wind and had high relative humidity matching outside conditions. The variety of roost sites used by barn owls elsewhere in SW Scotland suggested that this site was to some extent less well insulated than others. It is likely that roost sites under roofs, floorboards, inside chimneys of disused buildings or in natural cavities such as tree holes will have different thermal properties and will therefore provide a range of thermal conditions for roosting / nesting barn owls.

The value of wind tunnel studies and measurement of microclimate was that a biophysical model of heat loss could be developed which incorporated the effect of wind speed and wetting on plumage insulation not often included in other models. Discounting the effects of rain for the moment, the model suggested that by using the roost building at night barn owls may have been able to reduce heat loss on average by 18 % and by 8 % by roosting in trees, compared with roosting in the open. At night, the metabolic savings were due to lack of forced convection and from small radiative savings. During the day the roost site provided thermal benefits of 21 % compared with roosting in the open due to passive solar heating inside the roost and shelter from the stronger daytime winds. In contrast, tree roosts were poorer roost sites during the daytime and estimated to provide savings of only 3 % relative to roosting in the open because of the contribution of solar radiation to the energy balance of a bird in full sun.

The contribution of solar radiation to the energy balance of barn owls was significant only in conditions of low wind speed which compensated for cold air temperatures associated with sunny days. The energy exchange of barn owls was dominated by infrequent exposure to solar radiation, shown by the high occupancy of the roost building during daylight hours. Calculation of the energy balance of a barn owl at 1200 GMT each month indicated that on days of minimum solar radiation, solar radiation contributed only 3 % to total radiation absorbed but on days of maximum solar radiation represented 21 %, with an estimated energy saving of 24.5 %. Although significant, energy gains from solar radiation were small because of the low absorptivities of plumage associated with pale / white plumage. Evolution of plumage colouration in barn owls appears primarily to be associated with reducing prey detection by minimising shadow and for crypsis to avoid predators. The interaction between solar radiation and wind speed for light plumages should be considered more fully to establish the contribution of solar gains to the total energy balance of barn owls. Differences in heat loss for a barn owl foraging on cloudy and clear days were predicted but it should be remembered that barn owls are always able to conserve more energy by remaining in the roost and therefore, solar gains are unlikely to be associated with roosting behaviour. There are however, implications for the energy budget of a barn owl active on sunny days.

Weather patterns in SW Scotland were predicted to determine the rate of heat loss in barn owls because in general, rainfall was associated with relatively high temperatures and high wind speeds while dry periods were often associated with clear, cold and calm conditions especially during winter. The colder temperatures on these dry nights was found to partially compensate for wet plumage on wet nights and therefore the heat loss on wet nights was only 6 - 8 % greater than on dry nights. With no significant differences in temperature during the daytime, heat loss was estimated to be 9 - 17 % greater on wet days than on dry days. As a consequence of this, roosting in the building was estimated to provide savings of 14 - 17 % on wet nights but as much as 29 - 32 % on wet days. On days with snow cover, the biophysical model estimated that high rates of heat loss were most frequent on clear nights when air temperatures were well below freezing and radiation losses greater. On clear days with snow, barn owls had the lowest rates of heat loss because solar radiation and lower wind speeds compensated for lower air temperatures.

The heat loss of a barn owl was estimated to increase according to the combination of weather conditions such that maximum heat losses were calculated to occur on wet, windy and cold conditions and minimum rates on dry, calm and warm conditions. In this way savings of 25 - 37 % for barn owls are possible by roosting during wet, windy conditions but only 7 - 17 % during dry, warm conditions.

From January - May, barn owls occupied the roost building on average for 81 - 98 % of the daytime and 45 - 51 % of the night and therefore the general roosting behaviour of barn owls can be seen as a way of optimising energy savings by making use of higher energy savings during the daytime. The extent to which barn owls used the roost site to minimise metabolic heat production was however, not fully established. Although wetting by rainfall was estimated to result in the highest rates of heat loss, no difference in use of the roost was found to occur between wet and dry days. There was a 10 % increase in occupation of the roost on clear than on cloudy nights and an increase of 10.5 % occupation on cold than on warm nights which were in line with earlier estimates of energy savings. There was however, no evidence that solar radiation was a factor influencing daytime exits. The effect of wind speed on roosting behaviour was contrary to the hypothesis that owls avoid windy periods because of high rates of loss. It was found that on windy nights barn owls were absent from the roost for 18.4 % more of the night than on calm nights. Although lacking supportive data, the suggestion was that barn owls found it difficult to locate prey in windy conditions.

To an extent, roosting behaviour of barn owls may be interpreted as a method of reducing the effects of low temperatures on metabolism. For subtropical and tropical barn owls, roost sites may however, be more important in preventing heat stress. Barn owls have been shown to respond to heat stress by increased respiratory evaporation through gular flutter but there remains considerable scope to examine other physiological adaptations to heat stress and as importantly, to measure the microclimates experienced by barn owls in these areas.

It is important to realise that changes in the roosting behaviour of barn owls was a response to many factors, only one of which may have been to reduce the cost of metabolic heat production. Heat production from flight and specific dynamic action of feeding may help to compensate for high energy demands. In addition, weather conditions which increase energy expenditure in barn owls may not necessarily affect prey in the same way. Examination of the energetics and microclimates of field voles indicated that activity is unlikely to be influenced by wind speed due to the reduction in wind speed within grass runways. Periods of rain have been suggested to provide a reduction in predator detection and therefore, considering the high heat losses for barn owls at these times, it was surprising that greater occupation of the roost was not observed. The high surface area to volume ratio of small mammals such as field voles does suggest that activity will be strongly influenced by low temperatures, leading to greater activity during daylight hours in winter. During January and February, barn owls made a large proportion of daytime exits which can be interpreted as a response to the increased availability of prey. The 2 - 4 hour short term activity rhythm of field voles may also explain an average exit time from the roost of 1.8 - 2.7 hours. Increased prey availability, however, would not account for a large number of afternoon exits during periods of snow cover. These exits probably occurred because barn owls needed to obtain greater energy intake rates at low temperatures and had to commence hunting earlier because of reduced foraging success with snow cover.

The models of energy expenditure during incubation suggested that the thermostatic cost of incubation for the female, including the cost of warming the eggs was not significantly different from the metabolic heat production of a female outside the nest site. The heat loss for an incubating female sitting on eggs was calculated to be 243 $kJday^{-1}$ and of that, 33.5 $kJday^{-1}$ was required to maintain eggs at around 35 ^{o}C. Transfer of heat from the brood patch provides an efficient mechanism of warming the eggs. The insulation of the nest combined with the thermal resistance of the eggs was estimated to almost fully compensate for the lack of feathering and increase in peripheral blood supply in this region.

The direct effects of weather on the female prior to laying, during laying and incubation are minimised due to the comparative insulation and favourable microclimate provided by the nest. The provision of food by the male and inactivity of the female during this time allows the female to accumulate the reserves required for egg synthesis. In this study, the male made as many as 12 visits per 24 hours to the nest box during the laying period. Weather conditions which reduce the hunting ability of the male at this time are important in determining food supply for the female and to avoid shortages, males are known to deliver surplus prey when foraging success is high (Langford and Taylor, 1992). The biophysical model indicated that heat production required by the incubating female was sensitive to changes in temperature of the nest box and therefore significant decreases in temperature were predicted to increase thermostatic costs at a time when provision of food by the male may also be affected. The correlation of barn owl laying dates with prey abundance and temperature immediately before laying reported by Taylor (in press) therefore indicates how food supply and the metabolic rate of the female are responsible for accumulation of sufficient energy reserves for egg production.

7.4 Energy Requirement, Mortality and Distribution of Barn Owls

Combining biophysical estimates of heat loss, roosting behaviour and flight costs, the daily energy requirement for free living barn owls was calculated to range from 428 $kJday^{-1}$ in January - February to 332 $kJday^{-1}$ in April. This agreed well with estimated energy intakes of wild barn owls during winter calculated from pellet examination (Taylor, in press) and indicated daily prey requirements of 3 to 4 average prey items. Agreement with this intake rate was also suggested by 2.5 - 3.7 exits from the roost building during January - May. When compared with a metabolised energy of 252 $kJday^{-1}$ for long eared owls in winter (Wijnandts, 1984) it appears that barn owls have relatively high energy requirements. The consequences of high energy requirements become critical when foraging success is poor because of low prey availability or poor weather conditions. This is likely to account for the high mortalities of barn owls during periods of snow cover when prey is unavailable and when low temperatures increase metabolism of a barn owl's limited fat reserves. Correlations between barn owl mortality and prey availability rather than weather conditions, however, suggest that provided prey is available, barn owls are able to balance energy budgets and compensate for short term reductions in foraging success.

The altitudinal limit of breeding barn owls at around 300 m in Britain and the latitudinal distribution of barn owls may therefore have come about from the problem of balancing a high energy requirement with a high rate of energy intake. The use of roost sites may only partially reduce energy demands in environments where the effect of climate is to increase metabolic heat requirements while at the same time altering prey availability. An ambitious task will therefore be to match predicted energy requirements with measured energy intake of barn owls and daily, seasonal and yearly changes in prey availability.

APPENDICES

APPENDIX 1 ENERGY INTAKE OF A CAPTIVE BARN OWL

A female barn owl was kept in an outdoor aviary (7 x 3 x 2 m) and fed on a diet of dead day-old pheasant chicks (*Phasianus colchicus*) for a period of 11 days. The owl was able to use a roost box and a series of wooden perches. The mass of the owl was determined at the beginning and end of the trial with a spring balance and was 360 and 355 g, respectively, representing a 1.4 % change in body mass. Plastic sheeting was placed below the roost box and perches to allow easier collection of uneaten food, pellets and faeces. The chicks given to the owl were divided randomly from a batch into groups of five and stored in the freezer at -20 °C. Five day-old chicks were *ad libitum*, as throughout the study, five chicks were never fully eaten. Before feeding, the fresh weight of each chick was determined on a digital balance accurate to 0.1 mg. During the afternoon, each day, all uneaten food, pellets and excreta were collected. The fresh weights of uneaten food and pellets were determined and samples were stored in the freezer at -20 °C together with excreta, for future analysis.

Following the feeding trial, the uneaten food, pellets and excreta, together with 10 fresh chicks, were dried in a convection oven at 70 °C for 48 hours. The energy content of each sample was then determined using an automatic adiabatic bomb calorimeter (Gallenkamp Ltd) and expressed in Joules per gram of dry matter (Jg^{-1}). The gross energy intake of the barn owl was found by subtraction of uneaten food from the total food provided. Energy metabolised was obtained by subtraction of the energy content of pellets and excreta from the gross energy intake.

Throughout the feeding trial, the barn owl had a fresh intake of 66.96 g (SE = 4.44). The water content of fresh chicks was 31 % (SE = 0.73) and the dry intake was equal to 18.47 g (SE = 1.65). The barn owl produced one pellet per day with the exception of a single day when no pellet was found and produced on average 3.38 g (dry mass) (SE = 0.22) of excreta.

The energy content of samples were 24.66 kJg^{-1}(SE = 0.24) for chicks, 25.82 kJg^{-1} (SE = 0.34) for uneaten chicks, 17.19 kJg^{-1} (SE = 0.30) for pellets and 13.28 kJg^{-1} (SE = 0.28) for excreta. From this, the gross energy intake for the barn owl was estimated to be 446.3 $kJday^{-1}$ (SE = 40.1) of which 357.3 $kJday^{-1}$(SE = 38.8) was metabolised, 44.9 $kJday^{-1}$ (SE = 5.2) was lost in pellets and 44.1 $kJday^{-1}$ (SE = 3.1) was lost in excreta (Table A1). Of gross energy intake the barn owl metabolised on average 80.1 % and lost 10.1 % and 9.9 % in pellets and excreta (Figure A1).

Mass (g)	**Fresh**		**Dry**		**n**
Intake	66.96	(4.44)	18.47	(1.65)	11
Pellets	7.26	(0.80)	2.56	(0.28)	10
Excreta	-	-	3.38	(0.22)	11
Water Content	**(%)**				
Chick	31	(0.73)			10
Uneaten Chick	38	(2.25)			11
Pellet	35	(1.57)			10
Excreta	-	-			-
Energy Content	**(kJg^{-1} dry matter)**				
Chick	24.66	(0.24)			10
Uneaten Chick	25.82	(0.34)			11
Pellet	17.19	(0.30)			10
Excreta	13.28	(0.28)			-
Energy Budget	**(kJ day^{-1})**		**% of G.E.I**		
Gross Energy Intake	446.3	(40.1)			
Metabolised	357.3	(38.8)	80.1		
Pellet	44.9	(5.2)	10.1		
Excreta	44.1	(3.1)	9.9		

Table A1. Food intake and energy budget of a female barn owl in an outdoor aviary for 11 days in October 1990 with mean daily temperature 7.5 - 13.2 °C and relative humidity 74.8 - 93.3 %.

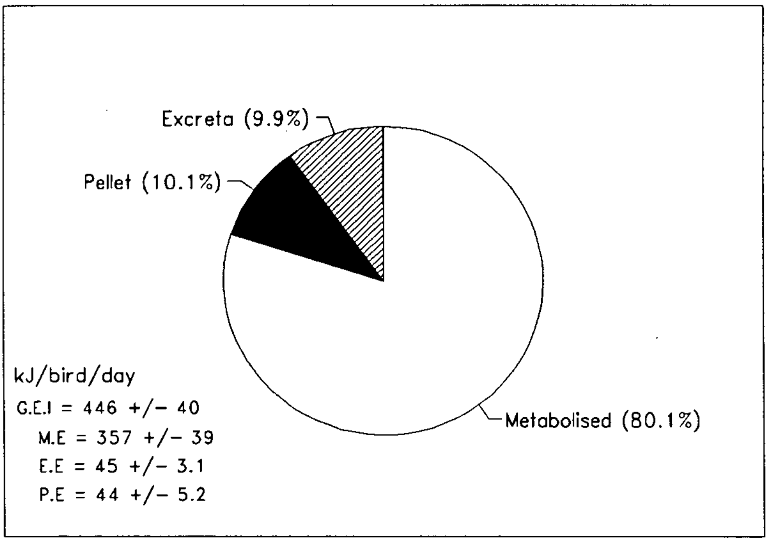


Figure A1. The energy budget of a female barn owl in captivity in an outdoor aviary for 11 days during October 1990 with mean daily temperature 7.5 - 13.2 °C and relative humidity 74.8 - 93.3 %. Energy is expressed as a percentage of gross energy intake.

APPENDIX 2 SPECTRAL PROPERTIES OF OWL PLUMAGE

The spectral properties of barn owl, short eared owl and tawny owl plumage samples were determined for wavelengths 400 - 800 nm. These were determined with a Model 6000 optical spectrum analyser using a stabilised light source (Monolight 6162) and controlled with 6800 System controller (Monolight Instruments Ltd) on a Compaq 386 personal computer.

Measurements were carried out on plumage samples used in wind tunnel studies. Samples were dry and free from dirt and were carefully positioned in the analyser ensuring that the plumage was not distorted. The reflectivity of dorsal and ventral plumage of torso and wing areas, for each species was determined. Between each determination the light spectra was rechecked. In a further experiment the dorsal pelage from a field vole was also examined.

	Reflectance %			
Spectra	**Dorsal**	**Ventral**	**Dorsal Wing**	**Ventral Wing**
Barn owl (male)	56	78	64	90
Barn owl (female)	54	75	58	87
S-eared owl (female)	50	55	51	64
Tawny owl (sex ?)	50	50	50	60
Field vole	63			

Table A2. Mean short wave reflectance of samples obtained by weighting spectral reflectivites according to solar irradiance (see text).

The mean short wave reflectance of plumage was determined by weighting the reflectivity spectra (Figure A2) according to the spectral irradiance (Wm^{-2} μm^{-1}) of solar radiation. This function was determined using the Planck formula according to Campbell (1977) with the temperature of the sun approximated as 6000K. The mean reflectance of the plumage samples was found to range between 50 in the tawny owl to 90% on the male barn owl (Table A2). The dorsal pelage of the field vole had a mean reflectance of 63 %.

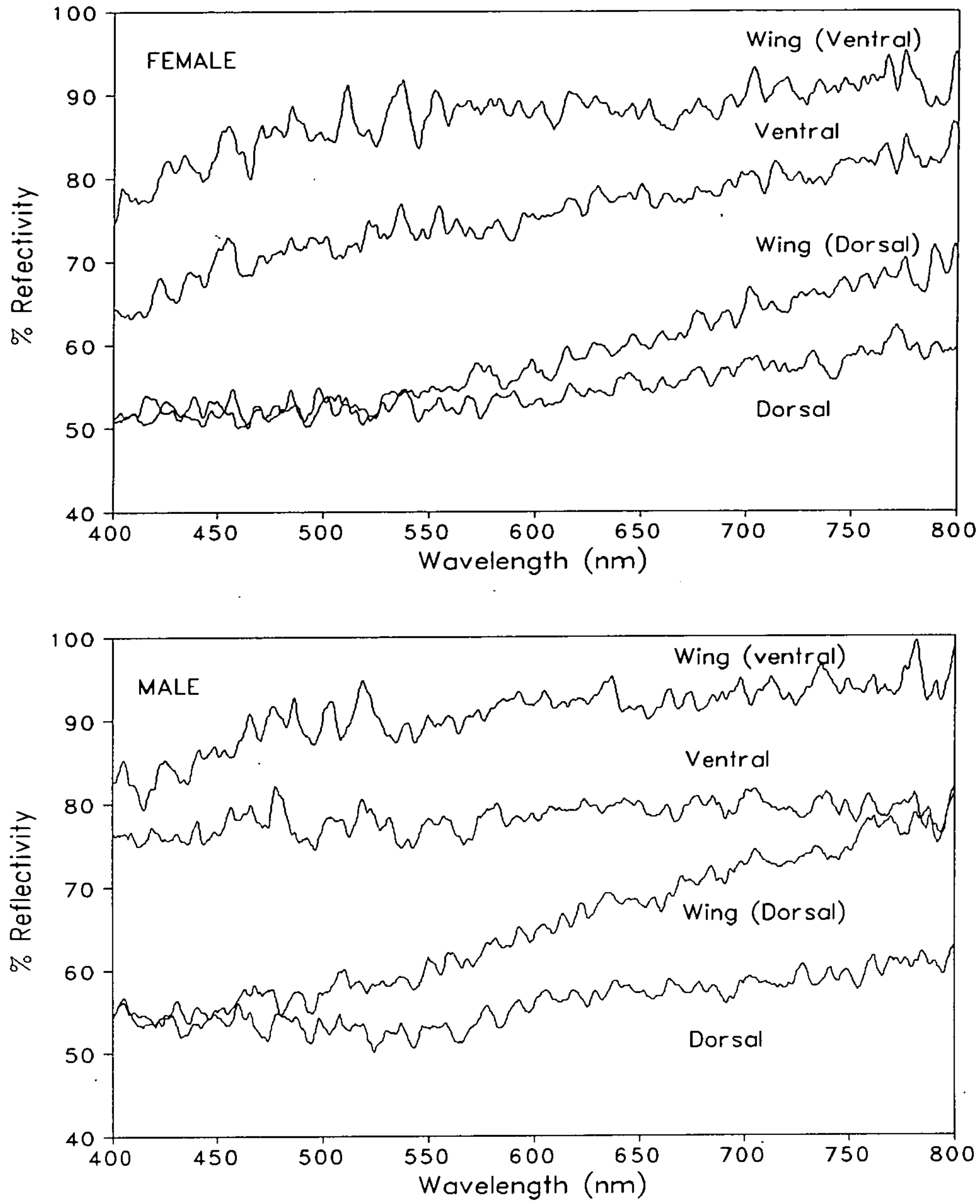


Figure A2. Spectral reflectivities of (i) female and (ii) male barn owl plumage from dorsal and ventral body and wing regions over the range in wavelengths 400 to 800 nm.

APPENDIX 3 METEOROLOGICAL AND MICROCLIMATE DATA 1990 - 1992

	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Temperature (°C)																
Outside Air	2.2	1.9	0.9	7.1	4.9	8.0	9.1	14.4	13.8	10.3	7.8	4.8	4.3	3.2	4.0	4.1
Roost	2.6	3.7	2.4	8.1	5.9	8.7	10.4	15.4	14.7	11.3	8.6	6.5	6.3	5.7	5.7	5.4
Nest Box (air)	-	-	-	6.2	6.6	9.4	12.0	17.2	16.8	13.1	7.4	3.8	2.1	1.6	3.3	4.5
Nest Box (surface)	-	-	-	6.0	6.5	9.1	11.7	16.8	16.4	12.8	7.5	4.0	2.4	1.9	3.5	4.6
Building Surface	-	-	-	-	6.4	10.4	11.4	15.9	15.3	11.6	7.3	3.8	1.8	1.6	3.1	2.3
Relative Humidity (%)																
Outside Air	93	97	95	95	86	82	88	92	92	93	97	98	99	99	98	96
Roost	96	99	96	95	85	80	86	89	90	90	98	99	100	99	99	97
Wind speed at 9m (ms^{-1})	2.8	2.5	2.2	2.1	2.7	2.4	2.2	2.4	2.2	2.3	2.2	3.0	2.4	2.3	3.3	3.1
Solar Radiation (MJm^{-2}day^{-1})	1.0	1.3	3.1	5.3	10.7	13.1	13.1	12.4	10.9	8.8	3.5	1.7	1.2	1.7	2.6	5.8
Rainfall																
Monthly Total (mm)	-	-	-	175	152	19	127	86	67	117	188	216	187	141	-	215

Table A3. Monthly summary of meteorological and microclimate data, measured at the field site from December 1990 to March 1992.

APPENDIX 4 METEOROLOGICAL DATA FROM ESKDALEMUIR OBSERVATORY 1990 - 1992

	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Air Temperature (°C)	2.6	0.7	0.5	5.5	5.5	9.1	9.5	15.1	13.9	11.1	7.7	4.3	2.3	2.0	3.4	4.8
Air Temperature (°C) 1951-1980	2.6	1.4	1.5	3.5	5.8	8.8	11.8	13.1	12.9	10.9	8.2	4.2	2.6	1.4	1.5	3.5
Wind speed (ms^{-1})	4.4	3.5	3.1	3.1	5.1	3.6	3.3	3.6	3.0	3.3	3.8	4.6	3.3	3.2	4.7	5.4
Wind speed (ms^{-1}) 1951-1980	4.6	4.6	4.3	4.6	4.2	4.0	3.8	3.5	3.4	3.9	4.1	4.4	4.6	4.6	4.3	4.6
Sunshine Hours	0.9	1.2	2.3	2.0	4.9	4.3	4.0	4.4	4.2	5.0	1.9	1.6	1.2	2.0	1.4	2.3
Sunshine Hours 1951-1980	1.2	1.4	2.2	2.9	4.5	5.3	5.5	4.6	4.3	3.3	2.5	1.8	1.2	1.4	2.2	2.9
Monthly Rainfall (mm)	245	191	149	170	151	18	109	86	65	103	191	231	184	148	176	254
Monthly Rainfall (mm) 1951-1980	171	158	100	123	82	98	92	107	124	147	160	153	171	158	100	123
Snow Days (9am)	12	16	13	0	0	0	0	0	0	0	0	1	3	0	4	4
Snow Days 1951-1980	4.7	10.6	9.0	4.3	0.8	0	0	0	0	0	0	1.9	4.7	10.6	9.0	4.3
Days of Snow / Sleet Falling	11	15	11	3	5	0	1	0	0	0	1	11	6	4	6	11
Days of Snow / Sleet Falling 1951-1980	9.6	13.8	11.9	11.6	5.7	1.3	0.1	0	0	0	0.5	6.6	9.6	13.8	11.9	11.6
Days of Hail / Ice Falling	5	8	2	3	8	0	0	0	0	0	0	8	5	0	3	7
Days of Hail / Ice Falling 1951-1980	2.5	3.8	2.9	5.3	4.4	3.3	0.8	0.2	0.4	0.4	1.2	0.1	2.5	3.8	2.9	5.3

Table A4. Monthly summary of meteorological data from Eskdalemuir Observatory for the study period and 1951 - 1980 long term average.

APPENDIX 5 BIOPHYSICAL ESTIMATES OF HEAT LOSS

	Estimated Heat Loss of Barn Owl in Open Site (Wm^{-2})							
	Wet Nights		Dry Nights		Wet Days		Dry Days	
January - March								
Windy - Cold	99.6	(0.8)	95.2	(0.5)	96.3	(1.0)	91	(0.8)
Calm - Cold	98.0	(1.0)	93.1	(1.2)	91.4	(2.4)	84.3	(1.1)
Windy - Warm	96.5	(0.6)	89.4	(2.3)	93.6	(1.0)	85.8	(1.7)
Calm - Warm	91.7	(2.3)	83.3	(1.4)	85.1	(1.1)	76.6	(0.9)
April - June								
Windy - Cold	96.3	(6.8)	89.0	(3.2)	87.3	(1.9)	79.5	(1.9)
Calm - Cold	90.4	(2.3)	87.9	(1.3)	78.7	(1.9)	71.9	(1.5)
Windy - Warm	86.9	(1.9)	85.2	(3.0)	80.0	(3.0)	69.4	(2.4)
Calm - Warm	83.5	(3.8)	79.3	(2.1)	72.4	(2.2)	67.3	(1.1)
July - September								
Windy - Cold	81.2	(1.5)	79.1	(3.1)	78.2	(1.6)	69.8	(2.2)
Calm - Cold	80.6	(2.1)	75.0	(1.1)	68.4	(1.8)	64.3	(1.2)
Windy - Warm	80.2	(1.4)	71.8	(0.8)	73.6	(2.1)	59.8	(1.9)
Calm - Warm	70.8	(1.5)	71.8	(1.0)	62.4	(3.0)	58.9	(0.6)
October - December								
Windy - Cold	99.0	(2.0)	96.8	(1.5)	93.7	(2.4)	82.9	(0.3)
Calm - Cold	89.8	(2.3)	88.0	(1.6)	90.0	(2.5)	80.4	(1.5)
Windy - Warm	91.6	(0.8)	83.3	(1.4)	90.4	(1.0)	83.8	(3.0)
Calm - Warm	78.9	(1.9)	75.0	(1.8)	77.2	(1.9)	79.1	(1.8)
	Estimated Heat Loss of Barn Owl in Roost Building							
January - March								
Windy - Cold	74.7	(0.2)	75.6	(4.3)	71.6	(0.7)	73.0	(1.3)
Calm - Cold	77.6	(0.7)	80.8	(1.2)	72.1	(1.7)	73.7	(1.0)
Windy - Warm	71.4	(0.7)	69.6	(0.5)	68.3	(0.7)	68.5	(1.1)
Calm - Warm	72.1	(1.2)	72.4	(0.9)	68.3	(0.7)	66.2	(1.2)
April - June								
Windy - Cold	73.6	(3.0)	74.2	(1.6)	65.6	(0.6)	61.1	(1.3)
Calm - Cold	74.3	(1.0)	77.1	(1.0)	63.4	(0.6)	62.4	(2.8)
Windy - Warm	67.4	(1.0)	70.8	(1.5)	59.0	(1.6)	55.3	(1.6)
Calm - Warm	69.6	(1.9)	70.0	(1.5)	59.9	(3.2)	57.4	(1.2)
July - September								
Windy - Cold	64.9	(1.0)	66.0	(2.5)	59.8	(1.1)	61.3	(3.6)
Calm - Cold	67.1	(1.5)	67.0	(0.9)	54.8	(1.4)	56.7	(1.6)
Windy - Warm	62.5	(0.7)	60.1	(0.5)	56.2	(1.1)	53.0	(1.1)
Calm - Warm	60.1	(1.2)	63.4	(0.6)	49.5	(1.6)	50.7	(1.3)
October - December								
Windy - Cold	73.9	(1.0)	84.3	(1.9)	68.4	(1.1)	66.0	(0.1)
Calm - Cold	73.9	(1.2)	78.2	(1.0)	71.8	(1.1)	70.6	(1.1)
Windy - Warm	70.0	(0.6)	71.4	(1.4)	68.7	(0.9)	66.1	(2.2)
Calm - Warm	66.5	(1.2)	70.0	(0.6)	63.0	(1.0)	70.3	(2.0)

Table A5. Estimated heat loss (Wm^{-2}) of a barn owl in the open and in the roost building for windy cold, calm cold, windy warm and calm warm conditions on wet and dry nights and wet and dry days. Values in brackets are standard errors of measurements.

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