

Winter survival strategies for small birds: Managing energy expenditure through hypothermia

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ABSTRACT

Theoretical studies on energy management in wintering small birds have focused on energy reserves. Here we extend these analyses to include energy expenditure controlled by nocturnal hypothermia. Our models indicate that even the minimal use of hypothermia, when dusk reserves are insufficient, can significantly increase the probability of surviving the winter. Optimal hypothermia, which allows employment of hypothermia even when dusk reserves are sufficient for surviving the night, outperforms minimal hypothermia only when the food supply in bad weather spells is very low. Our models illustrate the use of the dynamic state variable approach in a broader theoretical analysis involving multiple trade-offs among alternative strategies.

Keywords: dynamic optimization, energy management, fattening strategies, hypothermia, willow tits, winter survival.

INTRODUCTION

All organisms must make decisions crucial for survival and reproduction under environmental conditions of variability and uncertainty. Dan Cohen was among the first biologists who formalized this issue into a set of testable models (e.g. Cohen, 1966, 1970, 1971). One central life-history decision relevant to both plants and animals concerns the optimal amount of food reserves. Recently, the issue of optimal levels of fat reserves in small passerines has received considerable attention (Lima, 1986; McNamara and Houston, 1990; McNamara *et al.*, 1994; Clark and Ekman, 1995; Cuthill and Houston, 1997). A prominent theme in this work has been the prediction of daily foraging schedules and optimal fat reserves under unpredictable environmental conditions (Houston and McNamara, 1993; Bednekoff and Houston, 1994; McNamara *et al.*, 1994). Models of optimal fat reserves typically predict a daily foraging schedule consisting of intense foraging at dawn, and again at dusk, with less intensity during midday hours. They also predict larger levels of fat reserves at dusk under less predictable food availability. Other related themes have included short-term

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hoarding of food (McNamara *et al.*, 1990; Lucas and Walter, 1991; Brodin and Ekman, 1994; Hitchcock and Houston, 1994) and long-term hoarding (Brodin and Clark, 1997).

Efficient strategies of internal and external energy storage are clearly critical for surviving the winter, especially in northern latitudes. Certain species of birds, however, are known also to control their expenditure of energy during inclement weather, through the use of nocturnal hypothermia, defined as a shallow night-time reduction of body temperature to 30–38°C (reviewed in Reinertsen, 1996). So far, research on hypothermia and related phenomena has focused on physiological issues (Wang and Hudson, 1978; Bech and Reinertsen, 1988), although some authors have also included economic and ecological considerations (Hainsworth and Wolf, 1978; Reinertsen and Haftorn, 1986; Reinertsen, 1996). It is therefore pertinent to integrate the knowledge on hypothermia into a formal model of energy management in wintering small birds.

We present two sets of models designed to investigate the interactions among foraging, fat reserves and hypothermia. First, we consider analytical models for surviving a single day. These analytical models assume a daily balance of the energy budget and are hence not adequate for analyses involving long-term use of stored reserves. Our second set of models overcomes this limitation by using dynamic state variables, which are particularly suited for studying trade-offs between multiple interacting strategies (Clark and Mangel, 2000). In these models, the cost of hypothermia is taken to consist of an immediate but temporary increase in mortality risk, for example from predation. At the end of the paper, we briefly discuss the possibility that using hypothermia affects the animal's 'condition', with implications for future survival and foraging efficiency. Although we focus here on hypothermia in a small, wintering bird, our approach is relevant for other phenomena such as torpor and hibernation in various species under a wide range of environmental conditions (Wang and Hudson, 1978; Wang, 1989).

ENERGY BUDGET FOR A SINGLE DAY

We first consider the trade-off between foraging and using hypothermia in a simple, analytical model based on daily survival. We consider a small bird that forages during daylight hours in winter, building up its energy reserves to a maximum at dusk, and then uses these reserves overnight. If reserves are insufficient to survive the night (e.g. because of low ambient temperature), the bird can use hypothermia to reduce its energy use, but this has a cost which we first assume to consist of an increased immediate mortality risk. We assess the optimal combination of daily foraging effort and nocturnal hypothermia, where by 'optimal' we mean the strategy that maximizes survival probability.

Let f_0 denote the bird's net daily energy gain resulting from foraging, and let $S_1(f_0)$ be the probability that the bird survives the day's foraging. Night-time energetic costs without using hypothermia are f_n . The hypothermic variable θ is defined as the amount by which f_n is decreased by using hypothermia, where

$$0 \leq \theta \leq \theta_{\max} \quad (1)$$

with θ_{\max} representing the maximum possible use of hypothermia (per night). The probability of surviving the night is $S_2(\theta)$.

Case 1: f_n known in advance. If the bird knows f_n for the next night, it can choose f_0 and θ so as to balance its daily energy budget:

$$f_0 = f_n - \theta \quad (2)$$

In this case, the probability of surviving the 24 h day equals

$$S_{24}(\theta) = S_1(f_n - \theta)S_2(\theta) \quad (3)$$

The optimal level of hypothermia θ^* maximizes this expression, subject to $0 \leq \theta \leq \theta_{\max}$ and $\theta \leq f_n$.

For example, suppose first that the survival functions are exponential:

$$S_1(f_0) = c_1 \exp(-k_1 f_0) \quad (4)$$

$$S_2(\theta) = c_2 \exp(-k_2 \theta)$$

(where k_1, k_2 are constants), in which case

$$S_{24}(\theta) = c_1 c_2 \exp(-k_1(f_n - \theta) - k_2 \theta) \quad (5)$$

Here the trade-off between foraging and hypothermic risks is explicitly determined by the relative magnitudes of k_1 and k_2 . If $k_1 > k_2$, saving energy through hypothermia is less 'costly' than obtaining it by foraging, so that $\theta^* = \theta_{\max}$ (or $\theta^* = f_n < \theta_{\max}$). Likewise, if $k_2 > k_1$, then foraging is the better option and $\theta^* = 0$. However, this assumes that $f_0 = f_n$ - that is, all night losses are compensated by foraging. If there is a maximum amount $f_{0\max}$ of energy that can be gained by a day's foraging, and if $f_{0\max} < f_n$, then a minimal, positive level of hypothermia must be used, $\theta^* = f_n - f_{0\max}$.

The assumptions of equation (4) might be too strong. In the general case, we would have

$$S_1(f_0) = c_1 \exp(-k_1(f_0))$$

$$S_2(\theta) = c_2 \exp(-k_2(\theta))$$

where $k_1(f_0)$ and $k_2(\theta)$ denote functions. Maximization of the product $S_{24}(\theta)$, where $f_0 = f_n - \theta$, is equivalent to minimization of the expression

$$k_1(f_n - \theta) + k_2(\theta)$$

By calculus, θ^* satisfies $k_1'(f_n - \theta) = k_2'(\theta)$ (except for extreme solutions $\theta^* = 0$ or θ_{\max}). Although mathematically straightforward, this solution is perhaps too subtle for practical use, given the problem of estimating the two non-linear survival functions k_i .

Case 2: f_n uncertain. In Case 1, we assumed that the bird can predict f_n for the night to follow, and forage accordingly. It is more likely that the bird would sometimes encounter unexpectedly cold nights. What level of energy reserves f_0 should be used in this situation? Secondly, should the bird always attempt to balance its daily energy budget, retaining no surplus reserves, or should it store extra reserves as a hedge against unexpected cold weather?

Ignoring reserve storage for the moment, we can extend the above single-day deterministic model to allow for uncertain night-time costs. Assume that the bird 'knows' the probability density $\phi(f_n)$ for night costs f_n . Let $S(f_0, f_n)$ denote the 24 h survival probability, given f_0 and f_n , and using optimal hypothermia θ^* . For the exponential example, we have:

$$S(f_0, f_n) = \max_{\theta} c_1 c_2 \exp(-k_1 f_0 - k_2 \theta) = \begin{cases} c_1 c_2 \exp(-k_1 f_0) & \text{if } f_n \leq f_0 \\ c_1 c_2 \exp(-k_1 f_0 - k_2 (f_n - f_0)) & \text{if } f_0 < f_n \leq f_0 + \theta_{\max} \\ 0 & \text{if } f_n > f_0 + \theta_{\max} \end{cases} \quad (6)$$

(Note that this assumes no residual reserves at dawn.) Equation (6) is explained as follows. The bird uses the minimum hypothermia needed to survive the night, given f_0 = dusk reserves and f_n = night-time cost. If $f_n \leq f_0$, no hypothermia is needed and $S = c_1 c_2 \exp(-k_1 f_0)$. If $f_n > f_0$, hypothermia is used to make up the deficit, $\theta = f_n - f_0$, and $S = c_1 c_2 \exp(-k_1 f_0 - k_2 \theta)$. But if f_n is too large, namely $f_n > f_0 + \theta_{\max}$, hypothermia cannot make up the deficit and the bird dies, $S = 0$.

The trade-off here is apparent: low foraging intake f_0 reduces the risk from foraging, but incurs a higher risk of overnight mortality when f_n is large, and vice versa. The optimal f_0^* maximizes the overall daily probability of survival $E_{f_n}\{S(f_0, f_n)\}$. However, failure to forage sufficiently to cover the possibility of a very cold night risks certain death whenever such a night does occur. Hence the optimal f_0^* will be such as to ensure survival except in extremely rare situations.

Results

We consider the following example (related to the parameters used later in the long-term model; see Table 1): $c_1 = c_2 = 1$, $k_1 = 0.025 \text{ g}^{-1}$, $k_2 = 0.01 \text{ g}^{-1}$, $\theta_{\max} = 0.5 \text{ g}$, $f_n = 0.8 \text{ g}$ with probability p_g and $f_n = 1.3 \text{ g}$ with probability $1 - p_g$, where p_g is a parameter. Thus night-time requirements are 0.8 g on a 'good' night and 1.3 g on a 'bad' night; we assume $f_{0\max} = 1.3 \text{ g}$.

Clearly, in this example, the optimal daily foraging effort is either $f_0^* = 0.3$ (survival on good nights: $f_0^* - (f_n - \theta_{\max}) = 0.3 - (0.8 - 0.5) = 0$) or $f_0^* = 0.8$ (survival on all nights: $f_0^* - (f_n - \theta_{\max}) = 0.8 - (1.3 - 0.5) = 0$), since intermediate values of f_0 would increase foraging mortality risk without improving nocturnal survival. It turns out that $f_0^* = 0.8$ (survival on all nights) unless the probability of a bad night, $1 - p$, is less than 0.008. Only

Table 1. Parameters used in the single-day model

Symbol	Meaning	Units	Basic value
f_0	Daily net energy gain	g	(decision variable)
$f_{0\max}$	Maximum daily net energy gain	g	1.3 g
$S_1(f_0)$	Survival probability, foraging	—	$c_1 \exp(-k_1 f_0)$
f_n	Night-time metabolic cost	g	0.8 g (good night), 1.3 g (bad night)
θ	Hypothermia variable	g	(decision variable)
θ_{\max}	Maximum hypothermia	g	0.5 g
$S_2(\theta)$	Survival probability, hypothermia	—	$c_2 \exp(-k_2 \theta)$
c_1, c_2	Survival function coefficients	—	1.0
k_1	Survival cost coefficient, foraging	g^{-1}	0.025 g^{-1}
k_2	Survival cost coefficient, hypothermia	g^{-1}	0.01 g^{-1}
p_g	Probability of a good night	—	(parameter)

if the probability of a bad night is extremely low is it optimal not to prepare for that possibility. Similarly, if night-time metabolic costs have a continuous distribution, daily foraging gains should prepare for all but the most extreme nights. This suggests that death due to overnight exhaustion of energy resources is likely to be a rare occurrence among birds capable of hypothermia.

DYNAMIC MODELS COVERING THE ENTIRE WINTER

The single-day model with uncertain night-time costs addresses one important aspect of energy management, namely the trade-off between obtaining energy by foraging and controlling energy expenditure via hypothermia. However, this model does not allow us to consider long-term aspects of energy management. For this, we require a dynamic state variable model (Clark and Mangel, 2000), with state $X(t)$ representing the level of reserves at dawn on day t in winter, $t = 1, 2, \dots, T$. The optimization problem then involves the optimal level of reserves, optimal daily foraging strategy and optimal hypothermia strategy. We introduce three models, of increasing complexity, to address these problems.

First, however, note that unless there is some cost associated with having large reserves, the optimal reserves strategy is obviously to maximize the level of reserves (Lima, 1986; McNamara and Houston, 1990; Houston and McNamara, 1999). Our dynamic models incorporate two costs that may increase with the level of reserves – metabolic cost and predation risk. The models use parameter values derived from data pertaining to Willow tits (*Parus montanus*) in Sweden (Brodin and Clark, 1997).

Case 1: No hypothermia. Our model without hypothermia resembles the earlier models of Lima (1986) and Houston and McNamara (1993) (see also Houston and McNamara, 1999, s. 9.3).

The main state variable $X(t)$ denotes the bird's energy reserves at dawn on day t ($t = 1, 2, \dots, T$) (see Table 2 for symbols). During the day the bird forages, using effort $e(t)$, defined as the portion of the total available time spent actively foraging ($0 \leq e(t) \leq 1$). Foraging effort $e(t)$ is the decision variable in our model. Daily food intake is $e(t) \cdot f$, where f represents the maximum possible daily food intake. Food intake f is a random variable determined by weather conditions, as described below.

Daily energy gain from food intake $e(t) \cdot f$ is:

$$\text{daily energy gain} = \beta e(t) \cdot f \quad (7)$$

where $\beta \leq 1$ denotes the assimilation coefficient. For simplicity, all energy-related variables are measured in grams of fat content, with 1 g equivalent to approximately 37.7 kJ.

Day-time metabolic costs, consisting of resting and activity costs, are given by:

$$\text{day-time metabolic costs} = c_{\text{day}} = (c_1(1 - e) + c_2e) \cdot (m_0 + x) \quad (8)$$

where c_1, c_2 are resting and activity cost coefficients, m_0 is lean body mass and x is fat reserves.

Thus metabolic costs increase with x , the level of fat reserves. Mass-dependent metabolic costs imply that greater foraging effort is needed to maintain a higher level of reserves. Since we assume (see below) that foraging activity incurs predation risk, it follows that higher levels of reserves incur indirect fitness costs in terms of predation. In addition (see

Table 2. Symbols used in the dynamic models

Symbol	Meaning	Range	Units	Basic value
t	Day in winter	$1, 2, \dots, T$	days	—
T	Time horizon	constant	days	60
$X(t)$	Fat reserves, start of day t	0 to X_{\max}	g	—
X_{\max}	Maximum fat reserves	constant	g	3.0
x_1	Initial fat reserves	constant	g	0.5
$e(t)$	Foraging effort, day t	0 to 1	—	—
f	Food supply	random	$\text{g} \cdot \text{day}^{-1}$	$f_g = 3.5$ $f_b = \text{parameter}$
β	Assimilation factor	constant	—	0.5
c_1, c_2	Day-time resting, activity metabolic rates	constants	day^{-1}	0.023, 0.028
m_0	Lean body mass	constant	g	10.0
$X_1(t)$	Fat reserves at dusk, day t	(equation 9)	g	—
p_{good}	Probability of good day following a good day	constant	—	0.9
c_0	Night-time basal metabolic cost	constant	g	0.3
c_{th}	Thermoregulation cost	random	g	$c_g = 0.5$ $c_b = 1.0$
μ_1	Fixed predation-risk coefficient	constant	day^{-1}	0.002
μ_2	Mass-dependent predation-risk coefficient	constant	$\text{g}^{-1} \cdot \text{day}^{-1}$	0.003
$J(t)$	Number of consecutive previous bad days	$0, 1, \dots, J_{\max}$	—	—
$F(x, j, t)$	Fitness function	(equation 14)	—	—
p_j	Probability that cold snap lasts j days	constants	—	0.2 ($j = 1-5$)
$p_g(j)$	Probability that day $t + 1$ is good, given that previous j days were bad	(equation 13)	—	—
θ	Degree of hypothermia	(equation 21)	g	—
$S_h(\theta)$	Probability of survival due to hypothermia	(equation 23)	—	—
μ_h	Hypothermia mortality coefficient	constant	g^{-1}	0.02

equation 12), we assume that the instantaneous predation risk increases with body mass (including fat reserves), implying a second fitness cost of high reserves. The advisability of including such mass-dependent fitness costs in models of overwinter survival tactics was stressed by Lima (1986) and McNamara and Houston (1990).

Energy reserves at dusk are equal to

$$X_1(t) = X(t) + \beta e(t) \cdot f - (c_1(1 - e) + c_2 e) \cdot (m_0 + x) \quad (9)$$

Both $X(t)$ and $X_1(t)$ are constrained by

$$0 \leq X, X_1 \leq X_{\max} \quad (10)$$

where X_{\max} denotes maximum capacity for fat reserves. The bird is assumed to die of starvation if either $X(t)$ or $X_1(t)$ becomes negative.

Night-time metabolic costs are $c_0 + c_{\text{th}}(t)$, where c_0 denotes basal metabolic cost and $c_{\text{th}}(t)$ denotes thermoregulatory cost, determined by current weather conditions (see below). In the absence of hypothermia, reserves at the start of day $t + 1$ are equal to

$$X(t + 1) = X_1(t) - c_0 - c_{\text{th}}(t) \quad (11)$$

with the condition that the bird dies overnight if this value is negative. The effect of hypothermia on energy reserves will be described later.

While searching for food, the bird is subject to predation. The instantaneous daily risk of predation is assumed to equal

$$\mu = \mu_1 + \mu_2(m_0 + x) \tag{12}$$

where μ_1, μ_2 are mass-independent and mass-dependent risk coefficients.

In modelling winter weather variability, we tried to be moderately realistic while also maintaining computational feasibility. A highly realistic model would be a time-dependent n th order Markov process for daily weather conditions. Discretized to include m state levels, such a model would involve m^{2n} time-dependent transition probabilities. We reduced this unmanageable dimension by making several simplifying assumptions. First, we ignored time dependence: this means that we are considering a typical ‘mid-winter’ situation. Secondly, we considered just two weather states, labelled ‘g’ (‘good’) and ‘b’ (‘bad’). Finally, we assumed that bad weather occurs in spells lasting j days ($j = 1, 2, \dots, J_{\max}$), where j is a random variable, with $p_j = \text{Pr}(\text{current spell lasts exactly } j \text{ days})$, $\sum p_j = 1$. The transition probabilities for good weather days are $p_{\text{good}} = \text{Pr}(\text{day } t + 1 \text{ is good} \mid t \text{ is good})$ and $p_{\text{bad}} = 1 - p_{\text{good}}$.

The assumption of possibly protracted bad-weather spells is in our opinion much more realistic than the alternative assumption of serial independence (as in Brodin and Clark, 1997), or of a first-order Markov process (as in Lima, 1986). Energy requirements are more critical under our assumption than under such alternatives, because the bird must hedge against the onset of several consecutive days of low temperature and restricted access to food sources, and manage its energy expenditure over such protracted spells.

If day t is bad, let $p_g(j)$ denote the probability that $t + 1$ is good, where j denotes the number of consecutive previous bad days. Using Bayes’ formula, we have

$$\begin{aligned} p_g(0) &= p_{\text{good}} \\ p_g(1) &= p_1 \\ p_g(2) &= p_2 / (p_2 + \dots + p_{J_{\max}}) \\ &\vdots \\ &\vdots \\ &\vdots \\ p_g(J_{\max}) &= 1 \end{aligned} \tag{13}$$

The weather conditions on day t determine nocturnal thermoregulatory costs $c_{\text{th}} = c_g$ or c_b . We also assume that weather conditions on a given day t affect the bird’s access to food supplies on day $t + 1$, with $f(t + 1) = f_g$ or f_b respectively. Thus a bad day is doubly stressful, resulting in high overnight metabolic costs and low food accessibility on the next day.

To include weather in the model, we thus require a second state variable $J(t)$ = number of consecutive previous bad days. Daily foraging (and other) decisions are assumed to depend on the current values of both state variables $X(t)$ and $J(t)$.

We adopt overwinter survival (i.e. survival until day T) as the fitness criterion, and define the fitness function as:

$$F(x, j, t) = \text{maximum probability that the bird survives from dawn on day } t \text{ to dawn on day } T, \text{ given that } X(t) = x \text{ and that } J(t) = j \tag{14}$$

The maximization in this definition refers to the choice of search effort $e(s)$ on each day s from t to T . This effort is assumed to depend on the current day's morning reserves $x = X(t)$; for example, a bird with large reserves will presumably forage less than if it has low reserves; effort $e(t)$ may also depend on the current weather state $j = J(t)$. The fitness function $F(x, j, t)$, and the optimal search strategy $e^*(x, j, t)$, are computed using dynamic programming (Houston and McNamara, 1999; Clark and Mangel, 2000).

The dynamic programming equations are

$$F(x, j, T) = 1 \text{ for all } x \geq 0 \text{ and for all } j \quad (15)$$

$$F(x, j, t) = \max_{0 \leq e \leq 1} S_p(e, x)[p_g(j)V_g + (1 - p_g(j))V_b] \quad (16)$$

where $S_p(e, x)$ denotes the probability of surviving predation while foraging,

$$S_p(e, x) = \exp(-e \cdot (\mu_1 + \mu_2(m_0 + x))) \quad (17)$$

and where the probabilities $p_g(j)$ are given by equation (13), and V_g, V_b are given by

$$V_g = F(x + \beta e f_j - c_{\text{day}} - c_0 - c_g, 0, t + 1) \quad (18)$$

$$V_b = F(x + \beta e f_j - c_{\text{day}} - c_0 - c_b, j + 1, t + 1) \text{ for } j < J_{\text{max}} \quad (19)$$

Here c_{day} is given by equation (8), and $f_0 = f_g$ and $f_j = f_b$ for $1 \leq j \leq J_{\text{max}}$. We also have

$$F(x', j', t + 1) = 0 \text{ if } x' < 0 \quad (20)$$

That is, the bird starves if it runs out of reserves. (See chapter 5 in Clark and Mangel, 2000, for an explanation of why the condition in equation (20) is not $x' \leq 0$.)

The dynamic programming equations (15) and (16) are obtained by the usual argument, as follows. First, the terminal condition follows directly from the definition, equation (14), and the specification that the bird is alive if, and only if, $x \geq 0$. To derive equation (16), consider a certain level of effort $e(t) = e$ on day t . The probability of surviving the day's foraging is $S_p(e, x)$. Given that the bird does survive the day, it will encounter a good night with probability $p_g(j)$, or a bad night with probability $1 - p_g(j)$. Following a good night, reserves at the start of day $t + 1$ will equal

$$x' = x + \beta e f_j - c_{\text{day}} - c_0 - c_g$$

(from equations 8, 9 and 11). Thus the probability of surviving from day $t + 1$ to T equals $V_g = F(x', 0, t + 1)$, as in equation (18); note that $J(t + 1) = 0$ here because the night of day t is good. Similarly, following a bad night, future survival equals V_b , as in equation (19). Combining these probabilities and maximizing with respect to e leads to equation (16).

Case 2: Minimal hypothermia. Birds under hypothermia are less responsive than sleeping birds, so it is likely that hypothermia is associated with higher rates of predation than regular night-time sleep (Hainsworth *et al.*, 1997; Reinertsen, 1996). Hence hypothermia may be perceived as an emergency measure taken when some lower threshold of energy reserves has been reached (Hainsworth *et al.*, 1977; Reinertsen and Haftorn, 1983; Graf

et al., 1989). In the next model, we assume that (i) hypothermia is used, when necessary, to prevent exhaustion of overnight reserves; (ii) the level of hypothermia, or minimum night-time body temperature, may vary within a set limit as a function of the potential energetic deficits, determined by the night-time ambient temperature and energy reserves (Reinertsen and Haftorn, 1983); and (iii) a higher level of hypothermia (lower body temperature) is associated with higher predation risk.

The energy savings due to hypothermia equal the potential deficit

$$\text{energy savings} = -(X_1(t) - c_0 - c_{th}) = \theta \tag{21}$$

provided this deficit is positive (see Fig. 1). In other words, hypothermia is used to reduce thermoregulatory costs, but only sufficiently to achieve overnight survival; dawn reserves $X(t + 1)$ equal zero in this case:

$$X(t + 1) = \begin{cases} X_1(t) - c_0 - c_{th} & \text{if this is } \geq 0 \\ 0 & \text{if } X_1(t) - c_0 \geq 0 \text{ but } X_1(t) - c_0 - c_{th} < 0 \end{cases} \tag{22}$$

The probability of surviving predation due to hypothermia is denoted by $S_h(\theta)$:

$$S_h(\theta) = \exp(-\mu_h \theta) \tag{23}$$

where θ is given by equation (21) and μ_h is the mortality rate during hypothermia.

The dynamic programming equations for Case 1 – equations 15 and 16 – are the same for Case 2, but the expressions V_g , V_b are different. Write dusk reserves as

$$x_{1j} = x + \beta e f_j - (c_1(1 - e) + c_2 e)(m_0 + x) \tag{24}$$

where f_j is as described following equation (19). Then

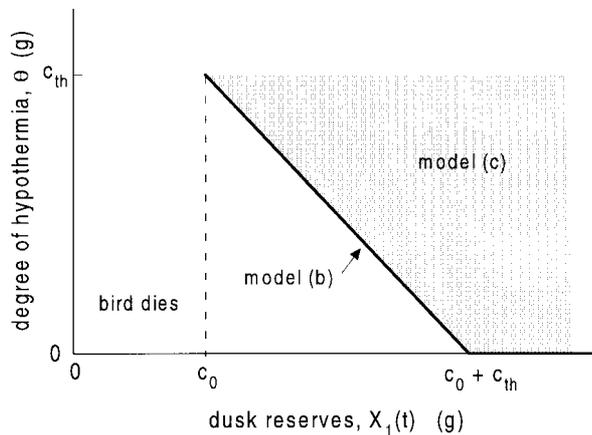


Fig. 1. Degree of hypothermia θ (i.e. energy saved overnight) for the dynamic models, Cases 2 and 3. In Case 2, the bird uses minimal hypothermia required for overnight survival (bold line). In Case 3, the bird can use any amount of hypothermia lying on or above this line (shaded area), the optimal amount being determined by the optimization component of the model.

$$V_g = \begin{cases} 0 & \text{if } x_{1j} < c_0 \\ F(x_{1j} - c_0 - c_g, 0, t + 1) & \text{if } x_{1j} - c_0 - c_g \geq 0 \\ S_h(-(x_{1j} - c_0 - c_g))F(0, 0, t + 1) & \text{if } x_{1j} \geq c_0 \text{ but } x_{1j} < c_0 + c_g \end{cases} \quad (25)$$

The expression for V_b is similar; replace ‘g’ by ‘b’ and use $j' = j + 1$ rather than $j' = 0$ in equation (25).

With the minimal hypothermia model just described, the bird is assumed to use hypothermia whenever this is necessary to prevent overnight exhaustion of energy reserves. Although the bird’s only decision in this case is its foraging strategy (or, equivalently, its dusk reserves level), this strategy also implicitly determines the use of hypothermia, since dusk reserves $X_1(t)$ determine the level of hypothermia required, depending on nocturnal conditions. Dusk reserves and hypothermia trade off in terms of survival: maintaining high reserves reduces the use of hypothermia, but is costly because of mass-dependent predation risk (equation 17), and also because metabolic costs are mass-dependent (equation 8), requiring additional foraging effort, which is itself risky. Hypothermia has an associated mortality risk, which we assume is proportional to the magnitude of hypothermia (equation 23). As suggested by the single-day model, the optimal trade-off between reserve storage and the use of hypothermia is determined in part by the relative risks associated with these two options. However, the frequency and duration of bad weather spells also influences this trade-off; analysing this aspect requires dynamic optimization models as developed here. There is further discussion later.

Case 3: Optimal hypothermia. The minimal hypothermia model only allows a bird to adjust minimum night-time body temperature to compensate for insufficient reserves for surviving that night. This model considers hypothermia as a short-term energy-saving mechanism used only in emergencies. However, empirical evidence suggests that hypothermia is not employed only under conditions of energy deficit (Kruger *et al.*, 1982; Reinertsen and Haftorn, 1986; Wang, 1989; Reinertsen, 1996). Hence, in the optimal hypothermia model, hypothermia can be used to maximize long-term winter survival and not only when reserves are insufficient for surviving the current night.

In the optimal hypothermia model, we allow the bird to choose any value of θ in the interval

$$(c_{th} + c_0 - x_{1j})^+ \leq \theta \leq c_{th} \text{ provided } x_{1j} \geq c_0 \quad (26)$$

where $(z)^+$ denotes the maximum of z and 0 (Fig. 1). This implies that $X(t + 1) = x_{1j} - c_0 - c_{th} + \theta$ satisfies

$$0 \leq X(t + 1) \leq x_{1j} - c_0 \quad (27)$$

The dynamic programming equations for this model are

$$F(x, j, T) = 1 \text{ for all } x \geq 0 \text{ and all } j \quad (28)$$

$$F(x, j, t) = \max_{0 \leq e \leq 1} S_p(e, x)(p_g(j)V'_g + (1 - p_g(j))V'_b) \quad (29)$$

where

$$V'_g = \max_{(c_g + c_0 - x_{1j})^+ \leq \theta \leq c_g} S_h(\theta)F(x_{1j} - c_0 - c_g + \theta, 0, t + 1) \quad (30)$$

and

$$V'_b = \max_{(c_b + c_0 - x_{ij})^+ \leq \theta \leq c_b} S_h(\theta)F(x_{ij} - c_0 - c_b + \theta, j + 1, t + 1) \tag{31}$$

provided $x_{ij} - c_0 \geq 0$ (with $V'_g = V'_b = 0$ if $x_{ij} - c_0 < 0$). Inspection of equations (24–31) shows that the Case 3 model extends Case 2 by allowing the bird to choose θ subject to condition (26).

Results

Our preliminary analyses revealed that a dominant factor determining fitness is the daily amount of food available in bad weather, f_b . We thus present model predictions as a function of f_b . We emphasize that these predictions all pertain to a bird using the optimal foraging strategy $e(t)$ as computed using the above dynamic programming algorithms for each of the three models. This strategy determines how much food the bird obtains in a day, and hence also determines the dusk reserves level $X_1(t)$. In addition, the optimal strategy allows for the use of ‘emergency’ hypothermia in the minimal hypothermia model, and optimal employment of hypothermia in the optimal hypothermia model.

With no hypothermia, survival probability drops sharply for f_b below a critical level f_{b1} , where $f_{b1} = 3.16$ g for the baseline parameters (Fig. 2A). In this case, maximum daily net food intake ($\beta f_b - c_2 m_0$) in bad weather is insufficient to cover nocturnal energy requirements ($c_0 + c_b$). Thus the bird progressively loses energy reserves in bad weather, the result being catastrophic in sufficiently prolonged cold spells. To counter this energy reduction, the bird attempts to build up a high level of dusk reserves X_1 during good weather (Fig. 2B). Similar results were obtained by Lima (1986) using a simulation model.

Including the possibility of minimum hypothermia in the model greatly enhances winter survival probability (Fig. 2A), and also reduces the need to maintain high levels of fat reserves (Fig. 2B). A key factor determining the winter survival and fat reserves is the mortality rate associated with hypothermia. Predictably, lower hypothermia-induced mortality is associated with a higher survival probability (Fig. 2A). In addition, a lower mortality rate during hypothermia allows the use of higher levels of hypothermia, thus enabling a bird to maintain lower levels of reserves (Fig. 2B).

The use of minimal hypothermia fails, however, if availability of food during bad weather, f_b , is below a second critical level f_{b2} , where $f_{b2} = 1.16$ g. In this case, the bird is unable to obtain sufficient food per day to fuel diurnal plus nocturnal metabolic needs, regardless of the degree of hypothermia employed ($\beta f_b - c_2(x_0 + x) < 0.5 \times 1.16 - 0.028 \times 10 = 0.30 = c_0$). Hence the bird’s reserves steadily decline during a bad spell of weather, even though emergency hypothermia ensures short-term survival for brief cold spells.

The predictions of the optimal hypothermia model are identical to those of the minimal hypothermia model when f_b is above the threshold value of f_{b2} . Below that value, however, the predictions of the models are distinctly different, with optimal hypothermia exceeding the minimal level, resulting in higher levels of survival (Fig. 3A, B). The reason for this difference is that, with the minimal hypothermia model, hypothermia is used only

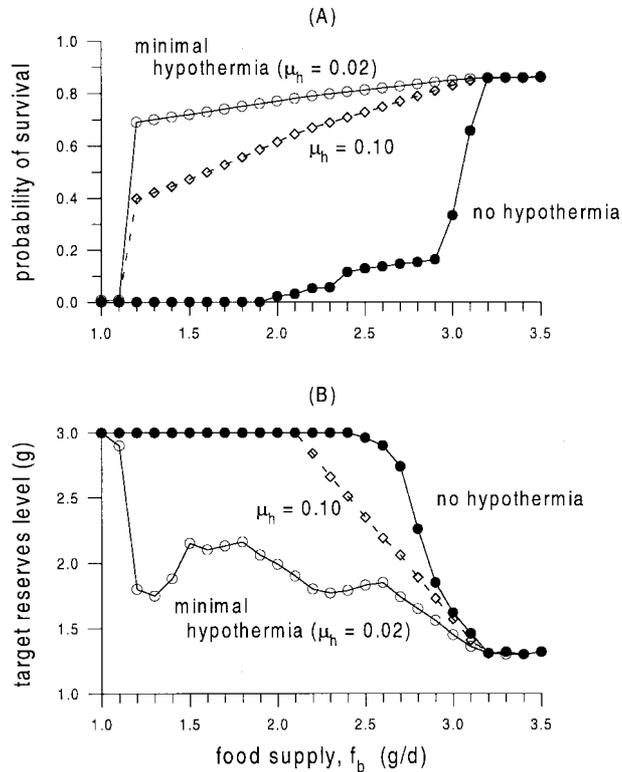


Fig. 2. (A) Probability of survival over 60 days in winter and (B) target dusk reserves $X_i(t)$ as functions of f_b = food supply accessible in bad weather. ●, Case 1 (no use of hypothermia); ○, Case 2 (minimal hypothermia, as in Fig. 1), $\mu_h = 0.02$; ◇, Case 2 (minimal hypothermia), $\mu_h = 0.10$.

to prevent overnight exhaustion of energy reserves, so whenever hypothermia is used, dawn reserves equal zero: $X(t+1) = 0$. In contrast, the optimal hypothermia model allows employment of an extra degree of hypothermia (Fig. 3B), which prevents dawn reserves from being exhausted immediately. Thus the bird can reduce the rate at which its reserves are exhausted during cold-weather spells, thereby increasing its overall chances of survival.

Combining the predictions shown in Figs 2 and 3, we conclude that, with the parameters and assumptions used:

- for $f_b > f_{b1} = 3.16$ g, hypothermia does not enhance survival;
- for $f_{b2} = 1.16$ g $< f_b < f_{b1}$, optimal hypothermia equals minimum hypothermia, and survival with minimal hypothermia is much higher than with no hypothermia;
- for $0.8 \leq f_b < f_{b2}$, optimal hypothermia exceeds minimal hypothermia, and greatly enhances survival probability relative to minimal hypothermia by preventing reserves from reaching zero except in a protracted spell of cold weather.

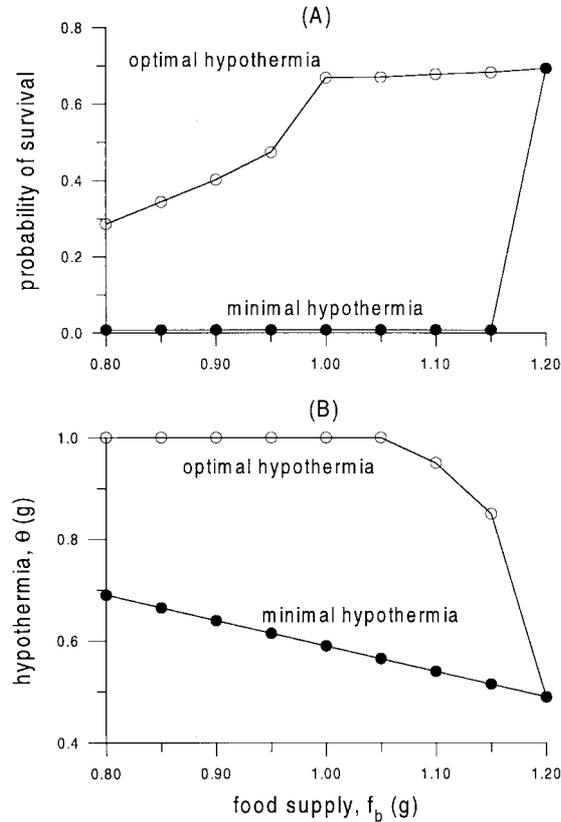


Fig. 3. (A) Probability of survival over 60 days and (B) degree of hypothermia θ on bad nights, as functions of f_b = food supply accessible in bad weather. ●, Case 2 (minimal hypothermia); ○, Case 3 (optimal hypothermia). Note change in scale of f_b -axis relative to Fig. 2. The curves for Cases 2 and 3 are identical for f_b values larger than depicted. Parameters as in Table 2; initial dawn reserves $x = 0.5$ g; number of previous days of bad weather $j = 1$.

DISCUSSION

Fat reserves and external food supplies

Our dynamic models help us to understand the fitness consequences of different adaptations that small birds are known to possess in order to survive harsh winter conditions. These adaptations, which include hoarding, foraging behaviour, fat reserves and hypothermia, are all interrelated in terms of costs and benefits. Conceptualizing the multiple trade-offs among alternative strategies is facilitated through the use of dynamic state variable models. (A simple analytical model of daily survival, while indicating the nature of the trade-off between foraging activity and hypothermia, could not fully address optimal energy management strategies in a fluctuating environment.) Here, hoarding strategies are treated only incidentally (see Brodin and Clark, 1997), but foraging, fat reserves and hypothermia are studied explicitly. For brevity, our discussion pertains explicitly only to the

possibility of insufficient food availability in inclement weather, but other model components such as high thermoregulation costs, c_{th} , low food quality, β , or increased frequency and duration of cold spells, would have similar implications.

Our models assume two effects of bad weather – increased thermoregulation costs and decreased availability of food. Under the extreme winter conditions we consider, fat reserves alone allow winter survival only if a bird has access to sufficiently large amounts of food during spells of bad weather. That is, even a small bird that lives under extremely cold winter conditions carries fat reserves sufficient for only a few very cold nights (King and Farner, 1966; Dawson and Marsh, 1988). Hence, such a bird must replenish a large portion of its energy reserves every day. If for any reason the bird progressively loses energy reserves during cold weather spells, then its chances of surviving the winter are much reduced. These results indicate the significance of strategies that affect the reliable supply of energy, such as long-term hoarding (to increase winter food availability, at least in good weather) or short-term rehoarding (for example, to provide concentrated small hoards in easily remembered and recovered locations).

Minimal and optimal hypothermia

Even minimal hypothermia can significantly increase winter survival probability compared to the use of fat reserves alone. This is because minimal hypothermia allows the bird to save on night-time energy expenditure when necessary. The degree to which hypothermia is employed depends on the rate of mortality associated with hypothermia relative to the mortality rate associated with fat reserves. A relatively higher rate of mortality during hypothermia results in less use of hypothermia and, correspondingly, higher target levels of dusk reserves (Fig. 2B). Hence, to understand further strategies of winter survival by small birds in northern latitudes, it is crucial to estimate the relative cost of hypothermia. The positive effect minimal hypothermia has on survival can explain the prevalence of the capacity to enter hypothermia under food shortage among birds (Walker *et al.*, 1983; Reinertsen and Haftorn, 1986; Wang, 1989; Reinertsen, 1996). That is, individuals of many species, even ones not under extreme winter conditions, may find themselves lacking sufficient energy reserves at dusk. Under such conditions, hypothermia may be the only means to prevent starvation.

The optimal hypothermia model suggests that, under a wide range of parameter values, wintering passerines should employ hypothermia only in emergencies, a prediction that concurs with some published data (Reinertsen and Haftorn, 1986; Reinertsen, 1996). However, the model has the additional twist that hypothermia is sometimes used to a greater degree than the minimum required for overnight survival, in order to decrease the rate at which reserves are reduced during spells of harsh weather. This also implies that birds employing optimal hypothermia can maintain higher levels of dawn reserves in midwinter when cold weather events are most prevalent. Indeed, it is known that birds maintain larger dawn reserves during harsh winters (Lehikoinen, 1987; Biebach, 1996; Cuthill and Houston, 1997), but the contribution of hypothermia to this phenomenon has not been empirically quantified. That is, higher levels of dawn fat reserves in mid-winter would be predicted even in species that do not employ hypothermia.

Our basic model specified maximum fat reserves as $x_{max} = 3$ g. It is likely, however, that Willow tits can carry greater loads of fat than this. Our model, therefore, might underestimate the benefits of carrying large reserves rather than using hypothermia. To test this

idea, we ran the models with $x_{\max} = 6$ g (see Table 3). Changing x_{\max} from 3 to 6 g increased fitness slightly (i.e. survival) when an inadequate food supply f_b resulted in very low fitness. However, it is clear from Table 3 that our original value of $x_{\max} = 3$ g is not a major determinant of model predictions; the advantages of hypothermia are much greater than those obtained by increased stores of fat. Of course, this conclusion is related to other model assumptions, particularly the relative magnitudes of mass-dependent predation risk while foraging, and the increased predation risk associated with using hypothermia. Empirical measurement of these risks would be invaluable, but may be difficult or impossible to obtain.

All our models incorporate a trade-off between maintaining high energy reserves and using hypothermia. In the single-day model, this trade-off involves only a comparison of the instantaneous costs of foraging and hypothermia (parameters k_1 , k_2 in Table 1). Hypothermia is avoided unless it is less costly, as an energy-saving method, than foraging is, as an energy-gaining method. Of course, some amount of daily input is always required, because hypothermia cannot reduce net energy expenditure to zero. Likewise, some hypothermia may be required if a bird's daily energy gain falls below its daily needs.

The trade-off between foraging and hypothermia is more complex in a dynamic, stochastic world. A high level of reserves reduces the frequency and amount of hypothermia required. But even if the instantaneous cost of hypothermia is high, relative to the costs of foraging for energy reserves, the occasional use of hypothermia when needed may be much less costly than the alternative strategy of maintaining sufficient body fat in winter to survive protracted periods of net energy loss, even if the latter is feasible. Thus, even though small animals may have relatively high daily energy requirements, maintaining fat levels well below the physiological maximum may well be an adaptive strategy, when used in combination with facultative hypothermia.

The importance of predation

An implicit prediction of our models is that, although wintering birds are at risk of dying from either starvation or predation, by far the leading source of mortality is predation (see Clark and Mangel, 2000, chapter 5). The reason for this prediction is that starvation is highly predictable – a bird that exhausts its energy supplies dies – and exhaustion of resources can be avoided, at least under normal weather fluctuations, by management of energy reserves and thermoregulation costs. Both strategies incur the risk of predation, but

Table 3. Fitness values $F(0.5, 1, 1)$ for the three dynamic models, under alternative constraints x_{\max} on maximum stored fat reserves

f_{bad}	No hypothermia		Minimal hypothermia		Optimal hypothermia	
	$x_{\max} = 3$	$x_{\max} = 6$	$x_{\max} = 3$	$x_{\max} = 6$	$x_{\max} = 3$	$x_{\max} = 6$
1.0 g	0	0	0.008	0.038	0.674	0.674
1.5 g	0.007	0.063	0.724	0.723	0.727	0.727
2.0 g	0.022	0.096	0.774	0.774	0.777	0.777
2.5 g	0.257	0.262	0.816	0.815	0.817	0.817
3.0 g	0.830	0.850	0.850	0.850	0.850	0.850

this is always probabilistic, not certain. In practice, however, an exception to this rule might occur as a result of an unusually prolonged spell of particularly bad weather, causing widespread starvation among local avifauna. Strategies designed to counter such conditions would be weakly selected, or not selected at all, given that such strategies would incur other costs, including increased predation risk.

There are no data available from which to estimate the three predation-risk coefficients, μ_1 , μ_2 , μ_h . Published values for survival rates of Willow tits studied between January and May 1997 in Southwestern Sweden were 91% for adults ($n=23$) and 48% for juveniles ($n=27$) (Ekman *et al.*, 1981). These values suggest that the absolute parameter values assumed here for predation risk on adults may be too high. On the other hand, the low survival rate for juveniles, who presumably suffer reduced access to food supplies under critical weather conditions (Clark and Ekman, 1995), suggests that fitness drops sharply when the parameter f_b is reduced. In Fig. 2, this drop occurs only when we assume a high value for the hypothermia coefficient μ_h , unless $f_b < 1.16$ g (in which case starvation does become an important cause of mortality). Ekman *et al.* (1981) assert that, in winter, 'juvenile willow tits are positively more often killed by predators than adults are', but whether this results from greater use of hypothermia, from carrying greater body fat, or from some other cause (such as being forced to forage in more exposed locations) is not clear. It is clear, however, that strong selection pressures should exist for both adults and juveniles to use a combination of energy management strategies that optimizes their overwinter survival probability.

Additional costs of hypothermia

Because of a lack of data, we made the simplifying assumption that night-time mortality rate is positively correlated with the current level of hypothermia. Although this is likely to be the case, hypothermia may incur other, perhaps more significant, costs. Hypothermia is associated with changes in the quality of sleep, most notably a reduction in rapid eye-movement sleep (Walker *et al.*, 1979, 1983; Graf *et al.*, 1989). The exact utility of rapid eye-movement sleep is unknown, but it is probably involved in recuperation of some bodily function (Horne, 1988; Amlaner and Ball, 1989). Hence, diminished rapid eye-movement sleep may cause a reduction in general alertness during the day, and perhaps also a long-term deterioration in body condition. Either of these effects can have a negative influence on foraging success and predator avoidance (see Dukas and Clark, 1995).

A few avian studies have indicated that birds attempt to maximize the quality of sleep. First, sleep in many birds involves a period of eye closure interrupted by 'peeks' of eye opening. Peeking allows a bird to scan the sleeping site for predators. Peeking rates and durations were monitored by Lendrem (1983, 1984) in two studies involving field observations of mallards, *Anas platyrhynchos*, and experimental manipulations of Barbary doves, *Streptopelia risoria*. Lendrem found that, when the perceived predation risk was lower, birds' peeking rates were lower, suggesting that peeking has negative effects on sleep which birds attempted to minimize. Secondly, some birds are capable of sleeping with one eye open and one hemisphere of the brain awake. The unihemispheric sleep allows these birds to sleep with one hemisphere and monitor predators with the other hemisphere at the same time. Rattenborg *et al.* (1999) found that mallards with lower perceived predation risk showed a 2.5-fold decrease in the proportion of time spent in unihemispheric sleep and a corresponding increase in bihemispheric sleep. This suggests that, compared with

bihemispheric sleep, unihemispheric sleep incurs some physiological costs that the birds attempt to minimize when possible.

It would be straightforward to develop an alternative dynamic model in which the effects of hypothermia are realized in terms of decreased body condition (but we have not done so). In this model, the costs of hypothermia would be spread over future days, rather than realized immediately. It is probable that the predictions of our present models would remain valid in the alternative case, at least in qualitative terms.

Ways of evaluating the models

Before testing any prediction about the optimal employment of hypothermia, one must evaluate critically the central assumption about the cost of hypothermia. One feasible although indirect way of assessing possible predation costs of hypothermia is to compare response to a model predator by birds that either sleep or undergo hypothermia. We predict a lower response rate and shorter response distance by individuals in hypothermia than sleep treatments. Such results would agree with our key assumption that hypothermia is associated with increased night-time predation rate. In addition, other costs of hypothermia could be assessed in a long-term study comparing key physiological and behavioural variables among treatments undergoing either regular sleep or hypothermia for a few months.

Our models suggest that a few measurable variables determine whether a bird should undergo hypothermia during a given night. First, if for any reason a bird does not have sufficient reserves for thermoregulation at regular sleep temperatures, it should enter hypothermia. Secondly, two closely related bird species may incur different hypothermia-related predation risks due to different sleeping habits (e.g. sleeping inside cavities or on branches) or differences in night-time predator activity. In that case, and assuming all other things being equal, birds will be more likely to enter hypothermia on a given winter night even when they have sufficient reserves if they belong to a population or species expected to experience a long winter with frequent spells of cold weather. Similarly, birds will be more likely to enter hypothermia on a given winter night even when they have sufficient reserves if they belong to a population or species with a higher uncertainty about food availability under bad weather conditions.

To summarize, the models analysed in this paper indicate that multiple aspects of energy management, including hoarding, foraging, fat storage and hypothermia, need to be considered jointly if we are to understand observed survival strategies in wintering birds. The dynamic state variable approach used here is highly appropriate for evaluating such interacting strategies, as well as others not explicitly considered here, such as social behaviour, territoriality and migration. The major insight of our models is that the optimal maintenance of fat reserves is insufficient for the survival of small birds under extreme winter conditions. Such birds must also have a relatively reliable supply of food, almost on a daily basis. When bad weather diminishes access to food, the optimal use of hypothermia is perhaps the only strategy enabling survival.

ACKNOWLEDGEMENTS

We thank Anders Brodin and an anonymous reviewer for detailed comments that led to an improved exposition throughout. The snow-covered ridges of Mt. Garibaldi kept us aware of the rigours of winter. We also thank Vladimir Pravosudov, who kindly sent us electronically a draft of a paper on

hypothermia by himself and J.R. Lucas, which will appear in the *Journal of Avian Biology*. This paper, which contains models and predictions fairly similar to ours, was received too late to be taken into account here.

REFERENCES

- Amlaner, C.J., Jr. and Ball, N.J. 1989. Avian sleep. In *Principles and Practice of Sleep Medicine* (M.H. Kryger, T. Roth and W.C. Dement, eds), pp. 50–63. Philadelphia, PA: W.B. Saunders.
- Bech, C. and Reinertsen, R.E., eds. 1988. *Physiology of Cold Adaptation in Birds*. New York: Plenum Press.
- Bednekoff, P.A. and Houston, A.I. 1994. Optimizing fat reserves over the entire winter: A dynamic model. *Oikos*, **71**: 408–415.
- Biebach, H. 1996. Energetics of winter and migratory fattening. In *Avian Energetics and Nutritional Ecology* (C. Carey, ed.), pp. 280–323. New York: Chapman & Hall.
- Brodin, A. and Clark, C.W. 1997. Long-term hoarding in the Paridae: A dynamic model. *Behav. Ecol.*, **8**: 178–185.
- Brodin, A. and Ekman, J. 1994. Benefits of food hoarding. *Nature*, **372**: 510.
- Clark, C.W. and Ekman, J. 1995. Dominant and subordinate fattening strategies: A dynamic game. *Oikos*, **75**: 205–212.
- Clark, C.W. and Mangel, M. 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford: Oxford University Press.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*, **12**: 119–129.
- Cohen, D. 1970. A theoretical model for the optimal timing of diapause. *Am. Nat.*, **104**: 389–400.
- Cohen, D. 1971. Maximizing final yield when growth is limited by time or limiting resources. *J. Theor. Biol.*, **33**: 299–307.
- Cuthill, I.C. and Houston, A.I. 1997. Managing time and energy. In *Behavioural Ecology* (J.R. Krebs and N.B. Davies, eds), pp. 97–120. Oxford: Blackwell.
- Dawson, W.R. and Marsh, R.L. 1988. Metabolic acclimatization to cold and season in birds. In *Physiology of Cold Adaptation in Birds* (C. Bech and R.E. Reinertsen, eds), pp. 83–94. New York: Plenum Press.
- Dukas, R. and Clark, C.W. 1995. Sustained vigilance and animal performance. *Anim. Behav.*, **49**: 1259–1267.
- Ekman, J., Cederholm, G. and Askenmo, C. 1981. Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P. cristatus*: A removal study. *J. Anim. Ecol.*, **50**: 1–9.
- Graf, R., Krishna, S. and Heller, H.C. 1989. Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.*, **256**: R733–R738.
- Hainsworth, F.R. and Wolf, L.L. 1978. The economics of temperature regulation and torpor in nonmammalian organisms. In *Strategies in Cold* (L.C.H. Wang and J.W. Hudson, eds), pp. 147–184. New York: Academic Press.
- Hainsworth, F.R., Collins, B.G. and Wolf, L.L. 1977. The function of torpor in humming-birds. *Physiol. Zool.*, **50**: 215–222.
- Hitchcock, C.L. and Houston, A.I. 1994. The value of a hoard: Not just energy. *Behav. Ecol.*, **5**: 202–205.
- Horne, J. 1988. *Why We Sleep*. Oxford: Oxford University Press.
- Houston, A.I. and McNamara, J.M. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scand.*, **24**: 205–219.
- Houston, A.I. and McNamara, J.M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- King, J.R. and Farner, D.S. 1966. The adaptive role of winter fattening in the white crowned sparrow with comments on its regulation. *Am. Nat.*, **100**: 403–418.

- Kruger, K., Prinzinger, R. and Schuchmann, K.L. 1982. Torpor and metabolism in hummingbirds. *Comp. Biochem. Physiol.*, **73A**: 679–689.
- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scand.*, **18**: 216–226.
- Lendrem, D.W. 1983. Sleeping and vigilance in birds. I. Field observations of the mallard (*Anas platyrhynchos*). *Anim. Behav.*, **31**: 532–538.
- Lendrem, D.W. 1984. Sleeping and vigilance in birds. II. An experimental study of the Barbary doves (*Streptopelia risoria*). *Anim. Behav.*, **32**: 243–248.
- Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology*, **67**: 377–385.
- Lucas, J.R. and Walter, L.R. 1991. When should chickadees hoard food? Theory and experimental results. *Anim. Behav.*, **41**: 579–601.
- McNamara, J.M. and Houston, A.I. 1990. The value of fat reserves and tradeoff between starvation and predation. *Acta Biotheor.*, **38**: 37–61.
- McNamara, J.M., Houston, A.I. and Krebs, J.R. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behav. Ecol.*, **1**: 12–23.
- McNamara, J.M., Houston, A.I. and Lima, S.L. 1994. Foraging routines of small birds in winter: A theoretical investigation. *J. Avian Biol.*, **25**: 287–302.
- Rattenborg, N.C., Lima, S.L. and Amlaner, C.J. 1999. Half-awake to the risk of predation. *Nature*, **397**: 398–399.
- Reinertsen, R.E. 1996. Physiological and ecological aspects of hypothermia. In *Avian Energetics and Nutritional Ecology* (C. Carey, ed.), pp. 125–157. New York: Chapman & Hall.
- Reinertsen, R.E. and Haftorn, S. 1983. Nocturnal hypothermia and metabolism in the willow tit *Parus montanus* at 63° N. *J. Comp. Physiol.*, **A151**: 109–118.
- Reinertsen, R.E. and Haftorn, S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol.*, **A156**: 655–663.
- Walker, L.E., Garber, A., Berger, R.J. and Heller, R.J. 1979. Sleep and estivation (shallow torpor): Continuous processes of energy conservation. *Science*, **204**: 1098–1100.
- Walker, L.E., Walker, J.M., Palca, J.W. and Berger, R.J. 1983. A continuum of sleep and shallow torpor in fasting doves. *Science*, **221**: 194–195.
- Wang, L.C.H. 1989. Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In *Advances in Comparative and Environmental Physiology*, Vol. 4 (L.C.H. Wang, ed.), pp. 361–401. Berlin: Springer-Verlag.
- Wang, L.C.H. and Hudson, J.W., eds. 1978. *Strategies in Cold*. New York: Academic Press.

