A MATHEMATICAL MODEL FOR THE ENERGY
ALLOCATION FUNCTION OF SLEEP

DISERTATION

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ABSTRACT

The function of sleep remains one of the greatest unsolved questions in biology. Schmidt [64] has proposed the unifying Energy Allocation Function of sleep, which posits that the ultimate function of sleep is effective energy allocation in the service of state-dependent division of labor, or repartitioning of metabolic operations. We present a mathematical model based on Schmidt’s Energy Allocation model.

The fundamental quantity we model is called biological debt ($D$). We define biological requirements ($R$) as the summation of maintenance obligations generated by all metabolic operations, biological investment ($I$) as the summation of completed functions servicing this requirements, and $D$ as the difference ($D = R - I$). We model $D$ as a discontinuous non-autonomous ordinary differential equation. We analyze bifurcations as well as existence and nonexistence of limit cycles. In order to apply the theory of averaging, we construct a smooth approximation to the equation for $D$, and show this approximation undergoes a saddle-node bifurcation of limit cycles.

We compare and contrast our model with the “two-process model” of sleep [9] and with empirical data of human neurobehavioural performance [48].

We define a division of labor parameter ($\lambda$) and use $D$ to develop an algorithm to compute the energy saved by sleep-wake cycling compared to continuous wakefulness. We quantify the contributions to energy savings from $\lambda$ and from metabolic rate reduction during sleep ($\rho$). We numerically compute energy savings with this method, finding substantially greater savings than previous estimates.
Some implications of the energy savings model include predictions that biological debt may govern sleep homeostasis; that short sleepers may increased metabolic rate in sleep compared to long sleepers, for whom energy savings may be primarily derived from metabolic rate reduction; and that dampening circadian amplitude during periods of sleep deprivation may be an adaptive feature.

We present an alternative energy savings calculation based on averaging theory and compare it to our original energy savings computation.

Finally, we develop a Markov Decision Process with a reward of net energy intake in order to find an optimal sleep-wake policy under a variety of conditions. We use this Markov Decision Process to optimize a policy under three different sets of conditions.
To my family. Without your love and support, I wouldn't have been able to make it this far.
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Chapter 1

INTRODUCTION

1.1 Biological Background on Sleep

The function of sleep remains one of the great unsolved questions in biology. We develop a mathematical model based on the proposition that energy allocation is the ultimate function of sleep [64]. Before we develop this model, we discuss some background on sleep (including prior theories) and review the Energy Allocation model. This background discussion largely follows [64].

1.1.1 Introduction

Sleep in most species can be defined using several common behavioral features, including species-specific posture and site, behavioral quiescence, elevated arousal threshold, regular daily occurrence influenced by a circadian clock, and rapid state reversibility [18, 32]. Furthermore, there is also an element of sleep homeostasis that includes compensation for sleep loss by both an increase in duration and intensity [61, 76]. Despite the recognition of sleep behavior across diverse phyla, there is no clear consensus regarding a fundamental underlying function of sleep in the animal kingdom. As sleep science pioneer Allan Rechtschaffen put it, “If sleep does not serve an absolutely vital function, then it is the biggest mistake the evolutionary process has ever made.” [60, 67]
There have been many proposed theories of sleep, some of which are discussed below. More thorough critiques of these hypotheses are given elsewhere [32,61].

1.1.2 Prior Theories of Sleep

Energy Conservation
One oft-cited theory on the function of sleep is energy conservation beyond that of quiet wakefulness [7,8]. However, REM sleep appears to be in conflict with this model, as it is a state of elevated brain activity. Furthermore, it has been argued that energy saved by metabolic rate reduction in sleep is inconsequential for this to be considered the primary function of sleep [32,61,86].

Immobilization
Another view is that sleep is an adaptive mechanism that keeps animals safe at a time when foraging is inefficient or dangerous, [49,62,82] and that also helps to conserve energy [69]. However, sleep has been observed in unsafe and exposed sites and may be even more dangerous than vigilant quiet wakefulness. In this hypothesis, sleep may actually considered to be maladaptive due to neurocognitive deficits during sleep and added sleep pressure following sleep deprivation, thereby increasing predation risk in wake [61].

Recuperation
Another common theory is that sleep is a time for recovery or recuperation [1,51,55]. Critics of this theory cite findings that whole-body synthesis of protein is greater in wake than in sleep and that protein synthesis is largely governed by feeding [13,14,24]. Furthermore, this hypothesis would predict that species with the largest bodies and brains would require the greatest amount of recovery. This is not the case, as large herbivores require the least amount of sleep, and those with the smallest bodies and
brains require the most sleep [68, 87]. It has also been proposed that restitution may occur to a similar degree in quiet wakefulness and sleep [31, 32].

**Neural network reorganization**

Other researchers think that sleep is “of the brain, by the brain, and for the brain” [28], or a time of neural network reorganization [4, 38–40, 42, 77–80]. Both REM and NREM potentially play specific roles in memory processing [71, 72, 81]. However, there are some species that show reductions in total sleep time for weeks at time during mating or migration seasons, but do not show reductions in mating success [43] nor deficits in learning operant tasks [59].

### 1.2 The Energy Allocation Model

In light of the hypotheses and evidence presented above and elsewhere, some have suggested that sleep may serve different functions for different species, even if no universal function is identified [12, 68]. However, the fact that sleep occurs throughout the diverse animal kingdom suggests that sleep has evolved to serve one underlying function in all species. Schmidt [64] has proposed a unifying theory of sleep: energy allocation. The Energy Allocation Model of Sleep is unifying in that it posits that many of the hypothesized functions of sleep are proximate functions; the ultimate function of sleep is optimal allocation of “limited energy resources to essential biological processes.” [64]

This theory is based on well-defined evolutionary principles in life history theory; namely, “all organisms have evolved to temporally allocate energy to basic functions such as growth, maintenance, and reproduction throughout their life histories from birth to death in a manner that maximizes reproductive output while meeting the
energy constraints of the ecological niche.” [63, 64] In the Energy Allocation model, this principle is applied on the shorter time scale of the circadian rest-activity cycle.

Some key elements of the Energy Allocation Model are as follows (quoted from [64]):

- Three energy allocation strategies or phenotypes are proposed: sleep-wake cycling; torpor; and continuous or predominant wakefulness (see Fig. 1.1). Each phenotype is associated with trade-offs regarding benefits and costs in an energy allocation economy, outlining the evolutionary selective pressures that influence expression of one or more phenotypes for a given species during its life history.

- Species employing the sleep-wake cycling phenotype have evolved to perform unique and essential biological processes during sleep so as to decrease the cumulative or peak energy requirements of wakefulness, dedicate more energy reserves to the needs of waking niche exploitation, and reduce total daily energy expenditure (EE) through a repartitioning of energy resources across behavioral states. Species employing torpor, by contrast, experience the greatest energy savings, but many critical biological processes normally performed during sleep are sacrificed in torpor. Although continuous wakefulness may maximize niche exploitation, it harbors the greatest burden on daily EE.

- NREM and REM sleep perform the same core function in endotherms. Both sleep states reallocate energy utilization away from the high demands of wakefulness into other essential biological operations when the organism is outside of its temporal niche of waking specialization and/or when it is no longer profitable to expend energy on waking-related activities. REM sleep, by eliminating both thermoregulatory defense and skeletal muscle tone, enhances energy allocation
for somatic and CNS-related functions, thereby allowing even greater energy resources to be dedicated for REM sleep-specific biological activities.

In the Energy Allocation Model of Sleep, energy is allocated to two broad categories: waking effort (vigilance and mobility) and biological investment (all other biological activities not requiring vigilance or mobility). Waking effort includes foraging to capture energy, vigilance to avoid predation, and reproduction. Biological investment includes cellular repair and housekeeping, neural network reorganization, immune function, and growth or maintenance of reproductive organs and supporting neurophysiology. For a more comprehensive discussion, see [64].

In the sleep-wake cycling phenotype, energy to waking effort is upregulated during wake and downregulated during sleep, while energy to biological investment is upregulated during sleep and downregulated during wake (see Figure 1.1). It is these state-dependent processes properly coupled with circadian-dependent processes that provides efficient energy utilization. The model posits that selection favors those organisms that allocate energy in a way that maximizes survival and reproduction, and thus the ultimate function of sleep is energy allocation.
Figure 1.1: Three phenotypes of energy allocation proposed in the energy allocation mode. A) Wake-Predominant or constant wakefulness, B) Sleep-Wake Cycling, and C) Torpor or Hibernation. WE: Waking Effort; BI: Biological Investment. (Found in [64].)
1.3 The Mathematical Model

For the model presented in this section, we assume that maintenance requirements are inherent to all biological systems if operational integrity is to be preserved. In our model, biological requirements ($R$) represent the summation of maintenance obligations generated by all metabolic operations. Biological investments ($I$), in contrast, are defined as the summation of completed functions servicing these requirements (see discussion in section 1.2). We also assume that natural selection favors organisms that manage energy expenditures while limiting biological debt ($D$), the difference between $R$ and $I$.

1.3.1 Equations

We model biological requirements ($R$) and biological investments ($I$) with the following differential equations (the dot represents the time derivative):

$$\dot{R} = p_W r_W(t) + p_B(t) r_B(t)$$
$$\dot{I} = r_B(t) x_B(t),$$

(1.3.1)

where $t$ is time (in days), $p_W$ is the cost (to biological requirements) for spending energy on waking effort, $p_B$ is the cost (to biological requirements) for spending energy on biological investments, and $x_B$ is the conversion from energy to biological investments. Furthermore, $r_W$ and $r_B$ are the rates of energy deployed toward waking effort and biological investments, respectively. Comparing an organism to a machine, $r_W$ refers to the rate of energy deployed for “running” the machine (energy acquisition, predation avoidance and reproduction), whereas $r_B$ to “maintenance” and “upgrading” of the machine [64]. Note that both $r_W$ and $r_B$ contribute to growth in biological requirements, but only $r_B$ contributes to biological investment.
As biological debt ($D$) is the difference between these quantities ($D = R - I$), we may also write

$$\dot{D} = p_W r_W(t) + (p_B(t) - x_B(t)) r_B(t).$$  \hspace{1cm} (1.3.2)

We assume the cost to pay back $D$ is proportional to $D$, so we define

$$p_B(t) = p_B D(t),$$  \hspace{1cm} (1.3.3)

where $p_B$ is a proportionality constant. We also define

$$x_B(t) = C(t) \frac{D(t)}{1 + D(t)^2},$$  \hspace{1cm} (1.3.4)

where $C(t)$ is a periodic function representing the circadian system. Furthermore, let $0 \leq t_s \leq 1$ be the proportion of time spent in sleep. We assume that wake occurs during the first part of the day ($0 \leq t < 1 - t_s$) and sleep occurs during the last part of the day ($1 - t_s \leq t < 1$). In light of this, we define $r_W$ and $r_B$ to be

$$r_W(t) = \sum_{n=-\infty}^{\infty} r_{Ww}[n,n+1-t_s](t) + r_{Ws}[n+1-t_s,n+1](t)$$  \hspace{1cm} (1.3.5)

$$r_B(t) = \sum_{n=-\infty}^{\infty} r_{Bw}[n,n+1-t_s](t) + r_{Bs}[n+1-t_s,n+1](t),$$  \hspace{1cm} (1.3.6)

where $\chi$ is the indicator function, $r_{Ww}$ is $r_W$ in wake, $r_{Ws}$ is $r_W$ in sleep, $r_{Bw}$ is $r_B$ in wake, and $r_{Bs}$ is $r_B$ in sleep.

Substituting equations 1.3.3 and 1.3.4 into 1.3.2, we get a differential equation in terms of $D$, namely

$$\dot{D} = p_W r_W(t) + p_B r_B(t) D(t) - r_B(t) C(t) \frac{D(t)}{1 + D(t)^2}.$$  \hspace{1cm} (1.3.7)

We consider $C$ of the form

$$C(t) = m_C (1 - \alpha \sin (2\pi (t - 0.25 + 0.5t_s))),$$  \hspace{1cm} (1.3.8)

where $m_C$ is the mean value of $C$, and $\alpha$ determines the amplitude. We require $0 \leq \alpha < 1$, so that $C(t) > 0$ for all $t$. The argument of sine in (1.3.8) was chosen so
that the circadian curve has a period of one day and so that the peak of the circadian curve occurs in the middle of the sleep phase. We also require all of the parameters in the equation above to be nonnegative.

The conversion factor (1.3.4) contains two independent efficiency multipliers. First, the circadian process, \(C(t)\), participates as an efficiency multiplier in the conversion of energy to biological investments, providing greater efficiency during the habitual sleep phase and less during the wake phase. This circadian model is intended to reflect the assumed role of circadian molecular clocks in regulating metabolic processes at the local or cellular level. The second efficiency multiplier component of \(x_B(t)\) is \(\frac{D}{1 + D^2}\), which is dependent on the level of \(D\) in order to model a reactive homeostasis in the conversion of energy to \(I\). The curve of this reactive homeostatic component is low at low levels of \(D\), peaks at some moderate level of \(D\), (here, at \(D = 1\)) and decreases asymptotically to 0 as \(D \to \infty\); this shape reflects greatest efficiency in energy conversion at some moderate level of \(D\) but with decreasing efficiency at either low or high levels of \(D\).

1.3.2 Comparison to the Two-Process Model

We briefly mention here the Two-Process Model of sleep regulation proposed by Borbély [9, 10] to compare and contrast to our model. The two processes proposed are a sleep homeostat (process S) and a circadian process (process C). The sleep homeostat increases while awake (increasing pressure to sleep) and decreases while asleep. The model proposes that the wake-sleep cycled is governed by process S and process C. Process C, an oscillator, acts as a "gate" for process S; when S interacts with C, activity state changes.

In the mathematical model presented above, we think of biological debt (\(D\)) as
analogous to process $S$, a homeostatic process. However, in contrast with the two-process model, the circadian component in our model model ($C$) does not act as a “gate.” Instead, it has a multiplier effect on efficiency of biological investment.

### 1.3.3 Existence and Uniqueness of Solutions

Because of $r_W$ and $r_B$, (1.3.7) is not continuous (hence not differentiable) in $t$ at “transition points,” points where the organism enters the sleep state or the wake state. Therefore, the problem is to find an absolutely continuous function that satisfies (1.3.7) except on the Lebesgue measure-zero set of “transition points.” This is referred to as a solution “in the sense of Carathéodory” [26] or “in the extended sense” [15]. We show that such a solution exists, is unique, and is smooth between transition points.

To show this, we need to show that the right hand side of (1.3.7) is Lipschitz continuous. We then show that solutions exist for all time when $r_W$ and $r_B$ are constant, and then we “cut and paste” these solutions together over successive intervals. First, we need a lemma.

**Lemma 1.3.1.** For all $(x, y) \in \mathbb{R}^2$,

\[
\left| \frac{xy - 1}{(1 + x^2)(1 + y^2)} \right| \leq 1
\]

**Proof.** Make a polar change of coordinates: $x = r \cos \theta$ and $y = r \sin \theta$ where $r \geq 0$ and $0 \leq \theta < 2\pi$. Then

\[
\left| \frac{xy - 1}{(1 + x^2)(1 + y^2)} \right| = \left| \frac{r^2 \sin \theta \cos \theta - 1}{r^4 \sin^2 \theta \cos^2 \theta + r^2 \sin^2 \theta + r^2 \cos^2 \theta + 1} \right|
\]

\[
= \left| \frac{0.5r^2 \sin 2\theta - 1}{0.25r^4 \sin^2 2\theta + r^2 + 1} \right| \leq \frac{0.5r^2 + 1}{0.25r^4 \sin^2 2\theta + r^2 + 1}
\]
\[
\leq \frac{0.5r^2 + 1}{r^2 + 1} \leq 1
\]

**Proposition 1.3.2.** Let \( f : \mathbb{R}^2 \to \mathbb{R} \) be defined
\[
f(t, x) = p_W r_{Wc} + p_B r_{Bc} x - r_{Bc} C(t) \frac{x}{1 + x^2},
\]
with \( C(t) \) as defined in (1.3.8), and \( p_W, p_B, r_{Wc}, \) and \( r_{Bc} \) nonnegative constants. \( f \) is globally Lipschitz in the second variable, uniformly with respect to the first. An upper bound for the Lipschitz constant is \( r_{Bc}(p_B + m_C(1 + \alpha)) \).

**Proof.** For \( x, y \in \mathbb{R} \),
\[
|f(t, x) - f(t, y)| = \left| p_B r_{Bc} (x - y) + r_{Bc} C(t) \left( \frac{y}{1 + y^2} - \frac{x}{1 + x^2}\right) \right|
\]
\[
= r_{Bc} \left| p_B (x - y) + C(t) \left( \frac{y - x + xy(x - y)}{(1 + x^2)(1 + y^2)} \right) \right|
\]
\[
\leq r_{Bc} |x - y| \left( p_B + C(t) \left| \frac{xy - 1}{(1 + x^2)(1 + y^2)} \right| \right)
\]
\[
\leq r_{Bc} (p_B + m_C(1 + \alpha)) |x - y|
\]
where we used Lemma 1.3.1 and the fact that \( C \) is bounded above by \( m_C(1 + \alpha) \).

We cite the following theorem without proof to get existence of solutions when \( r_W \) and \( r_B \) are constant.

**Theorem 1.3.3.** (Corollary 2.6, [75]) Suppose \( f : \mathbb{R}^2 \to \mathbb{R} \) is globally Lipschitz in the second argument, uniformly with respect to the first. Define
\[
L(t) = \sup_{x \neq y \in \mathbb{R}} \frac{|f(t, x) - f(t, y)|}{|x - y|},
\]

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and suppose that $\int_{-T}^{T} L(t) \, dt < \infty$ for all $T > 0$. Then there exists a unique solution to the initial value problem

$$\dot{x} = f(t, x)$$

$$x(t_0) = x_0$$

for all $t \in \mathbb{R}$.

The following result, a corollary to Theorem 1.3.3, is that our system has a solution that exists and is unique, provided $r_W$ and $r_B$ are constant.

**Corollary 1.3.4.** The solution to the initial value problem

$$\begin{cases}
\dot{x} = p_W r_{Wc} + p_B r_{Bc} x - r_{Bc} C(t) \frac{x}{1 + x^2} \\
x(t_0) = x_0
\end{cases} \quad (1.3.9)$$

exists for all $t \in \mathbb{R}$, is smooth on $\mathbb{R}$, and is unique.

**Proof.** By Proposition 1.3.2, $L(t) \leq r_{Bc}(p_B + m_C(1 + \alpha))$, a constant. Existence and uniqueness follows from Theorem 1.3.3. Smoothness is clear from the differential equation. \qed

Finally, we get that solutions to (1.3.7) with initial value $D(0) = D_0$ exist by “gluing” solutions of (1.3.9) together.

**Proposition 1.3.5.** The solution to the initial value problem

$$\begin{cases}
\dot{D} = p_W r_W(t) + p_B r_B(t) D(t) - r_B(t) C(t) \frac{D(t)}{1 + D(t)^2} \\
D(0) = D_0
\end{cases} \quad (1.3.10)$$

exists for all $t \in \mathbb{R}$ and is unique.
Proof. On the interval $[0, 1 - t_s)$, $r_W$ and $r_B$ are constant, so Corollary 1.3.4 gives existence and uniqueness on the interval $[0, 1 - t_s]$. Say that $D(1 - t_s) = D_1$. Corollary 1.3.4 may be used again for $t \in [1 - t_s, 1)$ with this initial condition. Proceed like this for every interval $[n, n + 1 - t_s)$ and $[n + 1 - t_s, n + 1)$, $n \in \mathbb{Z}$ to get the result for all $t \in \mathbb{R}$. \qed

Figure 1.2: Solution to (1.3.10) (with biological requirements ($\mathcal{R}$) and biological investments ($\mathcal{I}$) separated out, see (1.3.1)). In this plot, $\mathcal{I}$ is reset to 0 and $\mathcal{R}$ is reset to the value of $D$ at the start of each day. The initial value was chosen so $D$ is periodic (see Chapter 2). Initial value: $D(0) \approx 0.241$. Parameter values: $p_W = 1.3$, $p_B = 0.7$, $t_s = 1/3$, $r_{Ww} = 0.65$, $r_{Bw} = 0.35$, $r_{Ws} = 0.175$, $r_{Bs} = 0.525$, $m_C = 5$, $\alpha = 0.5$.\[ \]
Chapter 2

ANALYSIS

2.1 Two Dimensional Reformulation

In this section, we assume \( \mathcal{D} \) is a solution of (1.3.10) with some (possibly given) initial condition. We first establish the fact that once \( \mathcal{D} \) is positive, it stays positive.

**Lemma 2.1.1.** Suppose \( b^* = \mathcal{D}(t^*) > 0 \) for some \( t^* \). Then \( \mathcal{D}(t) > 0 \) for all \( t > t^* \).

*Proof.* Let \( \mathcal{D}_\ell(t, b^*) \) be the solution to the initial value problem

\[
\begin{cases}
\dot{\mathcal{D}}_\ell(t) = p_B r_B(t) \mathcal{D}_\ell(t) - C(t) r_B(t) \frac{\mathcal{D}_\ell(t)}{1 + \mathcal{D}_\ell(t)^2} \\
\mathcal{D}_\ell(t^*) = b^*
\end{cases}
\]

(2.1.1)

Now \( \mathcal{D}_\ell = 0 \) is a fixed point of the differential equation in (2.1.1), so its trajectory will not cross 0. Hence \( \mathcal{D}_\ell(t) > 0 \) for all \( t > t^* \). Since \( \dot{\mathcal{D}}(t) \geq \dot{\mathcal{D}}_\ell(t) \) for all \( t \), and \( \mathcal{D}(t^*) = \mathcal{D}_\ell(t^*) \) we see that \( \mathcal{D}(t) \geq \mathcal{D}_\ell(t) > 0 \) for all \( t > t^* \). \( \square \)

**Lemma 2.1.2.** Suppose \( \mathcal{D}(t^*) = 0 \) for some \( t^* \), and suppose \( r_W(t^*) > 0 \). Then \( \mathcal{D}(t) > 0 \) for all \( t > t^* \).

*Proof.* Since (1.3.10) implies that \( \dot{\mathcal{D}}(t^*) = p_W r_W(t^*) > 0 \), and \( \dot{\mathcal{D}} \) is right-continuous (see (1.3.5) and (1.3.6)), there exists \( \varepsilon > 0 \) such that \( \dot{\mathcal{D}}(t) > 0 \) on the open interval \( (t^*, t^* + \varepsilon) \). So \( \mathcal{D} \) is increasing on that interval. Thus, \( \mathcal{D}(t) > 0 \) for \( t \in (t^*, t^* + \varepsilon) \). The result follows from Lemma 2.1.1. \( \square \)
The previous two lemmata give the following

**Proposition 2.1.3.** Suppose \( D(t^*) \geq 0 \) for some \( t^* \), and suppose \( r_W(t) > 0 \) for all \( t \). Then \( D(t) > 0 \) for all \( t > t^* \).

Equation 1.3.10 is a non-autonomous system that appears to have periodic solutions for some initial values. In order to study this property, we wish to analyze an associated two-dimensional autonomous system. By Proposition 2.1.3, when \( D \) starts positive, it stays positive. Therefore, we may consider an associated system in polar coordinates, namely

\[
\begin{aligned}
\dot{D} &= p_W r_W \left( \frac{\theta}{2\pi} \right) + p_B r_B \left( \frac{\theta}{2\pi} \right) D - C \left( \frac{\theta}{2\pi} \right) r_B \left( \frac{\theta}{2\pi} \right) \frac{D}{1 + D^2}, \\
\dot{\theta} &= 2\pi,
\end{aligned}
\]

where we consider \( D \) to be the radius and \( \theta \) to be the angle in polar coordinates. Here, 1 revolution is 1 day. We are interested in limit cycles when \( D > 0 \). Equivalently, we are interested in periodic solutions to (1.3.10). By abuse of language, we may refer to “limit cycles” of the one-dimensional system when there is no chance of confusion.

### 2.2 Nonexistence and Existence of Limit Cycles

For (2.1.2) to have a limit cycle, we must have

\[
\int_0^1 \dot{D}(t) \, dt = 0
\]

for some initial condition. Ruling out the uninteresting case of \( r_W = r_B = 0 \), this means that for part of the day, \( D \) is increasing, and part of the day it is decreasing. Rewriting (1.3.7) as

\[
\dot{D}(t) = p_W r_W(t) + r_B(t)D(t) \left( p_B - \frac{C(t)}{1 + D(t)^2} \right),
\]
we see heuristically that $D$ is can decrease only if $p_B$ and $D$ are "small enough," and $C(t)$ is "large enough". We aim to make some of this precise in this section.

For here and the remainder of the paper, define

\[
\begin{align*}
    r_{W,\text{min}} &= \min \{r_{Ww}, r_{Ws}\} \\
    r_{W,\text{max}} &= \max \{r_{Ww}, r_{Ws}\} \\
    r_{B,\text{min}} &= \min \{r_{Bw}, r_{Bs}\} \\
    r_{B,\text{max}} &= \max \{r_{Bw}, r_{Bs}\}
\end{align*}
\]

and define

\[
\begin{align*}
    \overline{r}_W &= (1 - t_s)r_{Ww} + t_s r_{Ws} \\
    \overline{r}_B &= (1 - t_s)r_{Bw} + t_s r_{Bs}.
\end{align*}
\]  

(2.2.2)

First, we establish a condition on parameters for which there exist no limit cycles; namely, when $p_B$ is greater than or equal to the maximum value of $C$ (in our case, $(1 + \alpha)m_C$). If we think of $p_B$ as the "cost" of $r_B$ and $C(t)$ as "return on investment," then we say there are no limit cycles when the cost of spending energy is always greater then the return on investment.

**Proposition 2.2.1.** If $p_B \geq (1 + \alpha)m_C$, $D(0) > 0$, and $r_{W,\text{min}} > 0$, then

\[
\dot{D}(t) \geq p_Wr_{W,\text{min}} > 0
\]

for all $t > 0$. Thus, $\lim_{t \to \infty} D(t) = \infty$.

**Proof.** By Lemma 2.1.1, $D(t) > 0$ for all $t > 0$. Because $r_B(t) \geq 0$ and $D(t) > 0$, it suffices to show (see equation (2.2.1)) that $p_B > \frac{C(t)}{1 + D(t)^2}$ for all $t > 0$. But $C(t) \leq (1 + \alpha)m_C$ for all $t$, so

\[
\frac{C(t)}{1 + D(t)^2} \leq \frac{(1 + \alpha)m_C}{1 + D(t)^2} < (1 + \alpha)m_C \leq p_B.
\]
Therefore,
\[
\dot{D}(t) \geq p_W r_W(t) \geq p_W r_{W,\min} > 0,
\]
and
\[
D(t) \geq b_0 + t p_W r_{W,\min} \to \infty
\]
as \( t \to \infty \).

Because we are primarily interested in limit cycles, Proposition 2.2.1 tells us we only want to consider parameter values where \( p_B < (1 + \alpha)m_C \).

The following lemma and corollary give us a point, \( \beta \), such that when \( D > \beta \), it stays outside of \( \beta \), and in fact escapes to infinity.

**Lemma 2.2.2.** Suppose \( p_B < (1+\alpha)m_C \), and let \( \beta = \sqrt{\frac{(1 + \alpha)m_C}{p_B}} - 1 \). If \( D(t^*) > \beta \) for some \( t^* \), then \( D(t) > \beta \) for all \( t > t^* \).

**Proof.** If \( D(t^*) > \beta \), then
\[
\frac{C(t^*)}{1 + D(t^*)^2} < \frac{(1 + \alpha)m_C}{1 + \beta^2} = p_B.
\]
Thus,
\[
\dot{D}(t^*) = p_W r_W(t^*) + r_B(t^*) D(t^*) \left( p_B - \frac{C(t^*)}{1 + D(t^*)^2} \right) \geq 0. \tag{2.2.4}
\]

Now suppose, toward a contradiction, that \( N = \{ t > t^*: D(t) \leq \beta \} \) is non-empty. Let \( t_0 = \inf N \). Since \( D \) is continuous, \( D(t_0) = \beta \). By the mean value theorem, there exists \( t_1 \in (t^*, t_0) \) such that \( \dot{D}(t_1) < 0 \). But, since \( D(t_1) > \beta \), we see (as in (2.2.4)), that \( \dot{D}(t_1) \geq 0 \).

**Proposition 2.2.3.** Suppose \( p_B < (1 + \alpha)m_C \), and let \( \beta = \sqrt{\frac{(1 + \alpha)m_C}{p_B}} - 1 \). If \( r_{W,\min} > 0 \) and \( D(t^*) > \beta \) for some time \( t^* \), then
\[
\dot{D}(t) \geq p_W r_{W,\min} > 0
\]
for all \( t > t^* \). Thus, \( \lim_{t \to \infty} D(t) = \infty \).
Proof. By Lemma 2.2.2, $D(t) > \beta$ for all $t > t^*$. So, for $t > t^*$,

$$\frac{C(t)}{1 + D(t)^2} < \frac{(1 + \alpha)m_c}{1 + \beta} = p_B.$$ 

Thus,

$$\dot{D}(t) = p_Wr_W(t) + r_B(t)D(t) \left( p_B - \frac{C(t)}{1 + D(t)^2} \right) \geq p_Wr_{W,min} > 0.$$ 

The final statement follows as in Proposition 2.2.1. □

Proposition 2.2.3 gives an important condition for “escape from homeostasis” [54]. Namely, if $D > \beta$, the organism will never recover.

The next two propositions give conditions on the parameters for which limit cycles do not exist.

**Proposition 2.2.4.** Suppose $\bar{r}_W > 0$ and $r_{B,max} > 0$. If $p_W \geq \frac{m_C \cdot r_{B,max}}{2 \bar{r}_W}$, then (1.3.10) has no limit cycle for $D > 0$.

Proof. Suppose to the contrary, that (1.3.10) has a limit cycle for $D > 0$. Then, for some positive initial condition,

$$0 = \int_0^1 \dot{D}(t) \, dt = p_W((1 - T_s)r_W + T_s r_{W,s}) + \int_0^1 p_Br_B(t)D(t) - r_B(t)C(t) \frac{D(t)}{1 + D(t)^2} \, dt.$$ 

Using the facts that $\frac{x}{1 + x^2} < \frac{1}{2}$ for $x > 0$ and $\int_0^1 C(t) = m_c$, we see

$$\int_0^1 r_B(t)D(t) \, dt = -\frac{p_W}{p_B} \frac{r_W}{\bar{r}_W} + \frac{1}{p_B} \int_0^1 r_B(t)C(t) \frac{D(t)}{1 + D(t)^2} \, dt$$

$$\leq -\frac{p_W}{p_B} \frac{r_W}{\bar{r}_W} + \frac{r_{B,max}}{2p_B} \int_0^1 C(t) \, dt$$

$$= \frac{1}{p_B} \left( -p_W \frac{r_W}{\bar{r}_W} + \frac{m_C}{2} \right).$$

If $p_W \geq \frac{m_C \cdot r_{B,max}}{2 \bar{r}_W}$, then $\int_0^1 r_B(t)D(t) \, dt \leq 0$, a contradiction to Proposition 2.1.3. □
Proposition 2.2.5. If
\[
\frac{(m_C(1 + \alpha) - p_B)^3}{p_B} \leq p_W^2 \left( \frac{\bar{r}_W}{r_{B,\text{max}}} \right)^2,
\]
then (1.3.10) has no limit cycle for \( D > 0 \).

Proof. Suppose to the contrary, that (1.3.10) has a limit cycle for \( D > 0 \). Then, for some positive initial condition, (as we saw in Proposition 2.2.4)
\[
\int_0^1 r_B(t) D(t) dt = -\frac{p_W}{p_B} \bar{r}_W + \frac{1}{p_B} \int_0^1 r_B(t) C(t) \frac{D(t)}{1 + D(t)^2} dt
\leq -\frac{p_W}{p_B} \bar{r}_W + \frac{m_C(1 + \alpha)}{p_B} \int_0^1 r_B(t) D(t) dt.
\]

Rearranging the above inequality gives
\[
\left(1 - \frac{m_C(1 + \alpha)}{p_B}\right) \int_0^1 r_B(t) D(t) \leq -\frac{p_W}{p_B} \bar{r}_W.
\]

Since we have a limit cycle for \( D > 0 \), Proposition 2.2.1 implies that \( \left(1 - \frac{m_C(1 + \alpha)}{p_B}\right) < 0 \). Therefore,
\[
\int_0^1 r_B(t) D(t) dt \geq \frac{p_W \bar{r}_W}{m_C(1 + \alpha) - p_B},
\]
hence
\[
\int_0^1 D(t) dt \geq \frac{p_W \bar{r}_W}{(m_C(1 + \alpha) - p_B)r_{B,\text{max}}}
\]

Now, rearranging our assumed inequality gives
\[
\frac{p_W \bar{r}_W}{(m_C(1 + \alpha) - p_B)r_{B,\text{max}}} \geq \sqrt{\frac{m_C(1 + \alpha)}{p_B}} - 1.
\]

But then \( D(t) \geq \sqrt{\frac{m_C(1 + \alpha)}{p_B}} - 1 \), for some \( t \). By Proposition 2.2.2, (1.3.10) has no limit cycle for \( D > 0 \), a contradiction. \qed
In the preceding propositions, note that we fail to have a limit cycle when \( m_C \) is “too small.” We now want to show that if \( m_C \) is “large enough,” there do exist limit cycles. To do this, we need a modified version of the Poincaré-Bendixson Theorem that works for discontinuous ODE.

**Theorem 2.2.6.** (Theorem 1, [50]) Consider the planar autonomous system

\[
\dot{x} = f(x). \tag{2.2.5}
\]

Let \( \Omega \subseteq \mathbb{R}^2 \) satisfy the following conditions

(A1) \( \Omega \) is an open domain in \( \mathbb{R}^2 \), divided into a finite number of open sub-domains \( \Omega_i \), such that \( \bigcup \Omega_i = \Omega \).

(A2) If \( \overline{\Omega}_i \) and \( \overline{\Omega}_j \) are not disjoint and \( i \neq j \), then \( \overline{\Omega}_i \cap \overline{\Omega}_j = \Gamma_{ij} \), where \( \Gamma_{ij} \) (joint boundaries) are piecewise smooth.

(A3) \( f \) is Lipschitz in all sub-domains \( \Omega_i \) and possibly discontinuous along \( \Gamma_{ij} \) (also called discontinuity curves).

(A4) The vector field \( f \) defines a direction in each point in \( \Omega \). In particular, at every point of \( \Gamma_{ij} \) the vector field \( f(x) \) specifies into which \( \Omega_i \) the flow is directed.

Further suppose \( f \) is bounded in \( \Omega \). Suppose that \( K \) is a compact region in \( \Omega \), containing no fixed points of (2.2.5). If all solutions of (2.2.5) are in \( K \), for all \( t \geq t_0 \), then (2.2.5) has a closed orbit in \( K \).

**Note 1.** We need only use Theorem 2.2.6 when \( 0 < t_s < 1 \). If \( t_s = 0 \) or \( t_s = 1 \), we may use the normal Poincaré-Bendixson Theorem. In what follows, we assume \( 0 < t_s < 1 \).

We claim that there exists \( m_C \) the system (2.1.2) satisfies the conditions of Theorem 2.2.6 on a suitable domain, and therefore has a limit cycle.
First, for $\varepsilon > 0$, define $\Omega^\varepsilon = \{(D, \theta) : 0 \leq D < 1 + \varepsilon\}$. Define

$$\Omega^\varepsilon_w = \Omega^\varepsilon \cap \{(D, \theta) : D > 0 \text{ and } 0 < \theta < 2\pi(1 - t_s)\}$$

$$\Omega^\varepsilon_s = \Omega^\varepsilon \cap \{(D, \theta) : D > 0 \text{ and } 2\pi(1 - t_s) < \theta < 2\pi\}$$

to represent wake time and sleep time, respectively (see Fig. 2.1). It is clear that

$$\overline{\Omega^\varepsilon_w \cup \Omega^\varepsilon_s} = \overline{\Omega^\varepsilon}$$

, and that

$$\Gamma_{w,s} = \overline{\Omega^\varepsilon} \cap \{(D, \theta) : (D \geq 0 \text{ and } \theta = 0) \text{ or } (D \geq 0 \text{ and } \theta = 2\pi(1 - t_s))\}$$

is piecewise smooth (in fact, piecewise linear). So conditions (A1) and (A2) are satisfied. Condition (A4) is also clear. We prove (A3) in a lemma.
Lemma 2.2.7. Let \( f : \mathbb{R}^2 \to \mathbb{R}^2 \) be defined by the system (2.1.2). \( f \) is Lipschitz in \( \Omega^x_w \) and \( \Omega^y_s \).

Proof. \( \Omega^x_w \) and \( \Omega^y_s \) were chosen so that \( r_B \) and \( r_W \) are constant in each subdomain. We thus use \( r_{Bc} \) and \( r_{Wc} \) for these constants, and prove the result for both domains simultaneously.

For given \( (D_1, \theta_1) \neq (D_2, \theta_2) \), define
\[
L = \frac{d_p (f(D_1, \theta_1), f(D_2, \theta_2))}{d_p ((D_1, \theta_1), (D_2, \theta_2))}
\]
where \( d_p \) is the Euclidean metric on polar coordinates (given by the law of cosines).

By the definitions for \( f \) and \( d_p \), we see
\[
L = \frac{|p_B r_{BC} (D_2 - D_1) - r_{BC} \left( C \left( \frac{\theta_1}{2\pi} \right) \frac{D_2}{1+D_2^2} - C \left( \frac{\theta_1}{2\pi} \right) \frac{D_1}{1+D_1^2} \right) |}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)}}
\]

By the triangle inequality, we have
\[
L \leq \frac{r_{BC} \left( |p_B| |D_2 - D_1| + \left| C \left( \frac{\theta_1}{2\pi} \right) \frac{D_2}{1+D_2^2} - C \left( \frac{\theta_1}{2\pi} \right) \frac{D_1}{1+D_1^2} \right| + \left| C \left( \frac{\theta_1}{2\pi} \right) \frac{D_2}{1+D_2^2} - C \left( \frac{\theta_1}{2\pi} \right) \frac{D_1}{1+D_1^2} \right| \right)}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)}}
\]

As seen in the proof of Proposition 1.3.2, we may bound the third summand of the numerator:
\[
L \leq \frac{r_{BC} \left( |p_B| |D_2 - D_1| + \frac{D_2}{1+D_2^2} \left| C \left( \frac{\theta_1}{2\pi} \right) \frac{D_2}{1+D_2^2} - C \left( \frac{\theta_1}{2\pi} \right) \frac{D_1}{1+D_1^2} \right| + \left| C \left( \frac{\theta_1}{2\pi} \right) \frac{D_2}{1+D_2^2} - C \left( \frac{\theta_1}{2\pi} \right) \frac{D_1}{1+D_1^2} \right| \right)}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)}}
\]

Also, because the sine function is Lipschitz, and \( C \) is a shift and a dilation of the sine function, \( C \) is also Lipschitz, say with Lipschitz constant \( L_C \). We have
\[
L \leq r_{BC} \left( \frac{(p_B + m C(1 + \alpha)) |D_2 - D_1|}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)}} + \frac{D_2}{1+D_2^2} L_C |\theta_2 - \theta_1| \right)
\]

We bound each of these summands separately. First, note that
\[
\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)} \geq \sqrt{D_1^2 + D_2^2 - 2D_1D_2} = |D_2 - D_1|, \quad (2.2.6)
\]
so that
\[
\frac{(p_B + m_C(1 + \alpha)) |D_2 - D_1|}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos (\theta_2 - \theta_1)}} \leq p_B + m_C(1 + \alpha).
\]

For the second summand, use the substitution \(\Theta = |\theta_2 - \theta_1|\). We prove boundedness by cases. The case \(\Theta = 0\) is trivial. So suppose \(\Theta > 0\), and \(D_1 = D_2\). Then
\[
\frac{\frac{D_2}{1+D_2} L_C \Theta}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos \Theta}} = \frac{\frac{D_2}{1+D_2} L_C \Theta}{\sqrt{2D_2^2 (1 - \cos \Theta)}} = \frac{L_C \Theta}{(1 + D_2^2) \sqrt{2(1 - \cos \Theta)}} \leq \frac{L_C \Theta}{\sqrt{2(1 - \cos \Theta)}}.
\]

We see, by L'Hospital’s Rule, that
\[
\lim_{\Theta \to 0} \frac{\Theta^2}{1 - \cos \Theta} = \lim_{\Theta \to 0} \frac{2\Theta}{\sin \Theta} = \lim_{\Theta \to 0} \frac{2}{\cos \Theta} = 2,
\]
So \(\lim_{\Theta \to 0} \frac{\Theta}{\sqrt{1 - \cos \Theta}} = \sqrt{2}\). Because \(0 < t_s < 1\), we have
\[
0 \leq \Theta \leq 2\pi \max \{ (1 - t_s), t_s \} < 2\pi.
\]
From this, we see that \(\frac{L_C \Theta}{\sqrt{2(1 - \cos \Theta)}}\) is bounded above by compactness.

For the case \(D_1 \neq D_2\), \(0 < \Theta < |D_1 - D_2|\), we again use (2.2.6) along with the fact that \(\frac{D_2}{1+D_2} < 0.5\) to see
\[
\frac{\frac{D_2}{1+D_2} L_C \Theta}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos \Theta}} \leq \frac{0.5L_C \Theta}{|D_2 - D_1|} < 0.5L_C.
\]
Finally, for the case \(D_1 \neq D_2\), \(\Theta \geq |D_1 - D_2|\), we see that since \(\Theta\) is bounded below, the distance between the two points must be bounded below. But this gives boundedness of
\[
\frac{\frac{D_2}{1+D_2} L_C \Theta}{\sqrt{D_1^2 + D_2^2 - 2D_1D_2 \cos \Theta}} \leq \frac{L_C \Theta}{\sqrt{2(1 - \cos \Theta)}}
\]
since \(\Theta\) is bounded and the distance between two points is the denominator of the above expression.

Therefore, \(L\) is bounded above, and \(f\) is Lipschitz. \(\square\)
Having proven all of the conditions in Theorem 2.2.6, we have the following:

**Proposition 2.2.8.** If \( r_{B,\text{min}} > 0 \), there exists \( m^*_C > \frac{p_B}{1+\alpha} \) such that for all \( m_C > m^*_C \), \( f: \mathbb{R}^2 \to \mathbb{R}^2 \) (defined by (2.1.2)) has a stable limit cycle in \( K = \{(D,\theta): D \leq 1\} \), the closed unit disk.

*Proof.* By Proposition 2.2.1, if \( m^*_C \leq \frac{p_B}{1+\alpha} \), \( f \) has no limit cycle. By the discussion above and Lemma 2.2.7, \( f \) and \( \Omega^\varepsilon \) satisfy conditions (A1)-(A4) in Theorem 2.2.6. Furthermore, since \( f \) is continuous on the compact sets \( \overline{\Omega}^\varepsilon_w \) and \( \overline{\Omega}^\varepsilon_s \), \( f \) is bounded on \( \overline{\Omega}^\varepsilon = \overline{\Omega}^\varepsilon_w \cup \overline{\Omega}^\varepsilon_s \), hence bounded on \( K \subset \overline{\Omega}^\varepsilon \). Also, \( f \) has no fixed points, since \( \dot{\theta} \) is a nonzero constant.

Consider the boundary of \( K \), the unit circle. On this boundary,
\[
\dot{D} = p_W r_W \left( \frac{\theta}{2\pi} \right) + p_B r_B \left( \frac{\theta}{2\pi} \right) - 0.5p_B \left( \frac{\theta}{2\pi} \right) C \left( \frac{\theta}{2\pi} \right) \\
\leq p_W r_{W,\text{max}} + p_B r_{B,\text{max}} - 0.5p_B r_{B,\text{min}} m_C(1-\alpha),
\]

since \( C(t) > m_C(1-\alpha) \) for all \( t \). Therefore, if
\[
m_C > \frac{p_W r_{W,\text{max}} + p_B r_{B,\text{max}}}{0.5r_{B,\text{min}}(1-\alpha)},
\]
then \( \dot{D} < 0 \), and the trajectory stays in \( K \). Therefore, by Theorem 2.2.6, there is a stable limit cycle in \( K \).

We can make a slightly stronger statement about the existence of limit cycles.

**Proposition 2.2.9.** Suppose that a stable limit cycle exists for \( f \) for some \( m^*_C \), Call this limit cycle \( \mathcal{D}^*_s \). Then for all \( m_C > m^*_C \), a stable limit cycle exists inside the region bounded by \( \mathcal{D}^*_s \).

*Proof.* Choose \( \varepsilon > 0 \) so that \( \mathcal{D}^*_s \) is in \( \Omega^\varepsilon \). Choose \( K \) to be the compact set in the plane inside \( \mathcal{D}^*_s \), and suppose \( m_C > m^*_C \). Along \( \mathcal{D}^*_s \), the border of \( K \), we see \( \dot{D} < \dot{D}^*_s \). Thus, the trajectory stays in \( K \). So by Theorem 2.2.6, there exists a stable limit cycle in \( K \).
Proposition 2.2.8 tells us that the set $\mathcal{A} = \{m_C \geq 0: f \text{ has a stable limit cycle}\}$ is nonempty, while Proposition 2.2.9 tells us it is connected. Therefore, a bifurcation occurs at $\inf \mathcal{A}$. We may also say something about unstable limit cycles by considering the system as $t \to -\infty$.

**Proposition 2.2.10.** Suppose $r_{B, \min} > 0$ and $m_C > \frac{p_B}{1 + \alpha}$ is large enough so that a stable limit cycle exists. Call this limit cycle $D_s$. Define $K$ to be the compact set inside the disk of radius $\beta = \sqrt{\frac{(1 + \alpha) m_C}{p_B} - 1}$ centered at the origin and outside of the curve $D_s$. There exists an unstable limit cycle in the interior of $K$.

**Note 2.** We know that $D_s^\ast$ is inside the disk of radius $\beta$ centered at the origin by Proposition 2.2.3

**Proof.** The limit cycle $D_s$ is stable, so there exists $\varepsilon > 0$ such that the curve $D_s^\varepsilon = D_s + \varepsilon$ is in the stable set of $D_s$ and inside the disk of radius $\beta$. Thus, as $t$ moves in a negative direction in (2.1.2), the trajectory starting on $D_s^\varepsilon$ moves into $K^\varepsilon$, the set inside the disk of radius $\beta$ and outside the curve $D_s^\varepsilon$. By Proposition 2.2.3, the trajectory starting on the circle of radius $\beta$ also moves into $K^\varepsilon$. Defining $\Omega$ to be the disk of radius $\beta + 1$ centered at the origin, and $\Omega_w$ and $\Omega_s$ as before, we see that the “reverse” system (2.1.2) satisfies the conditions of Theorem 2.2.6 by proofs similar to those above. Therefore, there is an unstable limit cycle in $K^\varepsilon$. \[\square\]

Proposition 2.2.10 gives us a clue as to what type of bifurcation is happening. We see that for “small enough” $m_C$, no limit cycles exist (e.g. if $m_C < \frac{p_B}{1 + \alpha}$, see Proposition 2.2.1), whereas if $m_C$ is “large enough,” a stable and an unstable limit cycle exist. This suggests a saddle-node bifurcation of limit cycles. One proof approach is via the averaging theorem. However, this theorem requires that the system be “smooth enough,” but our system is not even continuous! We therefore
provide a smooth approximation to our system and show there is a saddle node bifurcation of limit cycles in this smoothed system by averaging.

## 2.3 Smooth Approximation

We want to provide a smooth \((C^\infty)\) approximation to the discontinuous \(r_W\) and \(r_B\).

To this end, define

\[
\Phi_0(t) = \begin{cases} 
\exp \left( -\frac{1}{1 - t^2} \right) & \text{for } |t| < 1 \\
0 & \text{otherwise}
\end{cases}
\]

**Proposition 2.3.1.** \(\Phi_0(t)\) is smooth and compactly supported.

**Proof.** It is clear \(\Phi_0(t)\) is compactly supported and smooth everywhere except at \(t = \pm 1\). We first show that it is continuous at these points. Indeed,

\[
\lim_{t \to 1^-} \exp \left( -\frac{1}{1 - t^2} \right) = 0 \quad (2.3.1)
\]

and

\[
\lim_{t \to 1^+} \exp \left( -\frac{1}{1 - t^2} \right) = 0.
\]

Thus, \(\lim_{t \to \pm 1} \Phi_0(t) = 0\).

The function \(g(t) = \exp \left( -\frac{1}{x} \right)\) is infinitely differentiable, with all derivatives being continuous at 0 (see [23], I.3.10). Thus, all derivatives of \(\Phi_0\) are continuous at \(\pm 1\).

\[\Box\]

For \(\delta > 0\), define

\[
\Phi(t, \delta) = \Phi_0 \left( \frac{2}{\delta} t \right),
\]

so that \(\Phi\) is supported on \(\left[ -\frac{\delta}{2}, \frac{\delta}{2} \right]\). We define

\[
W_w(t, \delta) = (r_{W_w} - r_{W_s}) \frac{\Phi(t, \delta)}{\int_{-\infty}^{\infty} \Phi(\tau, \delta) \, d\tau}.
\]
and

\[ W_s(t, \delta) = (r_{Ws} - r_{Ww}) \Phi(t - (1 - t_s), \delta) \int_{-\infty}^{\infty} \Phi(\tau, \delta) \, d\tau. \]

We also define

\[ W(t, \delta) = \sum_{n=\infty}^{\infty} W_w(t - n, \delta) + W_s(t - n, \delta). \]

Restrict \( \delta < \min \left\{ \frac{1 - t_s}{2}, \frac{t_s}{2} \right\} \), so that the intervals of support for the \( W_w \) and \( W_s \) do not overlap. With this restriction, need not worry about issues of convergence in the definition of \( W \). See Figure 2.3 for a plot.

![Graph of W](image)

Figure 2.2: Graph of \( W \). Parameters: \( t_s = \frac{1}{3}, r_{Ww} = 0.65, r_{Ws} = 0.175, \delta = 0.1 \)

**Lemma 2.3.2.** \( W \) is smooth, 1-periodic, and \( \int_0^1 W(t, \delta) \, dt = 0. \)

**Proof.** Clearly, \( W \) is smooth because \( W_w \) and \( W_s \) are smooth. Periodicity is clear by re-indexing:

\[ W(t + 1, \delta) = \sum_{n=\infty}^{\infty} W_w(t - n + 1, \delta) + W_s(t - n + 1, \delta) = W(t, \delta). \]
Finally, noting that \( W_w(t, \delta) = -W_s(t + (1 - t_s), \delta) \), we have

\[
\int_0^1 W(t, \delta) \, dt = \int_0^{\delta/2} W_w(t, \delta) \, dt + \int_{(1-t_s)-\delta/2}^{(1-t_s)+\delta/2} W_s(t, \delta) \, dt + \int_{1-\delta/2}^1 W_w(t+1, \delta) \, dt
\]

\[
= \int_{-\delta/2}^{\delta/2} W_w(t, \delta) \, dt + \int_{(1-t_s)-\delta/2}^{(1-t_s)+\delta/2} W_s(t, \delta) \, dt
\]

\[
= \int_{-\delta/2}^{\delta/2} W_w(t, \delta) \, dt + \int_{-\delta/2}^{\delta/2} -W_w(t, \delta) \, dt
\]

\[
= 0
\]

With these properties in mind, we use \( W \) to define a smooth approximation to \( r_w \) that is equal to \( r_w \) outside of small intervals.

\[
\tilde{r}_W(t, \delta) = \frac{r_{W_w} + r_{W_s}}{2} + \int_0^t W(\tau, \delta) \, d\tau.
\]

We now prove some properties about \( \tilde{r}_W \).

**Proposition 2.3.3.** \( \tilde{r}_W \) is smooth and 1-periodic in \( t \). Outside of \([n - \delta, n + \delta]\) and \([n + (1 - t_s) - \delta, + (1 - t_s) - \delta]\), for \( n \in \mathbb{Z} \) and small \( \delta \), we have \( r_W(t) = \tilde{r}_W(t, \delta) \).

Thus, for fixed \( t \),

\[
\lim_{\delta \to 0^+} \tilde{r}_W(t, \delta) = r_W(t).
\]

Furthermore,

\[
\int_0^1 \tilde{r}_W(t, \delta) \, dt = \overline{r_W} = \int_0^1 r_W(t) \, dt
\]

**Proof.** Smoothness is immediate from Lemma 2.3.2. The lemma also implies

\[
\tilde{r}_W(t + 1, \delta) = \frac{r_{W_w} + r_{W_s}}{2} + \int_0^{t+1} W(\tau, \delta) \, d\tau
\]

\[
= \frac{r_{W_w} + r_{W_s}}{2} + \int_0^t W(\tau, \delta) \, d\tau + \int_t^{t+1} W(\tau, \delta) \, d\tau
\]
\[
\begin{align*}
= r_{Ww} + r_{Ws} + \int_0^t W(\tau, \delta) \, d\tau + \int_0^1 W(\tau, \delta) \, d\tau \\
= r_{Ww} + r_{Ws} + \int_0^t W(\tau, \delta) \, d\tau \\
= \tilde{r}_W(t, \delta),
\end{align*}
\]
so \(\tilde{r}_W\) is 1-periodic.

Next, note that
\[
\begin{align*}
\int_{-\infty}^{\infty} W_w(t, \delta) \, dt &= \int_{-\delta/2}^{\delta/2} W_w(t, \delta) = r_{Ww} - r_{Ws} \\
\int_{-\infty}^{\infty} W_s(t, \delta) \, dt &= \int_{(1+t_s) - \delta/2}^{(1+t_s) + \delta/2} W_s(t, \delta) \, dt = r_{Ws} - r_{Ww}.
\end{align*}
\]
Since \(W_w\) is even, we have
\[
\tilde{r}_W(\delta/2, \delta) = \frac{r_{Ww} + r_{Ws}}{2} + \int_0^{\delta/2} W_w(\tau, \delta) \, d\tau = \frac{r_{Ww} + r_{Ws}}{2} + \frac{r_{Ww} - r_{Ws}}{2} = r_{Ww},
\]
and since \(W\) is zero on \((\delta/2, (1 - t_s) - \delta/2)\), \(\tilde{r}_W(t, \delta) = r_{Ww}\) on the same interval.

Furthermore,
\[
\tilde{r}_W((1 - t_s) + \delta/2) = r_{Ww} + \int_{(1+t_s) - \delta/2}^{(1+t_s) + \delta/2} W_s(\tau, \delta) \, d\tau = r_{Ww} + r_{Ws} - r_{Ww} = r_{Ws},
\]
and since \(W\) is zero on \(((1 - t_s) + \delta/2, 1 - \delta/2)\), \(\tilde{r}_W(t, \delta) = r_{Ws}\) on the same interval.

The above shows the statement is true on the the interval \([0, 1]\). To finish the proof, we use Lemma 2.3.2, which says \(\int_0^1 W(t, \delta) \, dt = 0\). Thus, \(r_W(t) = \tilde{r}_W(t, \delta)\) outside of the stated small intervals.

For the value of the integral, we use the result above, and note that since \(\tilde{r}_W\) is 1-periodic, that
\[
\int_{1-\delta/2}^{1} \tilde{r}_W(t, \delta) \, dt = \int_{-\delta/2}^{0} \tilde{r}_W(t, \delta) \, dt.
\]
Therefore, we have (letting \(t_w = 1 - t_s\)),
\[
\begin{align*}
\int_{0}^{1} \tilde{r}_W(t, \delta) \, dt &= \int_{-\delta/2}^{\delta/2} \tilde{r}_W(t, \delta) \, dt + \int_{\delta/2}^{t_w - \delta/2} \tilde{r}_W(t, \delta) \, dt + \int_{t_w - \delta/2}^{t_w + \delta/2} \tilde{r}_W(t, \delta) \, dt + \int_{t_w + \delta/2}^{1 - \delta/2} r_{Ws} \, dt
\end{align*}
\]
\[= \delta \frac{r_{w w} + r_{w s}}{2} + r_{w w}(1 - t_s - \delta) + \delta \frac{r_{w w} + r_{w s}}{2} + r_{w w}(t_s - \delta)\]

\[= \delta (r_{w w} + r_{w s} - r_{w w} - r_{w s}) + r_{w w}(1 - t_s) + r_{w s} t_s\]

\[= \overline{r}_W\]

Figure 2.3: Graph of \(r_W\) (dark blue) and \(\overline{r}_W\) (light blue). Parameters: \(t_s = \frac{1}{3}\), \(r_{w w} = 0.65\), \(r_{w s} = 0.175\), \(\delta = 0.1\)

To get a similar approximation for \(r_B\), we define

\[B_w(t, \delta) = (r_{B w} - r_{B s}) \frac{\Phi(t, \delta)}{\int_{-\infty}^{\infty} \Phi(t, \delta) \, d\tau}\]

and

\[B_s(t, \delta) = (r_{B s} - r_{B w}) \frac{\Phi(t - (1 - T_s), \delta)}{\int_{-\infty}^{\infty} \Phi(t, \delta) \, d\tau}.\]

Define

\[B(t, \delta) = \sum_{n=-\infty}^{\infty} B_w(t - n, \delta) + B_s(t - n, \delta).\]
From this, we can get an (smooth) approximation for $r_B$:

$$\tilde{r}_B(t, \delta) = \frac{r_{Bw} + r_{Bs}}{2} + \int_0^t B(\tau, \delta) \, d\tau.$$ 

Analogous results to Proposition 2.3.3 hold for $\tilde{r}_B$. As the proofs are the same, we omit them.

**Proposition 2.3.4.** $\tilde{r}_B$ is smooth and 1-periodic in $t$. Outside of $[n - \delta, n + \delta]$ and $[n + (1 - t_s) - \delta, +(1 - t_s) - \delta]$, for $n \in \mathbb{Z}$ and small $\delta$, we have $r_B(t) = \tilde{r}_B(t, \delta)$.

Thus, for fixed $t$,

$$\lim_{\delta \to 0^+} \tilde{r}_B(t, \delta) = r_B(t).$$

Furthermore,

$$\int_0^1 \tilde{r}_B(t, \delta) \, dt = \overline{r_B} = \int_0^1 r_B(t) \, dt$$

We wish to analyze the “smoothed” system

$$\frac{d \tilde{D}}{dt} = p_w \tilde{r}_W(t) + p_B \tilde{r}_B(t) \tilde{D}(t) - \tilde{r}_B(t) C(t) \frac{\tilde{D}(t)}{1 + \tilde{D}(t)^2}. \quad (2.3.2)$$

Proof of existence and uniqueness of solutions to (2.3.2) is similar to that of (1.3.7).

### 2.4 Averaging

Much of the discussion in this section follows [25], Chapter 4.

Consider $f$ of the form

$$\dot{x} = \varepsilon f(x, t); \quad x \in \mathbb{R}, \quad \varepsilon > 0 \text{ small}, \quad (2.4.1)$$

where $f : \mathbb{R}^2 \to \mathbb{R}$ is $C^\infty$, bounded on bounded sets, and of period $T > 0$ in $t$. The associated autonomous averaged system is defined as

$$\dot{y} = \varepsilon \frac{1}{T} \int_0^T f(y, t) \, dt := \varepsilon \overline{f}(y). \quad (2.4.2)$$

In this situation we have
Theorem 2.4.1. (The Averaging Theorem, Theorem 4.1.1, [25]) There exists a $C^\infty$ change of coordinates $x = y + \varepsilon w(y, t, \varepsilon)$ under which 2.4.1 becomes

$$
\dot{y} = \varepsilon \tilde{f}(y) + \varepsilon^2 f_1(y, t, \varepsilon),
$$

(2.4.3)

where $f_1$ is of period $T$ in $t$. Moreover

(i) If $x(t)$ and $y(t)$ are solutions to (2.4.1) and (2.4.2) based at $x_0, y_0$, respectively, at $t = 0$, and $|x_0 - y_0| = O(\varepsilon)$, then $|x(t) - y(t)| = O(\varepsilon)$ on a time scale $t \sim 1/\varepsilon$.

(ii) If $p_0$ is a hyperbolic fixed point of (2.4.2) then there exists $\varepsilon_0 > 0$ such that, for all $0 < \varepsilon < \varepsilon_0$, (2.4.1) possesses a unique hyperbolic periodic orbit $\gamma_\varepsilon(t) = p_0 + O(\varepsilon)$ of the same stability type as $p_0$. ($\gamma_\varepsilon$ may be a trivial periodic orbit, $\gamma_\varepsilon(t) \equiv p_0$).

(iii) If $x^*(t) \in W^s(\gamma_\varepsilon)$ is a solution of (2.4.1) lying in the stable manifold of the hyperbolic periodic orbit $\gamma_\varepsilon = p_0 + O(\varepsilon)$, $y^*(t) \in W^s(p_0)$ is a solution of (2.4.2) lying in the stable manifold of the hyperbolic fixed point $p_0$ and $|x^*(0) - y^*(0)| = O(\varepsilon)$, then $|x^*(t) - y^*(t)| = O(\varepsilon)$ for $t \in [0, \infty)$. Similar results apply to solutions lying in the unstable manifolds on the time interval $t \in (-\infty, 0]$.

For given small $\delta > 0$, let $f : \mathbb{R}^2 \to \mathbb{R}$ be defined

$$
f(x, t) = p_W \tilde{r}_W(t, \delta) + p_B \tilde{r}_B(t, \delta)x - \tilde{r}_B(t, \delta)C(t) \frac{x^2}{1 + x^2} + x^2 + y^2.
$$

Because $\tilde{r}_W$, $\tilde{r}_B$, and $C$ are each 1-periodic, $f$ is 1-periodic in $t$. Furthermore, $f$ is $C^\infty$, and bounded on bounded sets. We compute

$$
\bar{f}(y) = \int_0^1 f(y, t) \, dt = p_W \bar{r}_W + p_B \bar{r}_B y - \bar{r}_B C(t) \frac{y}{1 + y^2},
$$

where

$$
\bar{r}_B = \int_0^1 \tilde{r}_B(t, \delta)C(t) \, dt.
$$

(2.4.4)
Note that Propositions 2.3.3 and 2.3.3 were used above. Also note that

\[(1 - \alpha) m_C \tilde{r}_B \leq \tilde{r}_{BC} \leq (1 - \alpha) m_C \tilde{r}_B. \tag{2.4.5}\]

We compare the non-averaged system

\[\dot{x} = \varepsilon \left( p_W \tilde{r}_W(t, \delta) + p_B \tilde{r}_B(t, \delta) x - \tilde{r}_B(t, \delta) C(t) \frac{x}{1 + x^2} \right) \tag{2.4.6}\]

and the averaged system

\[\dot{y} = \varepsilon \left( p_W \tilde{r}_W + p_B \tilde{r}_B y - \tilde{r}_{BC} \frac{y}{1 + y^2} \right) \tag{2.4.7}\]

The fixed points of (2.4.7) are the zeroes of the cubic polynomial

\[f_p(y) = p_B \tilde{r}_B y^3 + p_W \tilde{r}_W y^2 + (p_B \tilde{r}_B - \tilde{r}_{BC}) y + p_W \tilde{r}_W. \tag{2.4.8}\]

Thus, there are either 1, 2, or 3 distinct real fixed points of (2.4.7).

For \(m_C > 0\), there is one and only one negative fixed point of (2.4.7). To see this, we use Descartes’ rule of signs with \(f_p(-y)\). If \(m_C\) is large enough so that \(\tilde{r}_{BC} \geq p_B \tilde{r}_B\), then Descartes’ rule of signs tells us that there is one and only one negative root for \(f_p\). On the other hand, if it is the case that \(\tilde{r}_{BC} < p_B \tilde{r}_B\), then Descartes’ rule of signs tells us that \(f_p\) has either one or three negative roots. If there were three negative roots, then \(f_p\) would have two negative zeroes. However, we have

\[f_p'(y) = p_B \tilde{r}_B y^2 - \tilde{r}_{BC} \frac{1 - y^2}{(1 + y^2)^2}, \tag{2.4.9}\]

which has at most one negative zero, namely

\[-\sqrt{- \frac{2 \tilde{r}_{BC} p_B + \tilde{r}_{BC}}{2 p_B \tilde{r}_B} \sqrt{8 \tilde{r}_B \tilde{r}_B \tilde{r}_{BC} + \tilde{r}_{BC}^2}}\]

when the argument inside the big square root is positive. Therefore, we rule out the case of three negative roots, and there must be only one.

We consider the discriminant of (2.4.8),
$-4p_B\tilde{r}_B^4(p_B - \tilde{r}_{BC})^3 + p_B^2\tilde{r}_B^2(p_B - \tilde{r}_{BC})^2$

$$+ 18p_B\tilde{r}_B^2p_W\tilde{r}_B^2(p_B - \tilde{r}_{BC}) - 4p_W^4\tilde{r}_W^4 - 27p_B^2p_W^2p_W^2 \quad (2.4.10)$$

Viewing this as a cubic in $(p_B - \tilde{r}_{BC})$, we see that if $\tilde{r}_{BC}$ is large enough, there are 3 real solutions to the cubic, hence 2 positive fixed points of (2.4.7). In light of (2.4.5), we may say if $m_C$ is large enough, there are two positive fixed points. These are a pair of hyperbolic fixed points, one stable and one unstable (because $f_p$ has positive leading coefficient).

Thus, for $\varepsilon > 0$ small enough and $m_C$ large enough, there exists a pair of hyperbolic periodic orbits for the smoothed system, one stable and one unstable, by Theorem 2.4.1.

### 2.5 Bifurcations

The discussion in the previous sections suggests a bifurcation, with $m_C$ as a bifurcation parameter. Indeed, this is the case. First, we re-write (2.4.6) and (2.4.7) with dependence on $m_C$:

$$\dot{x} = \varepsilon \left( p_W\tilde{r}_W(t,\delta) + p_B\tilde{r}_B(t,\delta)x - \tilde{r}_B(t,\delta)C(t,m_C)\frac{x}{1 + x^2} \right) \quad (2.5.1)$$

$$\dot{y} = \varepsilon \left( p_W\tilde{r}_W + p_B\tilde{r}_B - \tilde{r}_{BC}(m_C)\frac{y}{1 + y^2} \right) \quad (2.5.2)$$

**Theorem 2.5.1.** (Theorem 4.3.1, [25]) If (2.5.2) undergoes a saddle-node bifurcation at $m_C = m^*_C$, then, for $m_C$ near $m^*_C$ and $\varepsilon$ sufficiently small, the Poincaré map of (2.5.1) also undergoes a saddle-node bifurcation.

We only need to show that (2.5.2) undergoes a saddle-node bifurcation. For large enough $m_C$, there are a pair of fixed points, one stable, one unstable. Furthermore, if $m_C = 0$, then $\tilde{r}_{BC} = 0$ and (2.4.10) is negative. Therefore, by the intermediate value
theorem and the mean value theorem, there exists $m^*_C$ such that (2.4.10) is 0 and has a positive derivative (note that $\frac{\partial r_{BC}}{\partial m_C} > 0$). As the fixed points are solutions of the cubic (2.4.8), as $m_C$ decreases through $m^*_C$, these fixed points coalesce and annihilate each other. Thus, there is a saddle-node bifurcation.

By Theorem 2.5.1, for $\varepsilon$ small enough, the Poincaré map of (2.5.1) also undergoes a saddle-node bifurcation. Thus, (2.5.1) undergoes a saddle-node bifurcation of limit cycles.

In the next chapter, we use the “non-smoothed” system to compute energy savings afforded by sleep. We return to the smoothed system in Chapter 4, where we give an alternate way to compute energy savings based on averaging.
Chapter 3
ENERGY SAVINGS

3.1 Background

As we discuss in Chapter 1, sleep has long been considered an energy conservation strategy similar to torpor or hibernation [2, 8, 68]. This current perspective views metabolic rate reduction during sleep as the mechanism of energy savings. However, fundamental shortcomings have prevented the broad acceptance of sleep as an energy conservation strategy. Contrary to a downregulation of biological processes anticipated by this theory, it is now well established that diverse functions become upregulated during sleep (compared to wake), establishing sleep as a highly active metabolic state. These upregulated functions in sleep include macromolecule biosynthesis, intracellular transport and membrane repair [11, 46], neural network reorganization or memory consolidation [4, 42, 71, 79], immune function [34] and restorative processes [17, 51, 84]. Moreover, the current energy conservation hypothesis has been criticized as providing only limited energy savings. To illustrate, an 8 h metabolic rate reduction of 15-30% during sleep compared to quiet wakefulness results in a 5-15% decrease in total daily energy expenditure [37, 61, 85], a finding often cited as only a “cup of milk” for an adult human [61, 85]. Such modest savings have raised skepticism that energy conservation is the universal function of sleep shared by all species [32, 61, 86], particularly given sleep’s inherent costs related to lost mating and
foraging opportunities and increased predation risk from reduced behavioral responsiveness.

Previous calculations of energy savings derived from sleep are based only on metabolic rate reduction, a mathematical calculation that implicitly assumes all metabolic functions to be equally reduced during sleep compared to wake. However, the upregulation of many biological operations during sleep contradicts this assumption. Moreover, other processes are instead upregulated in wakefulness and downregulated in sleep, including excitatory neurotransmission, energy metabolism and responses to cellular stress [11, 46]. These data are consistent with a state-dependent division of labor as outlined in the energy allocation hypothesis of sleep [64]. This model postulates that state-dependent coupling of biological functions repartitions energy resources across circadian time. This coupling provides comparatively greater daily energy conservation than metabolic rate reduction when compared with the energy requirements of constant wakefulness [64]. Surprisingly, there are no published reports on energy savings from coupling biological processes with behavioral state.

A basic premise of the model is that a state-dependent division of labor occurs at the whole organism level. That is, repartitioning of metabolic operations is not restricted to a single organ or structure. Division of labor in the model defines the average repartitioning of metabolic functions according to behavioral state across all organ systems. We hypothesize that such whole organism repartitioning potentially increases energy savings derived from division of labor beyond what a single organ system could otherwise achieve. Specific mechanisms are viewed to coordinate behavioral state (brain) with periphery, including state-specific hormonal release (anabolic in sleep, catabolic in wake), autonomic innervation of peripheral tissues, and synchronization of peripheral and central circadian clocks [64].

Our calculation compares energy spent in a constant wakefulness phenotype to
energy spent in a sleep-wake cycling phenotype (see Fig. 1.1) by imposing the condition that certain biological functions must be carried out regardless of phenotype. Computed in this way, energy savings from sleep may be much greater than previous estimates, primarily due to state-dependent division of labor. Moreover, the model demonstrates that division of labor is constrained if energy deployment toward waking-related processes is maintained during the rest phase, whereas energy savings is amplified if such allocations during sleep are reduced. Sleep quota and the circadian system may further enhance energy conservation in the model. Under this model, we assert that the upregulation of central and peripheral biological processes during sleep is driven by the selective advantage of repartitioning metabolic operations, the principal mechanism by which sleep optimizes energy conservation across species.

3.2 Method

3.2.1 Definitions

Throughout the energy savings calculation, the parameters \( t_s, p_W, p_B, m_C, \) and \( \alpha \) remain fixed. The parameters we consider to be changing are the four rates used in the 4-tuple \( r = (r_{Ww}, r_{Bw}, r_{Ws}, r_{Bs}) \). Define the metabolic rates

\[
\mathcal{M}_w(r) = r_{Ww} + r_{Bw}
\]

\[
\mathcal{M}_s(r) = r_{Ws} + r_{Bs}
\]

for wake and sleep, respectively. Define the average metabolic rate

\[
\mathcal{M}_{avg}(r) = (1 - t_s)\mathcal{M}_w(r) + t_s\mathcal{M}_s(r) \tag{3.2.1}
\]

Parameter \( \rho \) is the proportion of metabolic rate reduction from wake to sleep:

\[
\rho(r) = \frac{\mathcal{M}_w(r) - \mathcal{M}_s(r)}{\mathcal{M}_w(r)} = 1 - \frac{r_{Ws} + r_{Bs}}{r_{Ww} + r_{Bw}}. \tag{3.2.2}
\]
Parameter $\rho$ may range from 0 to 1, where $\rho = 0$ means no metabolic rate reduction, and $\rho = 1$ means 100% metabolic reduction ($M_s = 0$).

The division of labor parameter ($\lambda$) is defined

$$
\lambda(r) = \frac{1}{2} \left( \frac{r_{Ww} - r_{Bw}}{r_{Ww} + r_{Bw}} + \frac{r_{Ws} - r_{Ws}}{r_{Bs} + r_{Ws}} \right) = \frac{1}{2} \left( \frac{r_{Ww} - r_{Bw}}{M_w(r)} + \frac{r_{Bs} - r_{Ws}}{M_s(r)} \right)
$$

$\lambda$ may theoretically take values between $-1$ and 1, but we consider values ranging between 0 and 1 to reflect the extent to which the “expected” processes are upregulated ($r_W$ in wake, $r_B$ in sleep). Note that $\lambda = 0$ means that the relative energy allocations are the same in both wake and sleep (i.e. $\frac{r_{Ww}}{r_{Bw}} = \frac{r_{Ws}}{r_{Bs}}$), while $\lambda = 1$ implies the downregulated processes vanish (i.e. $r_{Bw} = r_{Ws} = 0$).

Another quantity we will use to compute energy savings is “average $D$.” For a given $r$, if a stable limit cycle exists (see Chapter 2), we define average $D$

$$
D_{avg}(r) = \int_0^1 D'(t) \, dt,
$$

where $D'$ is the stable limit cycle solution of (1.3.10).

### 3.2.2 Energy Savings Computation

We compare three strategies in our energy savings calculations in which $\rho$ and $\lambda$ differ: **Strategy Wake**, **Strategy $\rho$**, and **Strategy $\lambda + \rho$**. **Strategy Wake** is a state of continual wakefulness (see Fig. 1.1), with $\rho = 0$ and $\lambda = 0$. In other words, there is no difference in wake and sleep states; $r_{Ww} = r_{Ws}$ and $r_{Bw} = r_{Bs}$. For **Strategy Wake**, define the ratio $R = \frac{r_W}{r_B}$. For **Strategy $\rho$**, we choose $\rho > 0$ and keep $\lambda = 0$. In this case, the relative allocations are the same, but metabolic rate is reduced during sleep.

For **Strategy $\lambda + \rho$**, we keep the same $\rho > 0$, and choose a positive target division of labor, $\lambda_T$ (see Section 3.2.5 for why a chosen target division of labor may not be achievable). In this case, both metabolic rate and relative allocations are different.

Denote the energy rates for each of these strategies $r_{Wake}$, $r_{\rho}$, and $r_{\lambda + \rho}$.
In order to compute energy savings, we must find \( r \) for each strategy so that \( D_{\text{avg}}(r) \) for the stable limit cycle solution of (1.3.10) is the same. We use the following relationships between parameters (justified in Section 3.2.5):

\[
\begin{align*}
    r_{Ws} &= \max \left\{ 0, \ (1 - \rho) \left( (1 - \lambda T) r_{Ww} - (\lambda T) r_{Bw} \right) \right\} \quad (3.2.5) \\
    r_{Bs} &= (1 - \rho)(r_{Ww} + r_{Bw}) - r_{Ws}, \quad (3.2.6)
\end{align*}
\]

where we assume all energy rates are nonnegative. Prior to the calculation, \( r_{Ww}, \rho, \) and \( \lambda_T \) are chosen. For all strategies, \( r_{Ww} \) is held constant. Within each strategy, we only vary one parameter, \( r_{Bw} \), to find \( r \) so that \( D_{\text{avg}}(r) \) is the same for each strategy.

For Strategy Wake, use \( \rho = 0 \) and \( \lambda_T = 0 \). Choose \( r_{Ww} \) and \( r_{Bw} \) so that a stable limit cycle solution for (1.3.7) exists to get \( r_{\text{Wake}} \). Compute \( D_{\text{avg}}(r_{\text{Wake}}) \) and \( M_{\text{avg}}(r_{\text{Wake}}) = r_{Ww} + r_{Bw} \).

For Strategy \( \rho \), keep \( r_{Ww} \) the same and \( \lambda_T = 0 \), but use the chosen value of \( \rho \). Using (3.2.5) and (3.2.6), find the value of \( r_{Bw} \) such that \( D_{\text{avg}}(r_{\rho}) = D_{\text{avg}}(r_{\text{Wake}}) \). Compute \( M_{\text{avg}}(r_{\rho}) \).

For Strategy \( \lambda + \rho \), keep \( r_{Ww} \) and \( \rho \) the same as in Strategy \( \rho \), but use the chosen value of \( \lambda_T \). Using (3.2.5) and (3.2.6), find the value of \( r_{Bw} \) such that \( D_{\text{avg}}(r_{\lambda+\rho}) = D_{\text{avg}}(r_{\text{Wake}}) \). Compute \( M_{\text{avg}}(r_{\lambda+\rho}) \).

Energy savings from \( \rho \) and \( \lambda \) may then be computed. Energy savings from \( \rho \) is

\[
S_{\rho} = \frac{M_{\text{avg}}(r_{\text{Wake}}) - M_{\text{avg}}(r_{\rho})}{M_{\text{avg}}(r_{\text{Wake}})},
\]

overall energy savings from \( \lambda \) and \( \rho \) is

\[
S_{\lambda+\rho} = \frac{M_{\text{avg}}(r_{\text{Wake}}) - M_{\text{avg}}(r_{\lambda+\rho})}{M_{\text{avg}}(r_{\text{Wake}})},
\]

and energy savings from \( \lambda \) is \( S_\lambda = S_{\lambda+\rho} - S_{\rho} \).
Figure 3.1: Method for calculating energy conservation. Horizontal axis is time (in days) in both columns. The vertical axis in the first column is metabolic rate, and in the second column is biological debt. Three strategies are differentiated based on total sleep time ($t_s$), metabolic rate reduction during sleep ($\rho$), and $\lambda$. a) Strategy Wake, b) Strategy $\rho$, c) Strategy $\lambda + \rho$. Right panels show the stable limit cycle solution of (1.3.10), biological debt ($D$) over three consecutive days. We impose the condition that daily average $D$ (orange) be held constant across conditions. Key: red (dashed) line is $r_W$, blue (dot-dashed) line is $r_B$, dark purple (solid) line is metabolic rate ($M$) such that $M = r_W + r_B$, and the light purple (dotted) line is average $M$. Standard parameters: $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $\alpha = 0.5$. 

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3.2.3 Existence of Solutions

The method given above is not complete; it is not clear that there exists an \( r_{Bw} \) that will match \( D_{avg}(r_{Wake}) \) for any given values of \( \lambda_T \) and \( \rho \). In fact, there will be some sets of parameters where such an \( r_{Bw} \) does not exist. However, we can say something about existence of solutions, and what to do when a solution does not exist. First, a lemma.

**Lemma 3.2.1.** Suppose that \( p_B < m_C(1 - \alpha) \) and define \( \beta(t) = \sqrt[3]{\frac{C(t)}{p_B}} - 1 \). If a stable limit cycle solution \( D(t) \) exists for Strategy Wake, then \( D(t) < \beta(t) \) for all \( t \).

*Proof.* Because \( D(t) \) is periodic and bounded on \( \mathbb{R} \), its maximum must occur at a point when \( \dot{D} = 0 \). Using (1.3.7), we see this happens when

\[
p_B r_B D^3 + p_W r_W D^2 + r_B (p_B - C(t)) D + p_W r_W = 0 \tag{3.2.7}
\]

For a fixed \( t \), we view (3.2.7) as a cubic in \( D \), and call it

\[
f(x) = p_B r_B x^3 + p_W r_W x^2 + r_B (p_B - C(t)) x + p_W r_W.
\]

We see that

\[
f'(x) = 3 p_B r_B x^2 + 2 p_W r_W x + r_B (p_B - C(t))
\]

and

\[
f''(x) = 6 p_B r_B x + 2 p_W r_W.
\]

Thus, for \( x > 0 \), \( f'(x) \) is increasing. We also see

\[
f'(\beta(t)) = 3 p_B r_B \left( \frac{C(t)}{p_B} - 1 \right) + 2 p_W r_W \beta(t) + r_B (p_B - C(t))
\]

\[
= 2 r_B (C(t) - p_B) + 2 p_W r_W \beta(t)
\]

\[
> 0.
\]
Finally, we see
\[ f(\beta(t)) = \left(1 + \beta(t)^2\right) \left(p_W r_w + r_B \beta(t) \left(p_B - \frac{C(t)}{1 + \beta(t)^2}\right)\right) \]
\[ = \left(1 + \beta(t)^2\right) p_W r_w \]
\[ > 0. \]

Because \( f(\beta(t)) > 0 \) and \( f'(x) > 0 \) for \( x \geq \beta(t) \), we have \( f(x) > 0 \) for \( x \geq \beta(t) \).

Therefore, the maximum of \( D(t) \) is less than \( \beta(t) \) for all \( t \), and thus \( D(t) < \beta(t) \) for all \( t \).

The significance of \( \beta(t) \) in Lemma 3.2.1 is that if \( 0 < D(t) < \beta(t) \), then
\[ p_B - \frac{C(t)}{1 + D(t)^2} < 0. \]

Therefore, increasing \( r_B \) decreases
\[ \dot{D}(t) = p_W r_w + r_B D(t) \left(p_B - \frac{C(t)}{1 + D(t)^2}\right). \] (3.2.8)

Clearly, decreasing \( r_W \) also decreases \( \dot{D} \). We use these facts to guarantee the existence of stable limit cycles for Strategy \( \rho \) and Strategy \( \lambda + \rho \), when one exists for Strategy Wake.

**Proposition 3.2.2.** Suppose that \( p_B < m_C(1 - \alpha) \). Suppose that a stable limit cycle solution exists for Strategy Wake (call the \( r_{Bw} \) rate for Strategy Wake \( (r_{Bw})_{\text{wake}} \)). Call this limit cycle \( D_s \). Define \( K \) to be the compact set inside of \( D_s \) in the plane.

For every \( 0 \leq \lambda_T \leq 1 \) and \( 0 \leq \rho < 1 \), there exists an \( r_{Bw} \) so that a stable limit cycle exists for Strategy \( \rho \) and Strategy \( \lambda + \rho \) inside \( K \).

**Proof.** It suffices to prove this for Strategy \( \lambda + \rho \), as setting \( \lambda_T = 0 \) is equivalent to Strategy \( \rho \).

From (3.2.5) and (3.2.6), we may choose \( r_{Bw} \) large enough so that \( r_{Ws} = 0 \), so that \( \dot{D} < 0 \) on \( D_s \) during the sleep period \((1 - t_s \leq t < 1)\). Furthermore, by Lemma
3.2.1 and (3.2.8), we may choose $r_{Bw}$ so large that $\dot{D} < 0$ on $D_s$ during the wake period $(0 \leq t < 1 - t_s)$. Therefore, by Theorem 2.2.6, there exists a stable limit cycle in $K$.

Suppose that a limit cycle exists for Strategy Wake with $D_{\text{avg}}(r_{\text{Wake}})$. For the energy savings computation, given a $\rho$ and $\lambda$, there may not exist an $r_{Bw}$ yielding the same $D_{\text{avg}}$. However, by Proposition 3.2.2, there does exist an $r_{Bw}$ that yields $D_{\text{avg}}(r_{\lambda+\rho}) \leq D_{\text{avg}}(r_{\text{Wake}})$. Therefore, since increasing $r_{Bw}$ decreases $D_{\text{avg}}$, we modify our energy savings computation:

$$r_{Bw} = \inf \{r_B \geq 0 : D_{\text{avg}}(r_{\lambda+\rho}(r_B)) \leq D_{\text{avg}}(r_{\text{Wake}})\}$$

where $r_{\lambda+\rho}(r_B)$ is the 4-tuple of energy rates dependent on $r_B$ calculated from (3.2.5) and (3.2.6). For Strategy $\rho$, run the calculation above with $\lambda = 0$.

### 3.2.4 Energy Savings Algorithm

In light of Proposition 3.2.2, if $p_B < m_C(1 - \alpha)$ and (1.3.10) has a stable limit cycle solution for Strategy Wake, then our computation is guaranteed to have a solution. We may write down an algorithm that takes inputs $p_W, p_B, m_C, \alpha, t_s, r_{Ww}, (r_{Bw})_{\text{Wake}}, \rho, \lambda_T$, and gives outputs $S_{\rho}, S_{\lambda},$ and $S_{\lambda+\rho}$:

1. Set $r_{\text{Wake}} = (r_{Ww}, (r_{Bw})_{\text{Wake}}, r_{Ww}, (r_{Bw})_{\text{Wake}})$ and define

$$r_{\rho}(r_{Bw}) = (r_{Ww}, r_{Bw}, (1 - \rho)r_{Ww}, (1 - \rho)r_{Bw})$$

(3.2.9)
as functions of $r_{Bw}$.

2. Compute $D_{\text{Wake}} = D_{\text{avg}}(r_{\text{Wake}})$ and $M_{\text{Wake}} = M_{\text{avg}}(r_{\text{Wake}})$ (see (3.2.4) and (3.2.1)).

3. Compute $r_{Bw,\rho} = \inf \{r_{Bw} \geq 0 : D_{\text{avg}}(r_{\rho}(r_{Bw})) \leq D_{\text{Wake}}\}.$

4. Compute $r_{Bw,\lambda+\rho} = \inf \{r_{Bw} \geq 0 : D_{\text{avg}}(r_{\lambda+\rho}(r_{Bw})) \leq D_{\text{Wake}}\}.$

5. Compute $M_{\rho} = M_{\text{avg}}(r_{\rho}(r_{Bw,\rho}))$ and $M_{\lambda+\rho} = M_{\text{avg}}(r_{\lambda+\rho}(r_{Bw,\lambda+\rho})).$

6. Compute $S_{\rho} = \frac{M_{\text{Wake}} - M_{\rho}}{M_{\text{Wake}}},$ $S_{\lambda+\rho} = \frac{M_{\text{Wake}} - M_{\lambda+\rho}}{M_{\text{Wake}}},$ and $S_{\lambda} = S_{\lambda+\rho} - S_{\rho}.$

3.2.5 Target Division of Labor

Using (3.2.6), we see that

$$
\rho(r) = \frac{r_{Ww} + r_{Bw} - (r_{Ws} + (1 - \rho)(r_{Ww} + r_{Bw}) - r_{Ws})}{r_{Ww} + r_{Bw}} = 1 - (1 - \rho)
$$
= \rho.

Furthermore, assuming that \((1 - \lambda_T)rw_w - (\lambda_T)rb_w \geq 0\) and using (3.2.5) and (3.2.6),

\[
\lambda(r) = \frac{1}{2} \left( \frac{rw_w - rb_w}{rw_w + rb_w} + \frac{(1 - \rho)(rw_w + rb_w) - 2rw_s}{(1 - \rho)(rw_w + rb_w)} \right) \\
= \frac{1}{2} \left( \frac{rw_w - rb_w}{rw_w + rb_w} + \frac{(1 - \rho)((rw_w + rb_w) - 2((1 - \lambda_T)rw_w - (\lambda_T)rb_w))}{(1 - \rho)(rw_w + rb_w)} \right) \\
= \frac{1}{2} \left( \frac{2rw_w - 2((1 - \lambda_T)rw_w - (\lambda_T)rb_w)}{rw_w + rb_w} \right) \\
= \frac{rw_w - rw_w + \lambda_T(rw_w + rb_w)}{rw_w + rb_w} \\
= \lambda_T
\]

On the other hand, suppose that \((1 - \lambda_T)rw_w - (\lambda_T)rb_w < 0\). If \(\lambda_T = 1\), for any \(rb_w > 0\), \(\lambda(r) < \lambda_T = 1\). If \(\lambda_T < 1\), then the assumed condition is equivalent to

\[
r_w = \frac{\lambda_T}{1 - \lambda_T}.
\]  
(3.2.11)

Using (3.2.11) along with that fact that

\[
\frac{x - 1}{x + 1} = 1 - \frac{2}{x + 1}
\]

is decreasing in \(x\), we see

\[
\lambda(r) = \frac{1}{2} \left( \frac{rw_w - rb_w}{rw_w + rb_w} + 1 \right) \\
= \frac{1}{2} \left( \frac{rw_w - 1}{rw_w + 1} + 1 \right) \\
< \frac{1}{2} \left( \frac{\lambda_T}{1 - \lambda_T} - 1 + 1 \right) \\
= \frac{\lambda_T}{1 - \lambda_T} \\
= \lambda_T
\]

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So in every case, \( \lambda(r) \leq \lambda_T \). This inequality explains why we use a “target” division of labor in our calculations; if \((\lambda_T)r_{BW}\) is large, a chosen level of division of labor may not be able to be met due to the restriction that energy rates must be nonnegative. Note that if \(\lambda_T = 0\), then \(\lambda = \lambda_T\).

### 3.3 Results

Using the method described above, we analyze the results from varying parameters \(\rho\), \(\lambda_T\), \(t_s\), and \(\alpha\). We found that varying \(p_W\), \(p_B\), \(m_C\), and \(R\) (the ratio \(r_W/r_B\) in Strategy Wake) did not have a substantial impact on energy savings (for further discussion on this point, see the final section of Chapter 4).

![Energy savings computation varying \(\lambda_T\) with \(t_s = 1/3\) and \(t_s = 1/2\). Note that in (a), the maximum \(\lambda\) is approximately 0.7, whereas in (b), \(\lambda_T\) is always reached. Parameters: \(\rho = 0.3\), \(\alpha = 0.5\), \(p_W = 1.3\), \(p_B = 0.7\), \(m_C = 5\), \(r_{WW} = 0.5\), \(R = 1\).](image-url)
This method demonstrates that a 30% reduction in metabolic rate ($\rho = 0.3$) for 8 h of sleep with $\lambda = 0$ provides a 7.5% daily energy savings ($S_{\rho}$) over *Strategy Wake* (Fig. 3.2a). This calculation is consistent with calorimetry data [37, 61]. However, these published observations do not calculate energy savings from repartitioning metabolic operations. Looking at $S_{\lambda + \rho}$, we also see that maximizing state-dependent $\lambda$ amplifies energy savings derived from sleep by approximately 4-fold over metabolic rate reduction alone, augmenting total energy savings to approximately 37% for an 8 h sleep quota. Notably, Fig. 3.2a demonstrates that $\lambda = 1$ may not be achievable under some combinations of parameters (hence the use of $\lambda_T$, target division of labor). In contrast, Fig. 3.2b demonstrates that under some conditions it is always possible for $\lambda = \lambda_T$.

One result of this model is that decreasing either sleep quota or metabolic rate during sleep limits biological investment ($I$) during sleep, forcing an increase in $r_B$ during wake to service biological requirements ($R$) and limit a rise in average daily biological debt ($D$). Despite these constraints, energy savings from state-dependent $\lambda$ equals or exceeds that from metabolic rate reduction across all sleep quotas for low to moderate $\rho$ (Fig 3.3a). The model also predicts that metabolic rate reduction is not required for sleep to conserve energy. As demonstrated in Fig 3.4, an 8 h sleep quota with $\lambda_T = 0.4$ provides a calculated daily energy savings of 24% without reducing metabolic rate ($\rho = 0$), and $\lambda_T = 0.7$ provides a 35% savings.

The Energy Allocation model reveals previously unforeseen interactions between division of labor and metabolic rate in energy conservation. For example, a combination of $\lambda$ and $\rho$ may enhance energy savings of sleep beyond what is achievable through $\lambda$ alone (Fig. 3.4). However, the relative contribution from $\lambda$ diminishes as $\rho$ increases towards its maximum value of 1 (i.e., 100% metabolic rate reduction). Large
Gains in energy savings with an increase in total sleep time are primarily derived from $\lambda$ for small $t_s$, whereas the gains come from $\rho$ for large $t_s$. Note that for low to moderate $\rho$ (a), $S_{\lambda} > S_{\rho}$, whereas for high $\rho$ (b), $S_{\rho} > S_{\lambda}$ for large $t_s$. Large $\rho$ and $t_s$ is suggestive of the torpor phenotype. Parameters: $\lambda = 0.4$, $\rho = 0.3$, $\alpha = 0.5$, $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $r_{Ww} = 0.5$, $R = 1$. 

Figure 3.3: Energy savings computation varying $t_s$ for a) $\rho = 0.3$ and b) $\rho = 0.5$. 

Figure 3.4: Energy savings computation varying $\rho$, when a) $\lambda_T = 0.4$ and b) $\lambda_T = 0.7$. Reductions in metabolic rate during the rest phase constrain $\lambda$, i.e. $\lambda_T$ is not met. Note that peak energy savings in (a) occur at about $\rho = 0.7$, whereas in (b) the peak is at about $\rho = 0.3$. Parameters: $t_s = 1/3$, $\alpha = 0.5$, $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $r_{Ww} = 0.5$, $R = 1$. 

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increases in $\rho$, however, are more compatible with torpor where reducing metabolic rate is the primary mechanism of energy conservation [22,41].

Figure 3.5: Energy savings computation varying $\alpha$ and a) $\lambda_T$ ($\rho = 0.3$) and b) $\rho$ ($\lambda_T = 0.4$). At low levels of $\lambda$, increasing $\alpha$ causes energy savings to decrease, whereas at higher levels of $\lambda$, increasing $\alpha$ increases energy savings. At low levels of $\rho$, increasing $\alpha$ causes energy savings to increase, whereas at higher levels of $\rho$, increasing $\alpha$ decreases energy savings. Parameters: $t_s = 1/3$, $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $r_{Ww} = 0.5$, $R = 1$.

We also identify interactions between the circadian system and both division of labor and metabolic rate reduction in energy conservation. Circadian amplitude ($\alpha$) provides additional daily energy savings in the presence of moderate $\lambda$ (e.g., $\lambda \geq 0.4$ in Fig. 3.5a), reflecting an efficiency multiplier function of the circadian process in converting energy to biological investment in the model. This circadian process is intended to model the role of central and peripheral molecular clocks in regulating metabolic functions at the local or cellular level [5,19,52]. In contrast, daily
energy savings are reduced when circadian amplitude is increased in the absence of $\lambda$. This latter effect results from inefficiencies in expending energy on state-dependent processes when comparatively out of phase with the circadian system. There is also a less pronounced interaction between $\rho$ and the circadian system in energy conservation (Fig. 3.5b). Increasing $\alpha$ for high values of $\rho$ decreases energy savings. This is, again, due to inefficiencies in addressing $R$ during sleep when metabolic rate reduction is high during the rest period.

3.4 Discussion

The Energy Allocation model identifies four variables that impact energy savings derived from sleep. These include: 1) state-dependent division of labor ($\lambda$), 2) metabolic rate reduction during sleep ($\rho$), 3) total sleep time ($t_s$), and 4) circadian amplitude ($\alpha$). The model not only quantifies the relative contributions of these variables in energy conservation, but also identifies specific interactions impacting energy savings. For example, metabolic rate typically decreases during the rest phase across species, including a 15-30% reduction during sleep [37, 61] and more than 90% reduction during hibernation [22, 41]. We show that a combination of state-dependent $\lambda$ and small reductions in metabolic rate during sleep may augment energy savings beyond what is achievable from $\lambda$ alone, but that the relative contribution from $\lambda$ diminishes as metabolic rate during the rest phase is reduced (Fig. 3.4). This interaction is consistent with the following proposition: Repartitioning of metabolic processes is the primary mechanism of energy savings for sleep, whereas metabolic rate reduction the principle mechanism for torpor.

State-dependent $\lambda$ achieves energy savings by preferentially coupling unique biological functions with either sleep or wake. Due to metabolic repartitioning, our calculations suggest that actual energy savings from sleep substantially greater than
what was reported previously from metabolic rate reduction, theoretically reducing total energy requirements by over 50% for species with long sleep quotas (Fig. 3.3). We hypothesize that state-dependent metabolic repartitioning occurs at the whole organism level, consistent with the great diversity of gene expression specifically coupled with either sleep or wakefulness in both central and peripheral tissues [11, 46, 47]. Whole organism energy expenditure influences an animal’s likelihood of overcoming energetic shortfall, accumulating energy reserves, and converting energy to offspring, thereby impacting its lifetime reproductive success. Our mathematical model suggests that the alternative strategy of continuous wakefulness increases biological requirements, constrains repartitioning of metabolic processes, and requires greater metabolic investments to limit rises in biological debt.

Prior work suggested that 8 h of sleep only reduces daily energy expenditures by 5-15% [37, 61, 83, 85]. However, these previous observations, often employing short-term sleep restriction, are not designed to determine differences in net energy savings between habitual continuous wakefulness and habitual sleep-wake cycling. Specifically, we have identified two critical limitations of these prior data. First, calculations from these earlier studies rely on the implicit assumption that all biological processes are equally reduced during sleep compared to wake, not accounting for state-dependent energy allocation. Second, these prior studies do not calculate the energy requirements needed to achieve comparable levels of biological debt when sleep-dependent processes are restricted as a result of protocol design. Our calculations, in contrast, suggest that daily energy requirements would be much greater for organisms to achieve habitual, long-term, continuous wakefulness while maintaining comparable levels of biological debt with respect to an alternative sleep-wake cycling strategy.

The proposed interactions in our model between $\lambda$, metabolic rate reduction, and
sleep quota are not intuitively obvious, but provide testable hypotheses on the optimization of sleep or torpor strategies employed across species for energy conservation. For example, sleep quotas vary widely by species, a finding that remains unexplained and lacking clear significance with constitutive variables such as body mass [44, 68]. The horse, cow and Caspian seal habitually sleep less than 4 h per day, whereas the brown bat, giant armadillo and the Lutrine opossum typically sleep more than 18 h per day (see [45] for a review). For short sleepers, the slope of energy savings for state-dependent $\lambda$ is greater than the relatively shallow slope for metabolic rate reduction during sleep. Long sleep quotas, in contrast, achieve comparatively greater total energy savings, but the slope of energy savings derived from $\lambda$ flattens (or even becomes negative) as sleep quota exceeds 12-14 h while the slope from metabolic rate reduction continues to increase (see Fig. 3.3).

These interactions predict short sleeping species to maintain a relatively elevated metabolic rate during sleep to optimize energy conservation through $\lambda$, a prediction requiring further investigation. Long-sleeping species, in contrast, should be more likely to reduce metabolic rate during sleep given its increasing gains toward energy savings as sleep quota approaches 24 h. Our review of the literature finds this latter prediction well supported: Species with habitual sleep quotas > 12 h also commonly reduce metabolic rate by as much as 70% during the rest phase by entering daily (shallow) torpor periods (e.g., see species-family comparisons in [21, 45]). Moreover, long sleeping endotherms are particularly prone to enter daily (nightly) torpor when challenged by energetic shortfalls [27, 41, 66], suggesting an adaptive capability to shift energy allocation strategies between primarily $\lambda$ (sleep) or metabolic rate reduction (torpor) depending on energy status.

The Energy Allocation model also ascribes an important role for the circadian system in energy conservation during conditions that favor repartitioning of metabolic
operations across circadian time (Fig. 3.5). However, if all biological processes are to be performed simultaneously without interruption (i.e., $\lambda = 0$), the model demonstrates the optimal strategy to reduce daily energy expenditures is to dampen or eliminate circadian amplitude. This interaction between the circadian system and state-dependent $\lambda$ is consistent with a growing body of literature suggesting a close relationship between circadian and sleep-wake mechanisms. Circadian amplitude of gene expression, for example, is markedly reduced during sleep deprivation [3, 53].

Sleep restriction in our model constrains $\lambda$ by limiting biological investment during the rest phase. As a result, such investments must increase during extended wakefulness (i.e., via increasing $r_B$ during wake) to limit a rise in daily biological debt. Prolonged wakefulness, therefore, theoretically necessitates the organism perform a greater proportion of biological functions simultaneously. We view dampening of circadian amplitude during sleep loss as an adaptive response to more efficiently service biological requirements during prolonged waking bouts when a state-dependent $\lambda$ must be reduced.

Given the calculated impact of sleep-wake cycling on reducing daily energy requirements, the Energy Allocation model argues that the ultimate (evolutionary) function of sleep is energy conservation through a repartitioning of biological operations. We suggest that basic principles of this general model may be applicable to all species, potentially providing insight into one of biology’s greatest questions: What is the selective advantage of sleep over the alternative behavioral strategy of quiet wakefulness? The answer, our model posits, resides in state-dependent division of labor ($\lambda$), a mechanism that amplifies energy savings as waking effort is eliminated during a metabolically active rest phase where unique biological processes are upregulated. This unifying perspective does not conflict with the many proposed physiological (proximate) functions of sleep, including the upregulation of protein biosynthesis,
immune function, neural network reorganization and restorative processes. On the contrary, the upregulation of these diverse functions during sleep is viewed to be in the service of $\lambda$, a mechanism by which daily energy conservation is optimized.
Chapter 4

ALTERNATIVE ENERGY SAVINGS CALCULATION

4.1 Introduction

Inspired by the averaging done in the analysis section, we may alternatively compute savings by using the averaged system

\[
\dot{z} = p_W \overline{r_W} + p_B \overline{r_B} z - \overline{r_{BC}} \frac{z}{1+z^2},
\]

where

\[
\overline{r_{BC}} = \int_0^1 r_B(t) C(t) \, dt = m_C \left( \overline{r_B} + \frac{\alpha}{\pi} (r_{Bs} - r_{Bw}) \sin (\pi t_s) \right),
\]

and \( \overline{r_B}, \overline{r_W} \) are defined in (2.2.3).

We compute energy savings in a method analogous to the one presented in Section 3.2, where the analogue of “\( D_{avg} \) of the stable limit cycle” is “stable fixed point.” Note that the fixed points of (4.1.1) are the zeroes of the cubic polynomial

\[
p_B \overline{r_B} z^3 + p_W \overline{r_W} z^2 + (p_B \overline{r_B} - \overline{r_{BC}}) z + p_W \overline{r_W}.
\]

4.2 Existence and Stability

One advantage of the alternate method over the method in 3.2 is an explicit criterion for when a stable fixed point exists for Strategy Wake. Define \( R = \frac{r_W}{r_B} \), where \( r_W \) and \( r_B \) are their respective values for Strategy Wake.
Proposition 4.2.1. Suppose $p_B < m_C(1 - \alpha)$. Then (4.1.1) has two distinct positive fixed points if and only if

$$R < \frac{\sqrt{m_C^2 - 20m_C p_B - 8p_B^2 + \sqrt{m_C(m_C + 8p_B)^{3/2}}}}{2p_W \sqrt{2}}.$$  \hfill (4.2.1)

Proof. We keep the requirement $p_B < m_C(1 - \alpha)$ from the original energy savings calculation. This implies $p_B < m_C$, so the square root in the numerator makes sense (this is also shown below).

For Strategy Wake, $\overline{r}_B = r_B$, $\overline{r}_W = r_W$, and $\overline{r}_{BC} = r_B m_C$. Note that zeroes of (4.1.3) are fixed points of (4.1.1), and (4.1.1) has two distinct positive zeroes if and only if its discriminant is positive (see the discussion of the similar cubic in section 2.4).

The discriminant of (4.1.1) is

$$r_{BP_B}^4 \left( -4 \left( 1 - \frac{m_C}{p_B} \right)^3 + \left( \frac{p_W r_W}{p_B r_B} \right)^2 \left( 1 - \frac{m_C}{p_B} \right)^2 ight.$$

$$+ 18 \left( \frac{p_W r_W}{p_B r_B} \right)^2 \left( 1 - \frac{m_C}{p_B} \right) - 4 \left( \frac{p_W r_W}{p_B r_B} \right)^4 - 27 \left( \frac{p_W r_W}{p_B r_B} \right)^2 \right). \hfill (4.2.2)$$

Viewing (4.2.2) as a quadratic in $\left( \frac{p_W r_W}{p_B r_B} \right)^2$, we see this discriminant is zero when

$$\left( \frac{p_W r_W}{p_B r_B} \right)^2 = \frac{1}{8} \left( -27 + 18 \left( 1 - \frac{m_C}{p_B} \right) + \left( 1 - \frac{m_C}{p_B} \right)^2 \pm \sqrt{m_C p_B} \left( 8 + \frac{m_C}{p_B} \right)^{3/2} \right) \hfill (4.2.3)$$

Claim 1. For $p_B < m_C$,

$$-27 + 18 \left( 1 - \frac{m_C}{p_B} \right) + \left( 1 - \frac{m_C}{p_B} \right)^2 - \sqrt{m_C p_B} \left( 8 + \frac{m_C}{p_B} \right)^{3/2} < 0$$

and

$$-27 + 18 \left( 1 - \frac{m_C}{p_B} \right) + \left( 1 - \frac{m_C}{p_B} \right)^2 + \sqrt{m_C p_B} \left( 8 + \frac{m_C}{p_B} \right)^{3/2} \geq 0$$

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Proof of Claim. Let \( x = \frac{mC}{p_B} - 1 \). The first part of the claim is equivalent to the statement that for \( x > 0 \),

\[
x^2 - 18x - 27 - \sqrt{x+1}(x+9)^{3/2} < 0.
\]

It is clear that at \( x = 0 \), the expression is negative. We also claim it is decreasing for \( x > 0 \). To see this, we take the derivative to get

\[
2x - 18 - \left( \frac{3}{2} \sqrt{x+1} \sqrt{x+9} + \frac{1}{2} (x+1)^{-1/2} (x+9)^{3/2} \right)
\]

\[
= 2x - 18 - (2x+6) \sqrt{\frac{x+9}{x+1}}
\]

\[
= 2 \left( x - 9 - (x+3) \sqrt{\frac{x+9}{x+1}} \right)
\]

\[
= 2 \left( x \left( 1 - \sqrt{\frac{x+9}{x+1}} \right) - 9 - 3 \sqrt{\frac{x+9}{x+1}} \right)
\]

\[
< 0
\]

For the second part of the claim, we try to show that for \( x > 0 \),

\[
x^2 - 18x - 27 - \sqrt{x+1}(x+9)^{3/2} \geq 0.
\]

At \( x = 0 \), the expression is 0. We also claim it is increasing for \( x > 0 \). Similar to what was shown above, the derivative is

\[
2 \left( x - 9 + (x+3) \sqrt{\frac{x+9}{x+1}} \right).
\]

For \( x > 9 \), the above is clearly positive. For \( 0 < x < 9 \), the following are equivalent:

\[
x - 9 + (x+3) \sqrt{\frac{x+9}{x+1}} > 0
\]

\[
\sqrt{\frac{x+9}{x+1}} > \frac{9-x}{3+x}
\]

\[
(x+9)(x+3)^2 - (x+1)(9-x)^2 > 0
\]

\[
32x^2 > 0.
\]

\(\square\)
With the claim proven, we choose (4.2.3) with the plus sign rather than the minus sign, and see that the discriminant is zero when

\[
\frac{p_{WR}W}{p_{BR}B} = \sqrt{\frac{1}{8} \left( -27 + 18 \left( 1 - \frac{m_C}{p_B} \right) + \left( 1 - \frac{m_C}{p_B} \right)^2 + \sqrt{\frac{m_C}{p_B} \left( 8 + \frac{m_C}{p_B} \right)^{3/2}} \right)},
\]

where we ignore the negative square root because all parameters are positive. Viewing the discriminant as a quartic in \( \frac{p_{WR}W}{p_{BR}B} > 0 \), we see that the expression above is the only zero of this quartic, the discriminant is positive when \( \frac{p_{WR}W}{p_{BR}B} \) is less than the expression above, and the discriminant is negative when \( \frac{p_{WR}W}{p_{BR}B} \) is greater than the expression above. Thus, we see by solving for \( R \), the discriminant (4.2.2) is positive when the given inequality holds.

Proposition 4.2.1 implies, in particular, that a stable fixed point exists. Suppose the parameters satisfy the conditions of Proposition 4.2.1, and let \( z^* \) be the minimum of the positive fixed points of (4.1.1) for Strategy Wake. That is, \( z^* \) satisfies

\[
0 = p_{WR}W + p_{BR}Bz^* - r_B m_C \frac{z^*}{1 + (z^*)^2},
\]

and is the minimum such positive value.

**Proposition 4.2.2.** \( z^* \) is a stable fixed point.

**Proof.** Define

\[
f_1(z) = p_B r_B z^3 + p_{WR}W z^2 + r_B (p_B - m_C) z + p_{WR}W.
\]

Let \( z^+ > z^* \) be the other positive root of \( f_1 \). Now, \( f_1'(z^*) \neq 0 \), otherwise \( z^* \) would be a repeated root, which contradicts positivity of the discriminant (for the same reason, \( f_1'(z^+) \neq 0 \)). Suppose, toward contradiction, \( f_1'(z^*) > 0 \). Then, \( f_1'(z^+) < 0 \). Since \( f_1'(z) \to \infty \) as \( z \to \infty \), this means there must be another root, which is a contradiction. Thus, \( f_1'(z^*) < 0 \).
From (4.1.1) for Strategy Wake, define
\[ f(z) = \varepsilon \left( pw r_W + p_B r_B z - r_B m_C \frac{z}{1 + z^2} \right), \]
and note that \( f(z) = \varepsilon \frac{f_1(z)}{1 + z^2} \). Then
\[ f'(z^*) = \varepsilon \frac{f_1'(z^*)}{1 + z^2} < 0. \]
Thus, \( z^* \) is a stable fixed point of (4.1.1) for Strategy Wake.

For \( r = (r_{Ww}, r_{Bw}, r_{Ws}, r_{Bs}) \), define
\[ h(r, z) = p_W r_W + p_B r_B z - r_B m_C \frac{z}{1 + z^2} \tag{4.2.5} \]
Given \( \rho \) and \( \lambda_T \), we seek an \( r_{Bw} \) so that \( r_{\lambda+\rho}(r_{Bw}) \) (defined in (3.2.10)) satisfies \( h(r_{\lambda+\rho}(r_{Bw}), z^*) = 0 \). Finding \( r_{Bw} \) almost amounts to solving a linear equation! However, we must ensure all energy rates are nonnegative and that \( z^* \) is still a stable fixed point for \( \dot{z} = \varepsilon h(r_{\lambda+\rho}(r_{Bw}), z) \). We return to these problems later. To conclude this section, note that because \( z^* \) is a stable fixed point for Strategy Wake, we know that
\[ r_B p_B - r_B m_C \frac{1 - (z^*)^2}{(1 + (z^*)^2)^2} < 0, \tag{4.2.6} \]
so
\[ p_B < m_C \frac{1 - (z^*)^2}{(1 + (z^*)^2)^2}. \tag{4.2.7} \]
Note 3. This implies that \( z^* < 1 \).

4.3 Further Condition on Parameters

For convenience, we define
\[ \xi = t_s p_W R + \frac{\alpha m_C}{\pi} \sin(\pi t_s) \frac{z^*}{1 + (z^*)^2} \tag{4.3.1} \]
\( t_s p_W R + \frac{\alpha}{\pi} \sin(\pi t_s) (p_W R + p_B z^*) \), \quad (4.3.2) 

(where \( R = \frac{r_W}{r_B} \) as above), as it will repeatedly appear in the following (we used (4.2.4) for the second equality for \( \xi \)).

Recall the definition (4.2.5). Expanding and rearranging \( h(r, z^*) \) gives

\[
h(r, z^*) = r_W w (1 - t_s) p_W + r_W s t_s p_W \\
+ r_B w \left( (1 - t_s) p_B z^* - (1 - t_s) m_C \frac{z^*}{1 + (z^*)^2} + \frac{\alpha m_C}{\pi} \sin(\pi t_s) \frac{z^*}{1 + (z^*)^2} \right) \\
+ r_B s \left( t_s p_B z^* - t_s m_C \frac{z^*}{1 + (z^*)^2} - \frac{\alpha m_C}{\pi} \sin(\pi t_s) \frac{z^*}{1 + (z^*)^2} \right)
\]

Using (4.2.4), we see

\[
h(r, z^*) = r_W w (1 - t_s) p_W + r_B w \left( -(1 - t_s) p_W \frac{r_W}{r_B} + \frac{\alpha m_C}{\pi} \sin(\pi t_s) \frac{z^*}{1 + (z^*)^2} \right) \\
- r_W s t_s p_W + r_B s \left( -t_s p_W \frac{r_W}{r_B} - \frac{\alpha m_C}{\pi} \sin(\pi t_s) \frac{z^*}{1 + (z^*)^2} \right) \quad (4.3.3)
\]

and, re-writing using (4.3.2) gives

\[
h(r, z^*) = r_W w (1 - t_s) p_W + r_B w (-p_W R + \xi) + r_W s t_s p_W + r_B s (-\xi) \quad (4.3.4)
\]

Therefore, using (3.2.10), we see that

\[
h(r_{\lambda + \rho}(r_{Bw}), z^*) = r_B w \mathcal{B}(r_{Bw}) - r_W \mathcal{W}(r_{Bw}) \quad (4.3.5)
\]

where

\[
\mathcal{W}(r_{Bw}) = \bigg\{ \begin{array}{ll}
- (1 - t_s) p_W - (1 - \rho)(1 - \lambda_T) t_s p_W + (1 - \rho) \lambda_T \xi & \text{if } r_{Bw} < r_W \frac{1 - \lambda_T}{\lambda_T} \\
- (1 - t_s) p_W + (1 - \rho) \xi & \text{if } r_{Bw} \geq r_W \frac{1 - \lambda_T}{\lambda_T} 
\end{array} \quad (4.3.6)
\]

and

\[
\mathcal{B}(r_{Bw}) = \bigg\{ \begin{array}{ll}
-p_W R + (1 - (1 - \rho)(1 + \lambda_T)) \xi - (1 - \rho) \lambda_T t_s p_W & \text{if } r_{Bw} < r_W \frac{1 - \lambda_T}{\lambda_T} \\
-p_W R + \rho \xi & \text{if } r_{Bw} \geq r_W \frac{1 - \lambda_T}{\lambda_T} 
\end{array} \quad (4.3.7)
\]
Abusing notation, we call \( h(r_{Bw}) = h(r_{\lambda+\rho(r_{Bw}), z^*}) \). Note that \( h(r_{Bw}) \) is continuous and piecewise linear (because \( W \) and \( B \) are piecewise constant).

In the original energy savings model, we expect increasing \( r_{Bw} \) will decrease stable average \( \mathcal{D} \). By the same token, we expect increasing \( r_{Bw} \) will decrease \( h \); in other words, \( B < 0 \). To ensure this, we impose an additional condition on the parameters.

**Proposition 4.3.1.** Let \( \eta = \frac{p_W r_W}{p_B r_B} \). If

\[
\alpha \leq \frac{\eta}{\eta + 1},
\]

Then \( B < 0 \).

The proof of this becomes clear after the following lemma.

**Lemma 4.3.2.** Let \( \eta = \frac{p_W r_W}{p_B r_B} \). If \( \alpha \leq \frac{\eta}{\eta + 1} \), Then \( \xi < p_W R \).

**Proof.** Viewing \( \xi \) as a function of \( t_s \) (\( 0 \leq t_s \leq 1 \)), we see that

\[
\xi'(t_s) = p_W R + \alpha \cos(\pi t_s) \left( p_W R + p_B z^* \right)
\]

We claim that \( \xi'(t_s) \) is never zero. Suppose, toward contradiction, that \( \xi'(t_s^*) = 0 \).

Then

\[
\cos(\pi t_s^*) = -\frac{p_W R}{p_W R + p_B z^*} \frac{1}{\alpha}
\]

\[
\leq -\frac{p_W R + p_B}{p_W R + p_B z^*}
\]

\[
< -1
\]

by Note 3. As \(-1 \leq \cos(\pi t_s) < 1\), this is a contradiction. Since \( \xi'(t_s) \) is continuous, never zero, and \( \xi'(0.5) > 0 \), we have \( \xi'(t_s) > 0 \) for all \( t_s \). Therefore, \( \xi(t_s) < \xi(1) = p_W R \). \( \square \)
To prove Proposition 4.3.1, note that Lemma 4.3.2 makes it obvious that $B < 0$ when $r_{Bw} > r_W \frac{1 - \lambda_T}{\lambda_T}$. On the other hand, suppose $r_{Bw} \leq r_W \frac{1 - \lambda_T}{\lambda_T}$. If $\lambda_T \geq \frac{\rho}{1 - \rho}$, then $1 - (1 - \rho)(1 + \lambda_T) < 0$ and $B$ is clearly negative. If $\lambda_T < \frac{\rho}{1 - \rho}$, then Lemma 4.3.2 says that

$$B < -(1 - \rho)(1 + \lambda_T)p_W R - (1 - \rho)\lambda_T t_s p_w < 0.$$ 

A restriction on $\alpha$ not only gives the desired mathematical behavior, it is also biologically reasonable. One interpretation of $\alpha$ is that it measures circadian temperature fluctuation, where $\alpha$ close to 0 means almost no fluctuation and $\alpha$ close to 1 means drastic fluctuation. The imposing of an upper bound for $\alpha$ in this interpretation is akin to the statement the circadian temperature fluctuation is low to moderate, a reasonable biological assumption.

4.4 Alternate Energy Savings Calculation

For this section, let $\eta = \frac{p_W}{p_B r_B}$ and assume that $\alpha < \frac{\eta}{\eta + 1}$, so that $B < 0$. Furthermore, for convenience we define $W_0 = W(0)$, $W_1 = W\left(r_W \frac{1 - \lambda_T}{\lambda_T}\right)$, $B_0 = B(0)$, and $B_1 = W\left(r_W \frac{1 - \lambda_T}{\lambda_T}\right)$.

4.4.1 Calculation of $r^*_{Bw}$

We are trying to find $r^*_{Bw} \geq 0$ such that $z^*$ is a fixed point of (4.1.1), i.e. $h(r^*_{Bw}) = 0$. As in the original energy savings calculation, it may not be possible to find $r^*_{Bw}$ so that $z^*$ is a stable fixed point, or even a fixed point at all. If $W_0 > 0$, then $h(0) < 0$ and $h' = B < 0$ (see Figure 4.1). In this case, there is no $r^*_{Bw} \geq 0$ such that $h(r^*_{Bw}) = 0$. As in the original energy savings calculation, we set $r^*_{Bw} = 0$. Otherwise, if $W_0 < 0,$
then \( h(0) > 0, \ h' = B < 0, \) and \( h \) is continuous. Therefore, we may find \( r^*_B w \) such that \( h(r^*_B w) = 0 \). First, we examine

\[
h\left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) = r_W \left( \frac{1 - \lambda_T}{\lambda_T} B_1 - W_1 \right) = \frac{r_W}{\lambda_T} \left( \lambda_T (p_W R - \xi + (1 - t_s)p_W) + (\rho \xi - p_W R) \right)
\]

Noting that Lemma 4.3.2 implies that \( p_W R - \xi + (1 - t_s)p_W > 0 \), we define

\[
\lambda^*_T = \frac{p_W R - \rho \xi}{p_W R - \xi + (1 - t_s)p_W},
\]

and see that if \( \lambda_T \leq \lambda^*_T \), then \( h\left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) \leq 0 \). Therefore \( r^*_B w \leq r_W \frac{1 - \lambda_T}{\lambda_T} \), whence \( r^*_B w = r_W \frac{W_0}{B_0} \). On the other hand, if \( \lambda_T > \lambda^*_T \), then \( h\left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) > 0 \). Therefore \( r^*_B w > r_W \frac{1 - \lambda_T}{\lambda_T} \), whence \( r^*_B w = r_W \frac{W_1}{B_1} \).

\[\text{Figure 4.1: Plots of } h(r_{\lambda+\rho}(0), z). \text{ On the left is the case where } W_0 < 0, \text{ in which case we find where } r^*_B w > 0 \text{ such that } h(r_{\lambda+\rho}(0), z^*) = 0. \text{ On the right } W_0 > 0, \text{ in which case we set } r^*_B w = 0, \text{ giving a new stable fixed point.}
\]

Parameters: on the left, \( p_W = 1.3, \ p_B = 0.7, \ r_W = 0.5, \ t_s = \frac{1}{3}, \ m_C = 5, \ 
\alpha = 0.5, \ \rho = 0.3, \ \lambda_T = 0.4, \ R = 1. \text{ On the right, } p_W = 0.7, \ p_B = 0.7, \ r_W = 0.5, \ t_s = 0.5, \ m_C = 5, \ \alpha = 0.99, \ \rho = 0.01, \ \lambda_T = 1, \ R = 1. \]
Putting this all together, and writing \( r^*_Bw \) as a function of \( \lambda_T \), we have

\[
r^*_Bw(\lambda_T) = \begin{cases} 
0 & \text{if } W_0(\lambda_T) \geq 0 \\
W_0(\lambda_T) & \text{if } W_0(\lambda_T) < 0 \text{ and } \lambda_T \leq \lambda^*_T \\
W_1 & \text{if } W_0(\lambda_T) < 0 \text{ and } \lambda_T > \lambda^*_T 
\end{cases}
\]  

(4.4.2)

4.4.2 Stability

With the initial calculation of \( r^*_Bw \) in hand, we want to check stability. Finding necessary and sufficient conditions will be difficult, convoluted, and not necessarily enlightening, so instead we provide some sufficient conditions that cover many cases.

First, we see that (4.2.7) and (3.2.10) give

\[
\frac{\partial h}{\partial z}(\lambda + \rho(r_Bw), z^*) = r_Bp_B - r_Bc - \frac{1 - (z^*)^2}{1 + (z^*)^2} < r_Bp_B - p_B \left( r_B + \frac{\alpha}{\pi} (r_B - r_Bw) \right)
\]

\[
= \begin{cases} 
\rho_B \frac{\alpha}{\pi} (1 - (1 - \rho)(1 + \lambda_T))r_Bw - (1 - \rho)\lambda_T r_W & \text{if } r_Bw \leq r_W \frac{1 - \lambda_T}{\lambda_T} \\
\rho_B \frac{\alpha}{\pi} (r_Bw - (1 - \rho)r_W) & \text{if } r_Bw > r_W \frac{1 - \lambda_T}{\lambda_T} 
\end{cases}
\]

:= h_w(r_Bw),

where the last line is a definition.

**Note 4.** \( h_w \) is continuous, and

\[
h_w \left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) = \frac{\rho}{\lambda_T} - 1 
\]

(4.4.3)

Suppose \( h(r_{\lambda + \rho}(r^*_Bw), z^*) = 0 \), so the choice of \( r^*_Bw \) makes \( z^* \) a fixed point. To guarantee stability of \( z^* \), we look at cases.
Suppose $\rho < \lambda_T$. Note that \( \frac{1 - \lambda_T}{\lambda_T} < \frac{1 - \rho}{\rho} \), so

\[
h_u \left( r_W \frac{1 - \rho}{\rho} \right) = 0.
\]

Now $h_u(0) < 0$ and

\[
h_u \left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) < 0
\]

(by Note 4). Since $h_u$ is linear on the interval $\left[ 0, \frac{r_W (1 - \lambda_T)}{\lambda_T} \right]$, $h_u < 0$ on that interval.

We see $h_u' > 0$ on the interval $\left( \frac{r_W (1 - \lambda_T)}{\lambda_T}, \frac{r_W (1 - \rho)}{\rho} \right)$. Thus, $h_u(r_{Bw}^*) < 0$ for

\[
r_{Bw}^* \leq r_W \frac{1 - \rho}{\rho},
\]

and therefore, $z^*$ is stable when this inequality holds.

On the other hand, suppose $\rho \geq \lambda_T$. By Note 4,

\[
h_u \left( r_W \frac{1 - \lambda_T}{\lambda_T} \right) \geq 0.
\]

Since $h_u$ is linear with a positive slope on $\left[ 0, \frac{r_W (1 - \lambda_T)}{\lambda_T} \right]$, we have that $z^*$ is stable when

\[
r_{Bw}^* \leq r_W \frac{(1 - \rho)\lambda_T}{1 - (1 - \rho)(1 + \lambda_T)}
\]

(4.4.5)

For the case where $W_0 \geq 0$, there is nothing to check, as $z^*$ is not a fixed point.

For the rest of this discussion on stability, we assume that $W_0 < 0$.

**Proposition 4.4.1.** Suppose $\lambda_T \leq \rho$, and

\[
R \geq \left( \frac{\rho}{\lambda_T} - 1 \right) + \frac{\rho}{\lambda_T} \frac{\rho}{1 - \rho} (1 - t_s).
\]

Then the $r_{Bw}^*$ given in (4.4.2) makes $z^*$ a stable fixed point for $\dot{z} = h(r_{\lambda+\rho}(r_{Bw}^*), z)$.

**Proof.** First, note that $R \geq \frac{\rho}{1 - \rho} (1 - t_s)$, so

\[
R(1 - \rho) \geq \rho(1 - t_s)
\]

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\[ p_W R (1 - \rho) \geq \rho (1 - t_s) p_W \]
\[ p_W R - \rho \xi \geq \rho (p_W R - \xi + (1 - t_s) p_W) \]
\[ \lambda^*_T \geq \rho. \]

Thus, \( \lambda_T \leq \lambda^*_T \), so \( r_{Bw}^* = r_W \frac{W_0(\lambda_T)}{B_0(\lambda_T)} \). Re-writing this, we see
\[
r_{Bw}^* = r_W \frac{(1 - \rho) \lambda_T}{1 - (1 - \rho)(1 + \lambda_T)} \frac{\xi - p_W \left( \frac{1 - t_s(1 - (1 - \rho)(1 - \lambda_T))}{(1 - \rho) \lambda_T} \right)}{\xi - p_W \left( \frac{R + (1 - \rho) \lambda_T t_s}{1 - (1 - \rho)(1 + \lambda_T)} \right)}.
\]

Note that the numerator and denominator of the rightmost fraction are negative, since \( W_0 \) and \( B_0 \) are negative, and we only factored out positive numbers from each. Therefore, we may say that \( z^* \) is a stable fixed point if
\[
\frac{1 - t_s(1 - (1 - \rho)(1 - \lambda_T))}{(1 - \rho) \lambda_T} \leq \frac{R + (1 - \rho) \lambda_T t_s}{1 - (1 - \rho)(1 + \lambda_T)}
\]
by (4.4.5). But this inequality is equivalent to the assumed inequality.

**Proposition 4.4.2.** Suppose \( \rho < \lambda_T \) and \( \lambda_T > \lambda^*_T \). If
\[
R \geq \frac{1 - t_s}{1 - \rho},
\]
then the \( r_{Bw}^* \) given in (4.4.2) makes \( z^* \) a stable fixed point for \( \dot{z} = h(r_{\lambda+\rho}(r_{Bw}^*), z) \).

**Proof.** Re-writing \( r_{Bw}^* = r_W \frac{W_1}{B_1} \), we see
\[
r_{Bw}^* = r_W \frac{1 - \rho}{\rho} \left( \frac{\xi - p_W \left( \frac{1 - t_s}{1 - \rho} \right)}{\xi - p_W R} \right).
\]

Note that the numerator and denominator of the rightmost fraction are negative, since \( W_1 \) and \( B_1 \) are negative, and we only factored out positive numbers from each. Therefore, we may say that \( z^* \) is a stable fixed point if the assumed condition holds, by (4.4.4).
Proposition 4.4.3. Suppose $\rho < \lambda_T$ and $\lambda_T \leq \lambda_T^*$. If

$$R \geq \lambda_T \left( \frac{\rho}{\lambda_T} - t_s + \frac{\rho}{\lambda_T} \frac{1}{1 - \rho} (1 - t_s) \right),$$

then the $r_{Bw}^*$ given in (4.4.2) makes $z^*$ a stable fixed point for $\dot{z} = h(r_{\lambda+\rho}(r_{Bw}^*), z)$.

Proof. By (4.4.4), we need to show that

$$\frac{\mathcal{W}_0}{\mathcal{B}_0} \leq \frac{1 - \rho}{\rho},$$

or (since $\mathcal{B}_0 < 0$),

$$\rho \mathcal{W}_0 - (1 - \rho) \mathcal{B}_0 \geq 0.$$

But this is just

$$p_W \left( R(1 - \rho) - \rho + t_s(\lambda_T (1 - \rho) + \rho^2) \right) + (1 - \rho)(\lambda_T - \rho) \xi > 0,$$

which is implied by the assumed condition. \hfill \Box

For all other cases, it is still required to check stability of solutions.

4.4.3 Energy Savings

We may now calculate energy savings:

$$\overline{S}_{\lambda+\rho}(\lambda_T) = \frac{r_W + r_B - ((1 - t_s)(r_W + r_{Bw}^*(\lambda_T)) + t_s(r_{Ws} + r_{Bs}))}{r_W + r_B}$$

$$= \frac{r_W + r_B - ((1 - t_s)(r_W + r_{Bw}^*(\lambda_T)) + t_s(1 - \rho)(r_W + r_{Bw}^*(\lambda_T)))}{r_W + r_B}$$

$$= \frac{\rho t_s r_W + r_B - (1 - \rho t_s)r_{Bw}^*(\lambda_T)}{r_W + r_B}$$

$$= \frac{\rho t_s R + 1 - (1 - \rho t_s)R \frac{\mathcal{W}_0(\lambda_T)}{\mathcal{B}_0(\lambda_T)}}{R + 1},$$

where we define $\mathcal{W}_\nu$ and $\mathcal{B}_\nu$:

$$\mathcal{W}_\nu(\lambda_T) = \begin{cases} 
0 & \text{if } \mathcal{W}_0 \geq 0 \\
-(1 - t_s) p_W - (1 - \rho)(1 - \lambda_T) t_s p_W + (1 - \rho) \lambda_T \xi & \text{if } \mathcal{W}_0 < 0 \text{ and } \lambda_T < \lambda_T^* \\
-(1 - t_s) p_W + (1 - \rho) \xi & \text{if } \mathcal{W}_0 < 0 \text{ and } \lambda_T \geq \lambda_T^* 
\end{cases}$$

(4.4.6)
and

\[ B_\nu(\lambda_T) = \begin{cases} 
- p_W R + (1 - (1 - \rho)(1 + \lambda_T)) \xi - (1 - \rho) \lambda_T t_s p_W & \text{if } \lambda_T < \lambda_T^* \\
- p_W R + \rho \xi & \text{if } \lambda_T \geq \lambda_T^* 
\end{cases} \]  

(4.4.7)

We calculate energy savings due to \( \rho \) (\( S_\rho \)) by setting \( \lambda_T = 0 \), and we calculate savings due to \( \lambda \) by subtraction, \( S_\lambda = S_{\lambda+\rho} - S_\rho \).

4.5 Comparison to Original Energy Savings Computation

This alternate method has several advantages over the original energy savings computation. The original computation relied on making a somewhat arbitrary choice for \( r_W \) and \( r_B \) in *Strategy Wake*. The alternate method does not rely on the individual values, but only on their ratio \( R \). Moreover, solving for \( r_{Bw}^* \) is essentially solving a linear equation, which is much less computationally expensive than finding a solution numerically.

Most advantages of the alternative computation of energy savings over the original stem from having explicit expressions to analyze. For instance, Proposition 4.2.1 gives us explicit conditions on the parameters to guarantee a stable solution for *Strategy Wake*, in addition to a condition on \( \alpha \) (see Proposition 4.3.1) to ensure the model behaves as expected. In the original computation, the only way to tell if a certain set of parameters would produce results was to run the computation. These given restrictions aid in choosing appropriate parameter values in the original calculation. We also get an expression in the parameters for \( \lambda_T^* \) (4.4.1), the maximum achievable \( \lambda \). Furthermore, this formulation allows for a deeper mathematical analysis, as differentiation of the results is possible.

Unfortunately, taking partial derivatives of the energy savings expression provides inscrutable results due to the number of parameters and the complicated expression.
However, faster numerical analysis at least allows us to survey more of these results in a reasonable amount of time. In particular, we find that the varying parameters $p_B$, $p_W$, and $m_C$ has little effect on energy savings. This matches our results in the original energy savings computation, but more extensive testing shows robustness with respect to sensitivity of parameters (see Fig. 4.2 for sample plots).

Finally, we want to demonstrate that this alternate method provides a good approximation for the smooth approximation model (see Section 2.3) via averaging (see Section 2.4). To show this, we first need a lemma.

**Lemma 4.5.1.** Recall the definitions

$$
\tilde{r}_{BC}(\delta) = \int_0^1 \tilde{r}_B(t, \delta)C(t) \, dt
$$

(see Section 2.3) and

$$
\bar{r}_{BC} = \int_0^1 r_B(t)C(t) \, dt.
$$

We have $\lim_{\delta \to 0^+} \tilde{r}_{BC}(\delta) = \bar{r}_{BC}$.

**Proof.** We see that

$$
|\tilde{r}_{BC}(\delta) - \bar{r}_{BC}| = \left| \int_0^1 (\tilde{r}_B(t, \delta) - r_B(t))C(t) \, dt \right|
\leq m_C(1 + \alpha) \int_0^1 \left|\tilde{r}_B(t, \delta) - r_B(t)\right| \, dt.
$$

Proposition 2.3.4 gives us the result. \qed

Next, we consider the systems

$$
\begin{cases}
\dot{y}(t; \delta) = \varepsilon \left( p_W \tilde{r}_W + p_B \tilde{r}_B y - \tilde{r}_{BC}(\delta) \frac{y}{1 + y^2} \right), \\
y(0) = y_0
\end{cases}
$$

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Figure 4.2: Sample plots for (alternate) energy savings varying a) $p_W$ ($p_B = 0.7$, $m_C = 5$, $R = 1$), b) $p_B$ ($p_W = 1.3$, $m_C = 5$, $R = 1$), and c) $m_C$ ($p_W = 1.3$, $p_B = 0.7$, $R = 1$), and d) $R$ ($p_W = 1.3$, $p_B = 0.7$, $m_C = 0.5$). The flatness is similar to results in the original energy savings computation. Changing other parameter values for the alternate energy savings computation shows similar flatness, as well. Domains in these graphs are based on (4.2.1) and (4.3.8). Parameter Values: $\alpha = 0.5$, $t_s = 1/3$, $\lambda_T = 0.4$, $\rho = 0.3$, $R = 1$. 

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which is the average of the smooth approximation given in \((2.4.7)\), and a modified version of \((4.1.1)\),

\[
\begin{aligned}
\dot{z}(t) &= \varepsilon \left( p_W r_W + p_B r_B z - r_{BC} \frac{z}{1 + z^2} \right) \\
 z(0) &= z_0
\end{aligned}
\]

\( (4.5.1) \)

**Proposition 4.5.2.** Let \(y^*(\delta)\) be the stable fixed point of \((2.4.7)\) and \(z^*\) be the stable fixed point of \((4.5.1)\), when they exist. For \(\varepsilon_0 > 0\), there exists \(\delta > 0\) such that 

\[ |z^* - y^*(\delta)| < \varepsilon_0. \]

**Proof.** \(z^*\) is the smaller positive root of

\[ p_B r_B z^3 + p_W r_W z^2 + (p_B r_B - r_{BC}) z + p_W r_W \]

and \(y^*(\delta)\) is the smaller positive root of

\[ p_B \tilde{r}_B z^3 + p_W r_W z^2 + (p_B r_B - \tilde{r}_{BC}(\delta)) z + p_W r_W \]

Lemma 4.5.1 and the fact that roots of polynomials are continuously dependent on their coefficients give the statement.

Proposition 4.5.2 in particular says that \(\lim_{\delta \to 0^+} y^*(\delta) = z^*\). In this sense, we say that this alternate energy savings method is a good approximation for \((2.4.7)\), as calculating energy savings relies on these fixed points. In turn, we have \((2.4.7)\) is a good approximation for the smooth approximation model \((2.3.2)\) times \(\varepsilon\), via the averaging theorem (Theorem 2.4.1).

To end this section, we provide plots of energy savings using both the original and alternate method as anecdotal evidence that they provide similar results.
Figure 4.3: Energy Savings using original calculation (black) and alternate calculation (green) varying parameters a) $\lambda_T$ ($\rho = 0.3, t_s = 1/3$), b) $t_s$ ($\rho = 0.3, \lambda_T = 0.4$), and c) $\rho$ ($\lambda_T = 0.4, t_s = 1/3$). Parameter Values: $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $\alpha = 0.5$, $R = 1$. 
5.1 Background

5.1.1 Energy Acquisition

If the ultimate evolutionary function of sleep is energy allocation, then differences in fitness (reproductive success or survival) will result in the optimization of energy allocation phenotypes over evolutionary time. For this study of optimization, we combine the Energy Allocation model of sleep with ideas from optimal foraging theory.

Models in optimal foraging theory assume that “the fitness of a foraging animal is a function of the efficiency of foraging.” [58] Such efficiency is measured in terms of some “currency,” often measured in intake rate (or net energy yield/feeding time), that correlates with fitness [65]. Instead of intake rate, the currency we use is net energy, with the constraint that biological debt ($D$) must be maintained at a moderate level. We have some choice as to what time scale to use: we may require $D$ to be periodic and try to optimize net energy on the time scale of a day, or we may require $D$ to be below some threshold and measure net energy on an “infinite” (lifetime) timescale with discounted futures (see Section 5.1.2). Although we adopt the latter approach here, we will sometimes see results where $D$ is periodic after all, so that we may discuss daily net energy.

For our purposes here, optimizing energy allocation over the course of a day is
the same as determining the optimal sleep-wake schedule. Because of this, we don’t assume a sleep quota ($t_s$) as we did when calculating energy savings. Instead, total sleep time per day is determined as a result of the optimization.

For our energy acquisition function, we use a modified version of the Jeschke steady-state satiation equation [35, 36],

$$Q = \begin{cases} 
\frac{1 + ad(b + c) - \sqrt{1 + ax(2(b + c) + ad(b - c)^2)}}{2abcd} & a, b, c, d > 0 \\
\frac{ad}{1 + abd} & b > 0, c = 0 \\
\frac{ad}{1 + acd} & b = 0, c > 0 \\
ad & b = c = 0 \\
0 & a = 0 \text{ or } d = 0
\end{cases} \quad (5.1.1)$$

where $Q$ is the energy acquisition rate, $a$ is the success rate (of encountering and acquiring food), $b$ is handling time per item of prey (the sum of attacking time and eating time), and $c$ is the digestion time per item of prey, and $d$ is the density of prey. The case where $b > 0, c = 0$ is exactly the Holling disk equation [30]. Notably, the energy acquisition has diminishing returns; as $d \to \infty$, the marginal rate goes to 0.

In our modification, we have a circadian component, ($C_Q$) so that success rate ($a$) depends on time of the circadian day. We assume that $C$ in (1.3.8), the efficiency of addressing biological investment ($I$), is exactly out of phase with $C_Q$, so that while circadian $I$ efficiency is upregulated, success rate efficiency is downregulated and vice versa. Furthermore, the circadian amplitude parameter ($\alpha$) plays the same role for both $C$ and $C_Q$; one value governs circadian amplitude for both. Not having $t_s$ as a parameter means we must re-define $C$ for this section. We define $C$ and $C_Q$ as

$$C(t) = m_C \left(1 - \alpha \sin (2\pi t)\right) \quad (5.1.2)$$

$$C_Q(t) = m_Q \left(1 + \alpha \sin (2\pi t)\right) \quad (5.1.3)$$
Additionally, we assume that the success rate $a$ is proportional to energy put toward waking effort ($r_W$). Therefore, we write $a(t) = r_W(t)C_Q(t)$.

We use parameter estimates of Jeschke [35] as a guide for parameters in our model.

### 5.1.2 Markov Decision Processes

**Introduction**

We model the problem of optimally allocating energy according to a schedule as a finite discrete infinite-horizon [57] Markov Decision Process (MDP). The definitions and discussion we give here follows [73]. MDPs can be thought of in the following way: an agent takes actions based only on a system’s current state (Markov). Making decisions and transitioning from state to state gives an reward. A particular finite MDP is defined by its finite state and action sets and by the one-step dynamics of the environment. Given any state and action, $s$ and $a$, the probability of each possible next state, $s'$, is

$$
\mathcal{P}_{ss'} = \Pr\{s_{t+1} = s'|s_t = s, a_t = a\}.
$$

There are called transition probabilities, and they add up to 1, i.e.

$$
\sum_{s'} \mathcal{P}_{ss'} = 1.
$$

Similarly, given any current state $s$ together with an action taken in that state $a$, there is a reward value, $R_s^a$. The state at time $t$ is $s_t$, the action taken at time $t$ is $a_t$, and the reward earned at time step $t$ is denoted $r_t$.

**Policy and Value Functions**

A policy, $\pi$, is a mapping from the set of states to the set of actions that prescribes an action based on the system being in a given state. A value, $V$, is a mapping from the set of states to $\mathbb{R}$, the real numbers. Given a policy, and a state $s$, the value
\( V^\pi(s) \) is defined as the expected value of the total reward assuming the system starts in state \( s \) and follows \( \pi \) thereafter. We write

\[
V^\pi(s) = E_\pi \left( \sum_{t=0}^{\infty} \gamma^t R_{st}^{\pi(a)} \mid s_0 = s \right),
\]

where \( 0 < \gamma < 1 \) is the discount factor. For values of \( \gamma \) close to 0, future decisions are discounted heavily whereas for values of \( \gamma \) close to 1, future decisions have more weight.

We now derive useful formulation for \( V^\pi \), known as the Bellman equation:

\[
V^\pi(s) = E_\pi \left( \sum_{t=0}^{\infty} \gamma^t R_{st}^{\pi(a)} \mid s_0 = s \right)
= \mathcal{R}_s^\pi(s) + E_\pi \left( \sum_{t=1}^{\infty} \gamma^{t-1} R_{st}^{\pi(a)} \mid s_0 = s \right)
= \mathcal{R}_s^\pi(s) + \gamma \sum_{s'} \mathcal{P}_{ss'}^{\pi(a)} E_\pi \left( \sum_{t=1}^{\infty} \gamma^{t-1} R_{st}^{\pi(a)} \mid s_1 = s' \right)
= \mathcal{R}_s^\pi(s) + \gamma \sum_{s'} \mathcal{P}_{ss'}^{\pi(a)} V^\pi(s') \tag{5.1.4}
\]

The Bellman equation tells us that if we know all \( \mathcal{P} \) and \( \mathcal{R} \) values, finding \( V^\pi \) is a matter of solving a system of linear equations.

We want to define what it means for a policy to be “optimal.” As a first step, we define an equivalence relation on policies: \( \pi \sim \pi' \) if and only if \( V^\pi(s) = V^{\pi'}(s) \) for all \( s \) in the state space, i.e. policies are equivalent when their value functions are the same. We abuse notation by referring to an equivalence class by one of its members.

We may put a partial order on this set of equivalence classes: \( \pi \geq \pi' \) if and only if \( V^\pi(s) \geq V^{\pi'}(s) \) for all \( s \) in the state space. When it exists, a policy greater than all others in this partial ordering is called an optimal policy, we call it \( \pi^* \). Under the setup provided here, it is obvious that an optimal policy exists, as there are only finitely many of them. The practical goal of MDPs is to find an optimal policy. One
important object for finding an optimal policy is the Bellman optimality operator, described in the next section.

**The Bellman Optimality Operator**

In this section, we mostly follow [70, 73, 74].

The methods used to find optimal policies for MDPs were developed first by Bellman [6], using principles of what he termed “dynamic programming.” When optimizing, we keep in mind Bellman’s Principle of Optimality:

An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision. [6]

To demonstrate how to find an optimal policy, we will use tools called Bellman Operators, which operate on value functions. For a given value function $V$, define the Bellman Optimality Operator $T^*$ state-wise:

$$(T^*V)(s) = \max_a \left( R_a^s + \gamma \sum_{s'} P_{as'}^s V(s') \right),$$

where the sum is over the set of all states, and the maximum over the set of all actions.

**Note 5.** Note that the value function $T^*V$ has an associated policy, by taking the actions chosen to produce the maximum.

Given a policy, we may use $T^*$ to “improve” the policy, according to the partial ordering of policies. Suppose we are given a policy $\pi$. Abusing notation, we define the policy $T^*\pi$ as follows:

$$(T^*\pi)(s) = \arg \max_a \left( R_a^s + \gamma \sum_{s'} P_{as'}^s V^\pi (s') \right),$$
where \( \text{argmax} \) is the maximizing argument (as opposed to the maximum value). With this definition, note that

\[
T^* V^\omega = V^{T^* \omega}.
\]

Therefore, (5.1.4) tells us that

\[
V^{T^* \omega}(s) = T^* V^\omega(s) \geq V^\omega(s)
\]

for all \( s \), and thus

\[
T^* \omega \geq \omega,
\]

(5.1.5)

where \( \geq \) is the partial order for (equivalence classes of) policies.

Suppose that the MDP has \( n \) states. The we may identify the space of value functions with the space \( \mathbb{R}^n \). This space is a Banach space when equipped with the sup norm, \( ||V||_\infty = \max_s |V(s)| \). Because \( T^* \) operates on a Banach space, we can show that it has a unique fixed point if it is a contractive map, using the Banach fixed point theorem. We show that it is indeed a contractive map.

**Proposition 5.1.1.** \( T^* \) is a contractive map on the space of value functions (i.e., for value functions \( V_1 \) and \( V_2 \), \( ||T^* V_1 - T^* V_2||_\infty \leq c ||V_1 - V_2|| \) for some \( 0 < c < 1 \)).

**Proof.** Suppose value functions \( V_1 \) and \( V_2 \) are given. We see

\[
||T^* V_1 - T^* V_2||_\infty = \max_s |T^* V_1(s) - T^* V_2(s)|
\]

\[
= \max_s \left| \max_a \left( \gamma \sum_{s'} P_{ss'}^a V_1(s') \right) - \max_a \left( \gamma \sum_{s'} P_{ss'}^a V_2(s') \right) \right|
\]

\[
\leq \max_s \left| \max_a \left( \gamma \sum_{s'} P_{ss'}^a (V_1(s') - V_2(s')) \right) \right|
\]

\[
\leq \max_s \left| \max_a \left( \gamma \max_s \left( |V_1(s) - V_2(s)| \right) \sum_{s'} P_{ss'}^a \right) \right|
\]

\[
= \gamma \max_s \left( |V_1(s) - V_2(s)| \right)
\]
Because \(0 < \gamma < 1\), \(T^*\) is a contractive map.

Therefore, the Banach fixed point theorem tells us that \(T^*\) has a unique fixed point, and that fixed point is \(\lim_{k \to \infty} (T^*)^k(V)\) for an arbitrary value function \(V\). We may use \(T^*\) to verify that our policy is indeed optimal.

The fixed point of \(T^*\) also satisfies the property that its value at any given state is the maximum such value among all policies.

**Proposition 5.1.2.** For \(s\) a state define the value function, define

\[
V^*_s = \max_{\omega} V^{\omega}_s.
\]  

\(V^*_s\) is the fixed point of \(T^*\). In other words, \(V^*_s\) satisfies

\[
V^*_s = \max_a \left( R_s^a + \gamma \sum_{s'} P_{ss'}^a V^*_s(s') \right),
\]

the Bellman optimality equation.

**Proof.** Re-writing (5.1.6) using (5.1.4) gives

\[
V^*_s = \max_{a,\omega} \left( R_s^a + \gamma \sum_{s'} P_{ss'}^a V^{\omega}_s(s') \right)
= \max_a \left( R_s^a + \gamma \sum_{s'} P_{ss'}^a \max_{\omega} V^{\omega}_s(s') \right)
= \max_a \left( R_s^a + \gamma \sum_{s'} P_{ss'}^a V^*_s(s') \right)
\]

Note that in (5.1.6), it was not assumed that different states would use the same maximizing policy. Proposition 5.1.2 tells us, among other things, that \(V^*_s\) is in the
image of $T^\ast$. By Note 5, $V^\ast$ has an associated policy, call it $\varpi^\ast$. We see that $V^\ast$
satisfies the Bellman equation (5.1.4) for $\varpi^\ast$,

$$V^\ast = \mathbb{R}_s \varpi^\ast(s) + \gamma \sum_{s'} P_{ss'}^{\varpi^\ast}(s)V^\ast(s'),$$

thus $V^\ast = V^{\varpi^\ast}$. By (5.1.6), we see that for any given policy $\varpi$, $V_\varpi(s) \leq V^\ast(s) =
V^{\varpi^\ast}(s)$ for all $s$. Therefore, $\varpi^\ast \geq \varpi$ for any policy $\varpi$, so it is the optimal policy
(equivalence class).

**The Policy Iteration Algorithm**

In this section, we offer methods of finding optimal policies.

One method that suggests itself is to choose an arbitrary value function $V$ and
repeatedly apply the Bellman optimality operator $T^\ast$ to $V$ until below some desired
error. When this happens, record the optimal policy. This so called “value iteration”
process may converge slowly.

Another method to find the optimal policy is “policy iteration.” [33] For this
method, start with an arbitrary policy $\varpi$. Compute $V^\varpi$ by solving a system of linear
equations. Next, find the optimal policy for $V^\varpi$ and update $\varpi$. Repeat this process
until $\varpi$ stops changing. We use this method, as it is guaranteed to terminate in a
finite number of steps and give an exact solution.

**5.1.3 Finite Markov Chains**

We include some brief remarks here on Markov Chains, mostly following [29].

Consider a system that can be in any of a finite set of states. Let the system be
observed at discrete moments of time $n = 0, 1, 2, \ldots$, and let $X_n$ denote the state
of the system at time $n$. Let the $X_n$ be random variables defined on a common
probability space. Suppose the transition probabilities between states satisfy the
Markov property:

\[ \Pr(X_{n+1} = s_{n+1}|X_0 = s_0, \ldots, X_n = s_n) = \Pr(X_{n+1} = s_{n+1}|X_n = s_n) \]

for every non-negative integer \( n \) and every choice of \( s_i \) in the state space. Furthermore, suppose the transition probabilities are not dependent on \( n \). We call such a stochastic process a finite Markov Chain ("finite" refers to the state space). For states \( s \) and \( s' \), call the probability of transition from \( s \) to \( s' \) \( \mathcal{P}_{ss'} \). A finite Markov chain has as an associated probability matrix \( \mathcal{P} \).

This notation is suggestive of our notation for transition probabilities in a Markov decision process. Indeed, an MDP together with a policy \( \varpi \) induce a Markov chain with the same state space and transition probabilities

\[ \mathcal{P}_{ss'} = \mathcal{P}_{\varpi(s)} \quad (5.1.8) \]

Therefore, after we have found an optimal policy for an MDP, we analyze the induced Markov chain.

We now give some definitions of helpful properties of Markov chains. Again, definitions and discussions are from [29].

A state \( s \) is recurrent if the probability of starting at \( s \) and returning to \( s \) in finite time is 1. Otherwise, a state is transient.

A nonempty set \( C \) of states is closed if no state inside \( C \) leads to any state outside of \( C \), i.e. \( \mathcal{P}_{ss'} = 0 \) when \( s \in C \) and \( s' \notin C \). We may construct a subchain of a Markov chain using \( C \) as the state space.

A closed set \( C \) is called irreducible if \( \mathcal{P}_{ss'} > 0 \) for all choices of \( s, s' \in C \). A closed set \( C \) is called recurrent is every state is recurrent. If an finite closed set is irreducible, then it is recurrent.
The period of a state $s$ is defined

$$\text{gcd} \{n \geq 1: (\mathcal{P}^n)_{ss} > 0\},$$

all states in an irreducible chain have the same period. If the period is 1, we say the chain is aperiodic.

Suppose $\pi(s)$ is defined for all $s$ in the state space such that $\pi(s) > 0$ for all $s$ and $\sum_s \pi(s) = 1$. We call $\pi$ a distribution. A stationary distribution is a distribution that satisfies

$$\sum_s \pi(s) \mathcal{P}_{ss'} = \pi(s').$$

The idea here is that if $\pi(s)$ is the probability that the system is in state $s$ for all $s$, then after one step forward in time, the probability the system will be in state $s$ is the same.

An important fact we will use about stationary distributions is in the following theorem, which we state here without proof [29]:

**Theorem 5.1.3.** A irreducible finite Markov chain has a stationary distribution. Furthermore, if the chain is aperiodic, then

$$\lim_{n \to \infty} (\mathcal{P}^n)_{ss'} = \pi(s'),$$

i.e., the stationary distribution is the “long term distribution.”

We will use these facts later when we analyze optimal policies.

### 5.2 Problem Setup

For our MDP, we “discretize” the differential equation, (1.3.7). We consider discrete time steps, discrete levels of $\mathcal{D}$, and discrete behavioral strategies (energy allocations). First, we choose a discrete time step, $\Delta t = \frac{1}{n_C}$, where $n_C$ is the number of discrete
circadian periods in one day. Next, we choose a discrete \( D \) step, \( \Delta D \). By Proposition 2.2.3, when \( D > \beta = \sqrt{\frac{m_C(1 + \alpha)}{p_B}} - 1 \), it cannot recover. Therefore, we round \( \beta \) down to the nearest multiple of \( \Delta D \) less than \( \beta \) (call it \( n_D \Delta D \)), and consider the discrete set of \( D \) levels \( \{\Delta D, 2\Delta D, \ldots, n_D \Delta D\} \). Finally, we choose \( n_\eta \) discrete behavioral strategies. A behavioral strategy is a triple \((r_W, r_B, F)\), where \( r_W \) and \( r_B \) are positive real numbers, and \( F \) is a boolean that determines whether or not the animal is acquiring energy (foraging) in the state. Here, we call the behavioral strategies active wake, quiet wake, sleep, torpor, and death. Active wake is the only time \( F \) is True.

The set of states for our MDP may be indexed by an ordered triple \((s_C, s_D, s_\eta)\), where \( s_C \) denotes circadian time of day, \( s_D \) denotes \( D \) level, and \( s_\eta \) denotes behavioral state (see Fig. 5.1). There is a death state at every circadian time, indexed by the triple \((s_C, 0, 0)\). If the system is not in a death state, it can be in any of the other behavior states and any other of the \( D \) levels. Note that there are \( n_C(4n_D + 1) \) total states.

There are restrictions on possible state transitions. States may only proceed from one circadian state to the next, i.e.

\[
s_C \to s_C + 1 \pmod{n_C}.
\]  
Furthermore, states transition to \( D \) levels based on the current state and (1.3.7). Specifically, given a state \( S = (s_C, s_D, s_\eta) \), with \( s_\eta = (r_W, r_B, F) \), we define the \( D \) transition function \( T_D \)

\[
T_D(S) = \left[ s_D + \Delta t \left( p_W r_W + p_B r_B s_D - r_B C(s_C) \frac{s_D}{1 + s_D^2} \right) \right]_{\Delta D},
\]

where \( \left[ \cdot \right]_{\Delta D} \) rounds to the nearest multiple of \( \Delta D \) (with x.5 multiples rounded to the nearest even multiple). Thus, a state may only transition to five possible states corresponding to behavior states; \( s_C \) and \( s_D \) are determined (see Fig. 5.2).
Figure 5.1: A schematic diagram for the states of the Markov Decision Process. The states are grouped by common $s_C$ in rounded rectangles and common $s_D$ in rectangles, here indexed by multiple of $\Delta t$ and $\Delta D$, respectively. States of the same color represent the same $s_\eta$ (green is active wake, yellow is quiet wake, red is sleep, blue is torpor, and grey is death). The arrows represent time moving forward one step. This process repeats every day in a cyclic fashion; note the “clock-like” shape.
Figure 5.2: A schematic diagram for the possible transitions in the Markov Decision Process. A state may transition to either death (if it is already in death or if $T_D(S) > n_D \Delta D$), or one of the other behavior states (active wake, quiet wake, sleep, and torpor) at a determined circadian level (5.2.1) and $D$ level (5.2.2). The decision or action to be made determines transition probabilities to those states.
A death state may only transition to another death state. A non-death state leads to death at the point when \( T_D(S) > n_D \Delta D \). We interpret this not as instant death of the organism, but that death is inevitable from this point. For all practical purposes, the system is in the death state.

We assume that from each state, there is a finite set of decisions (or actions) to choose. A decision is not necessarily the decision to transition into a particular behavior state (e.g., a “decision” to sleep), but instead a decision determines transition probabilities. See Fig. 5.3 for an example of decisions.

![Figure 5.3: Possible decisions in the MDP. In this arbitrary example, we are given the choice between two decisions. One decision gives the transition probabilities on the left, the other on the right. A decision is not necessarily a decision to enter a behavioral state, but a decision between probability distributions.](image)

Finally, we discuss rewards. The rewards are based on net energy, as that is our object of optimization. When \( F \) is True (in our case, only in active wake), the reward is

\[
\Delta t \left( Q(s_C, r_W) - (r_W + r_B) \right),
\]

where \( Q \) is defined in (5.1.1). The time \( s_C \) determines the value of \( C_Q \). On the other hand, when \( F \) is False, the reward is \(- (r_W + r_B) \Delta t \). The exception is when entering
death state from a non-death state. There must be some disincentive for death in the model (and it cannot be $-\infty$, otherwise the model could not distinguish death soon and death eventually), so we choose it to be some negative number, large in absolute value (we use $-1000$, for instance). When in a death state, the only action the decider can take is to stay in death; transitioning from death to death produces a reward of 0. Finally, we don’t want to discount the future too much in our model, so we choose values of $\gamma$ close to 1.

5.3 Numerical Experiments

Given a set of decisions, we try to find an optimal policy by methods described above, assuming the decider has perfect information. A given MDP and policy together is a Markov chain, in our analysis of the results, we analyze the Markov chain given by the optimal policy.

With the MDP described above, we run three different numerical experiments to find optimal policies, which we call Trials 1, 2, and 3.

Recall that a behavior state is defined by the triple $(r_W, r_B, \mathcal{F})$. For all trials, we use parameters $p_W = 1.3$, $p_B = 0.7$, $m_C = 5$, $\alpha = 0.5$ (thus, $\beta \approx 3.1168$), $m_Q = 0.5$, $b = 0.02$, $c = 0$, $d = 10$, and $\gamma = 0.999$. Furthermore, in order to discuss division of labor, we introduce the parameter

$$\lambda_W = \frac{r_W - r_B}{r_W + r_B}, \quad (5.3.1)$$

which reflects the extent to which waking effort is upregulated at a given time. We take $\lambda_W \geq 0$ to mean the system is “awake,” and $\lambda_W < 0$ to mean the system is “asleep.” Additionally, we assume that wake and torpor have the same $\lambda_W$, but a lower total metabolic rate.
5.3.1 Trial 1

We start with a straightforward deterministic model; that is, all transition probabilities are either one or zero. The decider gets to decide to which behavioral state it wants to go, and it gets its way (e.g., if the decider decides to go to sleep in the next time step, it will). We assume the decider will never decide to enter the death state while alive. The only way to enter the death state is if $D$ gets too high.

We use the four behavior states of active wake $(8.75, 1.25, True)$, quiet wake $(3.25, 1.75, False)$, sleep $(0.875, 2.625, False)$, and torpor $(0.1875, 0.5625, False)$. Alternatively, we may say that active wake has $M = 10$, $\lambda_W = 0.75$; quiet wake has $M = 5$, $\lambda_W = 0.3$; sleep has $M = 3.5$, $\lambda_W = -0.5$; and torpor has $M = 0.75$, $\lambda_W = -0.5$. We take $\Delta D = 0.01$, so $n_D = 311$. We also take $\Delta t = 1$ hour, so $n_C = 24$.

We find an optimal policy by by using the policy iteration algorithm [33]. We start with a value function that is identically 0. Applying the Bellman optimality operator induces a policy, which is our starting policy for policy iteration. Call the optimal policy we find $\pi^*$. We numerically verified this is indeed the optimal policy by showing that the Bellman optimality operator fixes $V^*$.

The optimal policy $\pi^*$ induces transition probabilities via (5.1.8). If we order the states lexicographically via their triples $(s_C, s_D, s_\eta)$ (the ordering of the $\eta$ position doesn’t matter), we see that $P^{nc}$ is block diagonal with block size $4n_D + 1$, as after $n_C$ time steps, the system is in the same circadian state in which it started (so, periodic). In each block, the upper- and leftmost element is 1, as this is the probability that the system is dead given it was dead yesterday. We analyze the subchains that these blocks represent.

We use Mathematica’s MarkovProcessProperties to analyze the Markov chain represented by the transition matrix $P^{nc} = P^{24}$. For Trial 1, we find that from any
initial state, the system settles into two cycles, or periodic policies. One cycle is the death cycle. We look at the non-death cycle.

The cycle has a period of 48 hours, or 2 days. Notably, the behavior of quiet wake is never chosen in this cycle. This is unsurprising, as being in quiet wake has no advantages in this trial; much energy is spent, none is acquired, and $\mathcal{D}$ is insufficiently addressed. For this cycle, over a 48-hour period, 9 hours are spent in active wake, 18 hours in sleep, and 21 hours in torpor (per day, that is 4.5 hours in active wake, 9 hours in sleep, and 10.5 hours in torpor). Torpor seems to be the optimal policy at points in the day when neither $C$ nor $C_Q$ is particularly high (that is, points when neither addressing $I$ nor acquiring energy is particularly efficient). See Fig. 5.4 for a summary.

![Figure 5.4: Trial 1 results. a) Long-term optimal policy with $\mathcal{D}$ (red). Average $\mathcal{D}$ for this policy: 1.041 (compare to $\beta \approx 3.117$). b) Long-term optimal policy with accumulated net energy (green). For this optimal policy, net energy is increasing. The horizontal axis is time in hours. The blue dots indicate behavioral state.](image)
5.3.2 Trial 2

In Trial 2, we move away from a deterministic model to a stochastic model. All of the parameters are the same as in Trial 1, as well as the methods for finding the optimal policy and analyzing the results.

In Trial 2, the decider may again choose what behavior state to enter into, but it may not get its way; there is a chance it will enter the sleep state. The probability of entering the sleep state increases as $D$ rises. We define the $D$-sleep function

$$ S(D) = \begin{cases} 
0.1 & \text{if } 0 < D < 1 \\
0.5 & \text{if } 1 \leq D < \sqrt{3} \\
0.8 & \text{if } \sqrt{3} \leq D < \beta \\
0 & \text{if } D \geq \beta 
\end{cases} $$

We may think of $S$ as the probability that you enter the sleep state given that you have not chosen to sleep. The points $D = 1$ and $D = \sqrt{3}$ were chosen because they are the point at which a local maximum occurs and an inflection point for $\frac{D}{1 + D^2}$ (an expression that appears in (1.3.7) and contributes to efficiency in addressing $I$), respectively.

We again consider blocks of $P^n$ each of which represents one circadian time. Within each of these blocks, we look for irreducible subchains. We seek stationary distributions of these irreducible subchains, which we know exist by Theorem 5.1.3. Moreover, this theorem also tells us that they describe long term behavior because these subchains are aperiodic.

For each circadian time, there are two irreducible subchains: the death subchain consisting of that one state, and a non-death one. We analyze the non-death irreducible subchains.
Figure 5.5: Distributions over behavioral states for each circadian time for Trial 2. We computed stationary distributions for non-death irreducible subchains (one non-death subchain per circadian time), and summed probabilities over all states with the same behavioral state. Horizontal axis is circadian time, and vertical axis is probability.

Figure 5.5 gives a summary of probabilities the system will be in a certain behavioral state at a given circadian time. With this information, we may compute the expected value of time spent in each behavioral state per day: 5.18 hours in active wake, 11.55 hours in sleep, and 7.27 hours in torpor. Note that, as in Trial 1, no time is spent in quiet wake (we posit the same reasons for this as in Trial 1).

Given a stationary distribution, we may also compute the expected value of $D$ at a given circadian time (Fig. 5.6). When we average over the course of one day, we find that average daily $D$ is approximately 0.9181.
5.3.3 Trial 3

Trial 3 is substantially different that Trials 1 and 2. One issue with Trials 1 and 2 are that they predict no quiet wake in an optimal policy, a prediction at odds with biological observations. In order to remedy this, we introduce a predation risk; it is now possible for the system to enter death stochastically, rather than dying only by having elevated $D$.

The principle we use here is that an organism is in less danger when vigilant (awake) than it is when not vigilant (asleep, or in torpor). Furthermore, we assume that an organism is in danger during the period of time in the day when its predators are active. In this particular trial, this corresponds with times when $C_Q$ is greatest. Thus, there is a trade-off: acquiring energy at a time that is efficient but risky vs. a time that is inefficient but safe.

Additionally, we split sleep into two behavior states (REM and NREM) so that there are now six behavior states (active wake, quiet wake, REM sleep, NREM sleep, torpor, and death). We assume REM and NREM have the same total metabolic rate,
but the value of $|\lambda_W|$ is greater in REM (see description of the Energy Allocation model, Section 1.2). Torpor has the same value of $\lambda_W$ as NREM.

We assume that REM sleep can only happen at low levels of $C_Q$ here, corresponding to certain circadian times of day. To justify this assumption, we note that the phase of $C_Q$ is the same as that of process $C$ in the two-process model [9], and process $C$, in turn, mirrors temperature rhythms. In the two-process model, there is only propensity for REM sleep near the nadir of the curve for process $C$.

One aspect of the EA Model is that REM sleep eliminates thermoregulatory defense and skeletal muscle tone, thereby enhancing energy allocation for somatic functions and functions related to the central nervous system [64]. Here, that is reflected by increasing $r_B$ and decreasing $r_W$ during REM. Furthermore, because of the loss of thermoregulatory defense and the need for homeostasis, we don’t allow the system to be in REM for consecutive periods (here, our $\Delta t = 0.5$ hours).

We define the five behavior states of active wake $(1.75, 0.25, True)$, quiet wake $(0.65, 0.35, False)$, REM sleep $(0.1, 0.6, False)$, NREM sleep $(0.175, 0.525, False)$ and torpor $(0.0375, 0.1125, False)$. Alternatively, we may say that active wake has $M = 2$, $\lambda_W = 0.75$; quiet wake has $M = 1$, $\lambda_W = 0.3$; REM sleep has $M = 0.7$, $\lambda_W = -5/7$; REM sleep has $M = 0.7$, $\lambda_W = -0.5$; and torpor has $M = 0.75$, $\lambda_W = -0.5$.

We take $\Delta D = 0.001$, so $n_D = 3116$. We also take $\Delta t = 0.5$ hour, so $n_C = 48$.

In Trial 3, the decider may again choose what behavior state to enter into, but it may not get its way and the choices are restricted. There is a chance the system will enter the death state. If it does not enter the death state, the decider gets its way. We assume predators are active during circadian periods 1 to 28, and inactive from circadian periods 28 to 48. When there is a predation risk, the probabilities are as follows: if the decider chooses to enter the active wake or quiet wake state, the probability the system will enter death is 0.0001; if the decision is to enter REM
or NREM sleep, the probability is 0.02; and if the decision is to enter torpor, the probability is 0.1. Therefore, wake is “safe,” sleep is “moderately dangerous,” and torpor is “dangerous” (it is more difficult to arouse an organism in torpor).

The actions are restricted based on the state the system is in. We assume REM can only be entered into during circadian periods 28 to 44. We now list out possible decisions:

- If the system is in active wake, it can decide to either stay in active wake, or transition to quiet wake.

- If the system is in quiet wake and in a time when REM can be entered into, then it can decide to enter any state except torpor. If the time is not right for REM, then any state excluding torpor or REM.

- If the system is in REM sleep, it may decide to enter any state except REM sleep.

- If the system is in NREM Sleep and in a time when REM can be entered into, then it can decide to enter any state. If the time is not right for REM, then any state excluding REM.

- If the system is in torpor, it can decide to either stay in torpor, or transition to sleep (REM if the time is appropriate).

We are interested in long-term behavior of the system. If the system enters a death state, the long term behavior is uninteresting. Because the system only enters death or the decider’s preference, we study the behavior assuming the system never enters death (i.e. what happens when the decider gets its way). Thus, we analyze results in the same fashion as in Trial 1.
**Figure 5.7**: Trial 3 results. a) Long-term optimal policy with $\mathcal{D}$ (red). Average $\mathcal{D}$ for this policy: 0.9131 (compare to $\beta \approx 3.117$). b) Long-term optimal policy with accumulated net energy (green). For this optimal policy, net energy is increasing. The horizontal axis is time in hours. The blue dots indicate behavioral state.

For Trial 3, as in Trial 1, starting from any state will lead to one of non-death cycle. The period of the cycle is 2 days. Notably, the behavior state of torpor is never chosen in an optimal policy, presumably because of its danger. For this cycle, the average daily schedule is 4.75 hours in active wake, 9.25 hours in quiet wake, 4.5 hours in REM sleep, and 5.5 hours in NREM sleep.

### 5.4 Discussion

The trials in the section above are not meant to predict conditions found in nature, nor do they reflect data. Rather, they serve as examples of this optimization model and how optimal policies change in response to differing conditions.

We make some observations

- As we have already speculated, the absence of quiet wake in Trials 1 and 2 are due to it being a fairly useless state (no energy acquisition nor efficient addressing of $\mathcal{I}$, with relatively high energy expenditure). In Trial 3, quiet
The table below provides a summary of the trials in Section 5.3. Non-$D$ values are expected values of hours per day in an optimal strategy.

<table>
<thead>
<tr>
<th>Trial</th>
<th>Active Wake</th>
<th>Quiet Wake</th>
<th>Sleep</th>
<th>Torpor</th>
<th>Avg. $D$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trial 1</td>
<td>4.5</td>
<td>0</td>
<td>9</td>
<td>10.5</td>
<td>1.041</td>
</tr>
<tr>
<td>Trial 2</td>
<td>5.18</td>
<td>0</td>
<td>11.55</td>
<td>7.27</td>
<td>0.9181</td>
</tr>
<tr>
<td>Trial 3</td>
<td>4.75</td>
<td>9.25</td>
<td>10</td>
<td>0</td>
<td>0.9131</td>
</tr>
</tbody>
</table>

- Wake is no longer quite as useless, as it has less predation risk than sleep or torpor, and uses less energy than active wake.

- Torpor is chosen surprisingly often in Trials 1 and 2, given the system cannot acquire energy and $I$ is not addressed sufficiently. Its main utility seems to be limiting energy expenditure.

- The absence of torpor in Trial 3 is probably due to its relatively high risk of predation.

- Note that average $D$ tends to be near 1. We guess this is because the system is most efficient at addressing $I$ when $D = 1$ (because it maximizes $\frac{D}{1+D^2}$).

- It makes sense that more time is spent in sleep in Trial 2 compared to Trial 1, because of its design (stochastic pressure to sleep with high $D$).

- Trial 3 appears "greedy" with respect to REM sleep, i.e. the optimal policy includes REM sleep whenever possible (see Fig. 5.7). It is reasonable for REM sleep to be preferred over NREM sleep, as REM sleep expends the same energy while having a more significant impact on $I$. Presumably REM sleep is chosen
whenever possible in order to be able to go into active wake to acquire energy as often as possible.

• It is curious that in Trials 1 and 3, the optimal policy showed a cycle of 2 days. We propose that since these 2 days have nearly identical strategies (in behavior and $\mathcal{D}$), that this is due to the discretization of the model; rather than being a meaningful result, this is a side effect of the method.

While the trials above are not predictive, we may attempt to design numerical experiments to more closely match experimental and observed data by getting better estimates for parameter values. While the Energy Allocation Model [64] and other biological conditions were taken into consideration (including parameter estimates from [35]), further experimenting with conditions will be necessary to produce biologically accurate results.
Chapter 6

FURTHER DIRECTIONS AND FINAL REMARKS

6.1 Further Comments on the Model

Monitoring of biological debt, while normalizing meaningful comparisons of energy savings calculations across strategies, demonstrates a well-defined temporal pattern that we postulate may impact sleep regulation. Biological debt in the model generally increases during wake and decreases during sleep, a behavior resulting from biological requirements exceeding investments during wake and investments predominating during sleep. Both the circadian system and state-dependent $\lambda$ contribute to its temporal pattern. For example, in the absence of both circadian amplitude ($\alpha = 0$) and state-dependent biological repartitioning ($\lambda = 0$) the system has a stable fixed point, and thus the stable limit cycle solution is the degenerate one. However, the temporal pattern of biological debt becomes a circadian-influenced wave in the absence of $\lambda$ when $\alpha > 0$, reflecting circadian-dependent efficiencies in servicing biological requirements. Finally, biological debt is transformed from a wave into a curve resembling Process S of the two-process model (see [9,10]) as $\lambda$ is introduced (Fig. 6.1a).

Modeling over successive days with varying levels of sleep restriction reveals a temporal pattern of biological debt that we suggest may play a homeostatic role in sleep regulation. For example, small amounts of sleep restriction show small but stable elevations in daily biological debt (Fig. 6.1b), consistent with an increase in
Figure 6.1: Temporal pattern of biological debt. a) Biological debt ($D$) in graphical form is modified by $\lambda$. The daily rise and fall of $D$ is transformed from a sinusoid-like curve when $\lambda = 0$ and $\alpha > 0$ to an appearance resembling Process S in the two-process model [9] when state-dependent $\lambda$ is introduced. b) $D$ at varying levels of $t_s$ over 12 days. Dashed lines pass through average $D$ over the previous day. Small reductions in $t_s$ yield limit cycle solutions with higher average $D$. However, drastic reductions lead to loss of a stable limit cycle. Compare this to empirical effects of sleep loss on human neurobehavioral performance [48].
homeostatic sleep pressure. However, more significant reductions of sleep may lead to sudden escalations over multiple days. This behavior of biological debt models empirical effects of sleep loss on human neurobehavioral performance and is consistent with homeostatic sleep propensity [9, 10, 48]. We hypothesize that an inability to moderate biological debt may represent an “escape from homeostasis” [54]. The mechanistic link, however, between biological debt and known signals of homeostatic sleep pressure, such as extracellular adenosine [20, 56], remains to be elucidated.

Finally, we hypothesize that biological debt may ultimately govern sleep homeostasis. Biological systems that cyclically repartition operations over time, as with either circadian-dependent or state-dependent coupling, face trade-offs with respect to such resource allocations. On the one hand, our model suggests that repartitioning of operations conserves energy through efficiencies in resource utilization, a potential advantage for species influenced by the predictability of the Earth’s rotation and the daily cycling of its ecology. On the other hand, biological debt will rise if sleep-dependent processes are restricted through sleep deprivation.

6.2 Further Directions in Modeling

While we addressed the topic briefly in the optimization section, further work is required to assess the role of coupling specific biological functions with either rapid eye movement (REM) or NREM sleep to further exploit division of labor for energy conservation in endotherms as the Energy Allocation hypothesis postulates [64]. One way to address this is to introduce a thermoregulatory component to the model. In REM sleep, thermoregulatory defense is eliminated, as well as skeletal muscle tone, allowing energy to be shunted to somatic and central nervous system related functions [64]. By keeping track of temperature relative to a certain set point and
driven by both environment and energy expenditure, it may be possible to model appropriate times in the sleep cycle for REM sleep.

Performing all processes simultaneously ($\lambda = 0$) theoretically increases cellular infrastructure requirements, an additional energy cost not currently addressed in the model. The principle at work here is that division of labor and specialization allow for less “hardware” to grow or be maintained. It is possible that our energy savings calculation is an underestimate when this extra cellular infrastructure to handle constant wakefulness is taken into account.

Another future direction is to model a response to sleep deprivation. Schmidt [64] has proposed a sleep deprivation response in the Energy Allocation model (see Fig. 6.2) based on reactive and predictive homeostasis. This response comes in two stages: short-term and prolonged sleep deprivation. In short-term sleep deprivation, energy to address $I$ is still downregulated in wake, as the body does not predict sleep deprivation will continue. In prolonged sleep deprivation, energy to address $I$ is now upregulated in wake to address deficits; this is reactive homeostasis. Energy allocated to waking effort is not downregulated, in order to meet the demands of longer waking bouts. During recovery sleep after prolonged sleep deprivation, energy to address $I$ is upregulated to a greater extent than in normal sleep. This is due to both predictive and reactive homeostasis: reactive in that it addresses deficits, and predictive in that it is preparing for the next waking bout. Additionally, this model predicts that a dampening of the circadian amplitude could be a potential deprivation response. Modeling a sleep deprivation response would complement the current model, giving a more complete picture of the Energy Allocation model.
Figure 6.2: Energy Allocation, Sleep Deprivation, and Homeostasis. (Found in [64])
6.3 Further Directions in Optimization

Some obvious ideas for future trials in the current optimization setup include varying the parameters (transition probabilities and parameters from (1.3.7) and (5.1.1)) and noting the effects of these changes, adding a thermoregulatory component (as discussed earlier to aid in REM and NREM transitions), and imposing different restrictions on state transitions.

One direction we can take with this optimization is to consider a continuous-time, continuous-state Markov Decision Process [57]. We may treat optimizing net energy as a problem of optimal control, where the decider controls, in our case, $r_W$ and $r_B$ in order to maximize net energy. We may find optimal controls by using, for instance, the Pontryagin maximum principle, or the Hamilton-Jacobi-Bellman equation [16].

Another approach would be to have the decider acting with imperfect information in a stochastic environment, and find an optimal policy with Q-learning [73]. In this situation, the decider learns new information with each decision, and updates his knowledge accordingly. One advantage to Q-learning is that it is a reasonable model for foraging; an animal has imperfect information in a stochastic environment and updates knowledge after making decisions. Some examples of stochastic variables in this model are density of prey, predator risk, encounter rate, and success rate.
BIBLIOGRAPHY


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