Interacting Circadian and Homeostatic Processes with Opportunity Cost: A Mathematical Model of Sleep with Application to Two Mammalian Species *

James H. Cardon¹, Eric R. Eide¹, Kerk L. Phillips^{1,2}, and Mark H. Showalter¹

¹Brigham Young University, Department of Economics, Provo, UT, USA ²US Congressional Budget Office, Washington, DC, USA

July 9, 2018 version 2018.07.a

Abstract

This paper introduces a new model of sleep for mammals. It extends the classic two-process model of sleep to account for differences in external circumstances. We apply this model to previously-collected data on elephants and sloths, comparing sleep patterns in the wild with sleep patterns in captivity. We find that the model does very well in explaining sleeping patterns for both types of animals, in both the captive state and in the wild state.

keywords: sleep, opportunity cost, dynamic models, elephant, sloth, animals

JEL classification: I19, J22

^{*}Useful comments from Dan Hamermesh are gratefully acknowledged. The views expressed in this paper are the authors' and should not be interpreted as those of the Congressional Budget Office.

1 Introduction

All known life forms must sleep (Walker, 2017). As with other essential biological functions like eating and breathing, insufficient sleep can lead to serious biological consequences, including death Carskadon and Dement (2011).

The most widely-used mathematical model of sleep, typically referred to as the two-process model, combines two types of biological processes, the circadian cycle and sleep pressure (also referred to as homeostasis) (Borbély (1982), Borbély and Achermann (1999) and Rempe et al. (2010)). The circadian cycle is a roughly 24-hour pattern of alertness and fatigue that also leads to daily cyclical patterns of body temperature, hunger, metabolic rate, etc.

Sleep pressure increases the longer a subject is awake, with a corresponding increase in the physical desire to sleep. This combination of the circadian cycle and sleep pressure creates a deterministic prediction for sleep patterns and is widely used to explore sleep patterns in humans and animals.

The two-process model summarizes the underlying biological forces determining the sleep cycle. However, the model does not account for substantial day-to-day variation in sleep patterns. From an economic perspective, the model is incomplete in that it ignores the fact that sleep is costly because it implies forgoing other activities that contribute to well-being. Economists would say that sleep has an opportunity cost that varies substantially across individuals and over time. As an example of such an opportunity cost, consider that animals in captivity tend to sleep more than their counterparts in the wild. Although biologically identical, all else equal, the cost of sleeping is much lower in captivity than in the wild because such animals have no

need to forage for food or to avoid predators. That animals vary their sleep in order to take advantage of time-varying opportunities is evidence that the deterministic two-process model is incomplete.

The main contribution of this paper is to incorporate the economic concept of opportunity cost into the widely-used and deterministic two-process model of sleep. Specifically, we augment the two-process model to allow subjects to trade off gains from sleep derived from the sleep cycle with gains from alternative, productive uses of time. We illustrate our model with an application to elephants and sloths in the wild and in captivity. For these animals, the opportunity cost of sleep can be represented by activities such as foraging for food and avoiding predators. In the context of a mathematical model of sleep, we assume animals choose to sleep or wake in order to optimize a more general objective function incorporating gains from waking activities as well as from sleep. We show that this can lead to different and better outcomes for the animals than choices conforming to mechanical models of sleep. Since the value of waking activity changes over time and across individuals, the model generates predictions about how certain variables affect sleep. We also demonstrate that the two-process model is a special case of our economic model of sleep.

We find that our model appropriately matches sleep patterns for wild and captive elephants and sloths. The model predicts that the opportunity cost of sleep for wild elephants is eight times greater than for captive ones, and is five times greater for wild sloths than sloths in captivity. This provides an economic explanation for why these animals sleep more in captivity than in the wild.

The remainder of the paper proceeds as follows: section 2 provides mathematical details of our extension to the two-process model; section 3 uses

our model to explain sleep patterns of elephants and three-toed sloths in captivity and in the wild; section 4 concludes.

2 Models of Sleep

2.1 Two-Process Model

We now provide the details of the two-process model. In the next section we present a more general sleep model which allows for choice in the timing of sleep as a function of the opportunity cost of sleep. We take our discussion and notation from Skeldon et al. (2014), but adopt a discrete-time framework rather than their continuous-time setup.

There is a baseline circadian cycle, which we will denote y_t . This is a weighted sum of sine waves of various frequencies and will fluctuate between -1 and +1. There are upper and lower bounds related to this cycle. We denote these H_t^u and H_t^l :

$$H_{t+1}^{u} = \bar{H}^{u} + ay_{t}$$

$$H_{t+1}^{l} = \bar{H}^{l} - ay_{t}$$

$$\bar{H}^{u} > \bar{H}^{l}$$

$$(2.1)$$

The homeostatic process which determines sleep versus waking is denoted H_t . If waking it rises toward an upper asymptote of μ and if sleeping it falls toward a lower asymptote of zero.

$$H_{t+1} = \begin{cases} H_t e^{-1/\nu_S} & \text{if sleeping} \\ \mu + (H_t - \mu)e^{-1/\nu_W} & \text{if waking} \end{cases}$$
 (2.2)

where ν_W is the constant half-life decay for the homeostatic process when

awake and ν_S is the half-life when sleeping.

If the subject is awake, H_t rises until it reaches the upper bound of H_t^u . At this point the subject sleeps and H_t falls until it reaches the lower bound H_t^l . This is illustrated in Figure 1.

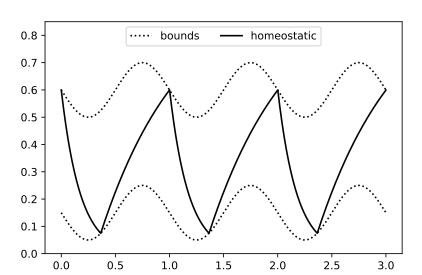


Figure 1: Two-Process Model

2.2 A Generalized Model

In the two-process model, the twin circadian bounds (H^u and H^l) determine the possibility of polyphasic sleep. Varying the parameters may admit the possibility for multiple sleep spells within a circadian cycle. When the homeostatic cycle is very steep (sleep pressure builds rapidly when awake and declines rapidly when asleep), the individual will cycle rapidly between sleeping and waking.

Now imagine there is an impediment or cost to switching between sleep

and waking. In this case, rather than switching instantaneously, the subject when waking would stay awake until the cost of switching to sleep fell below the loss due to distance from the central cycle. As we show below, this would lead to bounds on the homeostatic process very similar to those in the two-process model. In fact, if the switching cost were constant this would give us the exact upper and lower bounds hypothesized in that model. Both our model and the two-process model ignore the deeper cycles within the circadian cycle, such as REM and non-REM sleep. The physiological necessity of prolonged, restorative sleep justifies the assumption of a fixed cost of waking. A similar justification for non-sleep utility is that productive work (foraging or other work) also cannot be efficiently done in short bursts of activity and requires extended periods of time.

In addition, our model emphasizes the utility derived from waking activities, where utility is a general economic term used to define the well-being or welfare of a subject. Sleep restores physical and mental function to an optimal level, but at the cost of foregoing other activities which are also beneficial. Deviations from the mechanical sleeping behavior suggested by a model of circadian utility are common. Why might a subject be reluctant to sleep even when the homeostatic process is above the circadian cycle? For animals, hunger could be such a motivating force. The subject may choose to remain awake and search for food because the benefit of eating exceeds the cost of lost sleep¹.

In general this opportunity cost will not be constant, but may vary with the circadian cycle, and with external factors such as time of day or random

¹We note in the appendix that the two-process model can be interpreted as having an implicit fixed opportunity cost. However, that model cannot be used when the opportunity cost changes over time.

acts of nature. For example, a natural disaster like a fire or flood would greatly increase the cost of sleeping and alter optimal sleep timing. Seasonal fluctuations in weather and the availability of food would also affect sleep.

Suppose that instead of hard upper and lower bounds on the homeostatic process as conjectured in the two-process model, the subject faced gradually increasing pressure to sleep or wake as distance of the homeostatic process from a single, central circadian cycle increased. Including an opportunity cost of sleep in the form of waking utility allows the subject to balance the gains from productive work (or leisure) against utility losses from sleep. The result is "soft" boundaries that vary with the value of waking activities.

To formalize this intuition, we propose a utility function, U, with two components: one, U^y , based on adherence to the circadian cycle and another, U^w , based on non-circadian benefits. These are shown in the following:

$$U = U^{y}(H_{t}, y_{t}) + \chi U^{w}(H_{t}, A_{t})$$

$$U^{y}(H_{t}, y_{t}) = -|H_{t} - y_{t}|^{\kappa}; \ \kappa > 0$$
(2.3)

$$U^{w}(H_{t-1}, A_t) = (1 - A_t) \left[e^{z_t} \xi(\mu_W - H_{t-1}) \right]^{\gamma}$$
 (2.4)

The first component is based on a measure of distance of the homeostatic process (H_t) from the central circadian cycle (y_t) , while the second captures benefits from waking activity. The utility parameter χ is the relative weight given to U^w . Note that as the parameter κ in U^y approaches infinity, adherence to the circadian cycle dominates and we get the two-process model from 2.1 as a special case². The sleep state A_t is a binary variable equaling one when asleep and zero when awake. Non-circadian utility, U^w , will

This is because the disutility, U^y , goes to zero if $|H_t - y_t| < 1$, and it goes to infinity if $|H_t - y_t| > 1$.

depend on waking activities such as eating or providing shelter, which are, in turn, functions of non-sleep time. It is also a function of the homeostatic variable which is a measure of 'tiredness'. We use the previous period's value H_{t-1} since this is the level that will matter for exploiting opportunity costs. As H_{t-1} rises toward its upper bound, μ_W , the subject becomes less able to perform well at waking activities. The parameters ξ and γ modify the benefits from waking activities. Non-circadian utility while sleeping is assumed to be zero. However, there are dynamic benefits, since sleeping reduces tiredness and this is useful in the future when the subject wakes. Opportunity cost is given by the environmental state variable, z_t , which we assume follows an autogressive process.

Without loss of generality we can reformulate the homeostatic process as shown in equation (2.2). We reconfigure the equation so that the upper asymptote is μ_W and the lower one is μ_S , with $\mu_W > 0 > \mu_S$.

$$H_{t+1} = \begin{cases} \mu_W + (H_t - \mu_W)e^{-1/\nu_W} & \text{if } A_t = 0\\ \mu_S + (H_t - \mu_S)e^{-1/\nu_S} & \text{if } A_t = 1 \end{cases}$$
 (2.5)

Figures 2 - 4 illustrates the behavior of our model. In each figure the central circadian cycle is shown by the long dashed line. A small utility threshold away from this central cycle is shown by the two medium dashed lines. A large utility threshold is shown with the short dashed lines. The behavior of the homeostatic process is illustrated with the solid line.

Figure 2 shows the behavior with a fixed cost of switching between sleep and waking only. The is no opportunity cost so the subject cares only about circadian utility, switching between waking and sleeping only when the circadian disutility is larger than the small switching cost.

Figure 2: Behavior of the Generalized Model Fixed Switching Cost Only

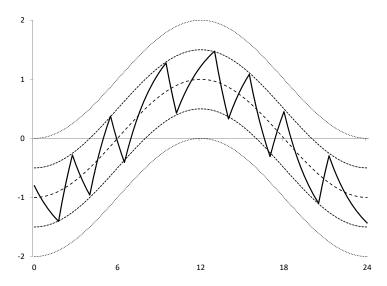


Figure 3 illustrates the behavior with an opportunity cost of sleep. The subject will switch from waking to sleep when the circadian disutility is greater than the switching cost plus the opportunity cost. They will switch from sleep to waking when the circadian disutility is greater than the switching cost *minus* the opportunity cost.

Figure 4 shows behavior when the opportunity cost varies over the course of the day. In this example there is zero opportunity cost between 6 p.m. and 6 a.m., but the opportunity cost is positive from 6 a.m. to 6 p.m. To model nocturnal animals, we could simply change the timing of productive waking hours from day to night.

Figure 3: Behavior of the Generalized Model Fixed Opportunity Cost of Sleep

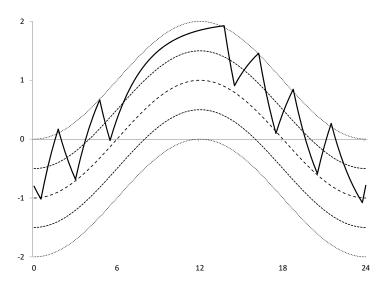
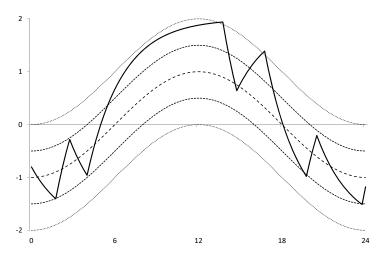


Figure 4: Behavior of the Generalized Model
Time-varying Opportunity Cost of Sleep



3 Modeling Sleep in Animals

There is a fairly extensive literature on sleep patterns of animals. One early summary of this literature is Campbell and Tobler (1984) which reports sleep duration for 150 species drawn from 200 studies. A more recent study by Siegel (2008) surveys the sleep behavior of insects, fish, amphibians, reptiles, birds and mammals. Phillips et al. (2010) show how a single model with different parameter values can explain variations in sleep patterns across seventeen mammal species. Almost all of these studies involved captive animals, however, and subsequent research has shown that captive sleep behavior can differ markedly from sleep behavior in the wild. Nearly 50 years ago, Hediger (1969) pointed out that the duration of sleep among animals should not be considered in isolation, but instead should considered together with other important factors of the animals biological make up. We would therefore expect most animals in the wild to sleep less than their counterparts in captivity. Sleep studies involving wild animals are difficult to conduct and still relatively rare, though advances in monitoring technology make them increasingly feasible.

In spite of technological barriers, for some animals data is available that permit comparisons for a species in the wild and in captivity. Gravett et al. (2017) report the study of two wild African elephant matriarchs and find an average daily sleep of 2.20 hours as compared with the 6.28 hours reported for captive zoo elephants from Tobler (1995). Rattenborg et al. (2008) and Voirin et al. (2014) examined the sleep behavior of three-toed sloths in the wild. They report that sloths in the wild sleep 9.63 hours per day on average. This is much less than the 15.85 hours reported by Galvao de Moura Filho et al. (1983) for captive sloths. Elephants and sloths are

interesting examples to consider because elephants are short sleepers and sloths are long sleepers.

We assume that herbivorous animals, such as elephants, use their time to either sleep or to forage. If the animal sleeps, the value of H_t will fall, but no non-circadian utility is generated. If the animal is awake it will forage and foraging generates consumption according to a mathematical representation we will refer to as a production function. This, in turn, generates utility. In our model foraging includes all activities which generate well-being for the animal, not just the search for food. This includes avoiding predation, caring for young, and even play.

Our model is agnostic on whether animals consciously choose sleep or not. Our formulation neither requires nor excludes that possibility. We treat the circadian utility described above as a given; animals are endowed with this as part of their genetic heritage. Forward-looking behavior can occur even if the animal has no concept of the future and does no explicit planning. All that is required is that it be aware of its environment and be able to infer the opportunity cost of sleep, which will consist primarily of the likely reward to searching for food and avoiding predation.

The circadian cycle is given by the following simple sine wave.

$$y_t = -\cos\left(\frac{t2\pi}{q}\right) \tag{3.1}$$

where q is the number of periods in a day.

Foraging productivity depends on the stock of sleep coming into the period, H_{t-1} (which was determined last period) and the environmental state, z_t . Circadian utility, however, depends on this stock now, which is its past value plus the increment upward or downward due to waking or

sleeping today. Finally, there is a fixed utility cost of λ for transitioning from waking to sleeping and back again. This is illustrated in the equation below, where we have substituted Equation (2.5) into the circadian utility function. Hence, the subject comes into the period knowing H_{t-1} and A_{t-1} , chooses A_t , and H_t evolves given this choice.

$$\max_{A_t} U = A_t \left[e^{z_t} \xi (\mu_W - H_{t-1})^{\eta} \right]^{\gamma}$$

$$- \chi \left[(1 - A_t) \left| \mu_W + (H_{t-1} - \mu_W) e^{-1/\nu_W} - y_t \right|^{\kappa} \right]$$

$$+ A_t \left| \mu_S + (H_{t-1} - \mu_S) e^{-1/\nu_S} - y_t \right|^{\kappa}$$

$$- \lambda |A_t - A_{t-1}|$$

We assume that the portion of foraging production related to the environment follows a stochastic autoregressive process.

$$z_t = \rho^{\frac{1}{q}} z_{t-1} + \sigma \varepsilon_t, \tag{3.2}$$

where ρ is the measure of autoregressive reversion to the mean measured in per hour terms and ε_t are independent and identically distributed random variables with mean zero and variance one.

The choice of A_t is a binary one; there is no marginal condition. Instead, the agent chooses the value of A_t which generates the greatest utility given current values for H_t , y_t and z_t .

3.1 Elephant Behavior

We now illustrate this model with an application to elephants. Gravett et al. (2017) monitored the sleep behavior of two African Elephant matriarchs for 35 days using an activity data logger implanted subcutaneously in their

trunks. Matriarch 1 averaged 2.3 hours of sleep per day, while Matriarch 2 slept an average of 1.8 hours. The standard deviations of sleep time were 1.3 and 1.0 hours. Figure 5 shows the recorded hours of sleep per day for both matriarchs over the course of the study. Both were polyphasic sleepers; Matriarch 1 sleeping an average of four spells per day and Matriarch 2 sleeping for five spells. Both had one main sleep episode averaging 1.3 and 0.8 hours, respectively. A number of shorter sleep episodes occurred usually before the main episode.

Tobler (1995) observed the sleep patterns of two groups of captive female Asian Elephants; one group at a zoo and the other at a circus. A total of 294 elephant-nights of sleep were observed over both groups. Sleep was determined by examining videotape. Zoo elephants slept an average of 6.28 hours per night with a standard deviation of 0.21. Circus elephants slept 3.52 hours per night with a standard deviation of 0.17. These numbers and those for wild African Elephants are reported in Table 1. They also found polyphasic sleep noting, "In all animals the hourly amount of sleep gradually increased during the course of the night, reaching a maximum between approximately 0100 and 0400 hours. The largest amounts of sleep invariably occurred after midnight."

We note that wild elephants slept only a third as many hours as captive elephants, and that the variability of time slept was five times as large. We hypothesize that wild elephants not only have higher opportunity costs of sleep time, but that the cost is also much more variable over time. Since the primary opportunity costs are likely time spent foraging for food and avoiding danger, it makes sense that these costs are both higher and more variable for elephants in the wild.

We attempt to match the sleep patterns of wild and captive zoo ele-

phants using our model. We calibrate our model first using the behavior of zoo elephants. We choose values for μ_S (lower asymptote for the homeostatic process) and σ (standard deviation of stochastic environmental shocks) to match the mean and standard deviation from the data to that for a simulation over 100,000 days with 144 periods of 10 minutes each per day. We then attempt to match the behavior of wild elephants by changing the values of ξ (the marginal productivity of time in foraging) and σ to match their mean and standard deviation. The parameter values and results of the simulations are reported in Table 2. We find that relative to captive zoo elephants, wild ones face an opportunity cost of time that is on average eight times greater. In addition, the volatility of the randomness in opportunity cost is thirteen times higher.

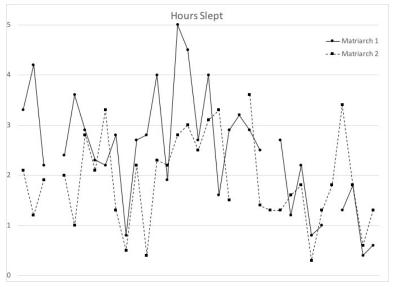
Our model also generates polyphasic sleep roughly in line with that for wild elephants. Figure 6 shows the sleep patterns for a stylized case where there are no random shocks to foraging productivity. In this case the elephant sleeps in five-equally spaced episodes over the night. In the wild the episodes are not equally spaced, but we are able to match the number of episodes by choosing a value of λ (sleep/wake switching cost) of 0.2. For comparison, the difference in the maximum and minimum for total utility per period over the course of a day is 29.35.

Table 1: Average and Standard Deviation of Hours of Sleep per Day for Adult Elephants

type	average	standard deviation
captive zoo	6.28	0.21
captive circus	3.52	0.17
wild	2.20	1.03

Data from Gravett et al. (2017) and Tobler (1995).

Figure 5: Daily Hours of Sleep by Two Wild Elephant Matriarchs 14 April - 18 May



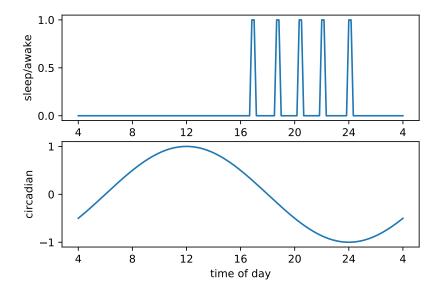
Data from Gravett et al. (2017).

What do we learn from this exercise about elephant sleep? Our model fits the observed sleep behaviors of wild and captive elephants remarkably well. We also find elephants in the wild have an opportunity cost of sleep that is eight times greater than that of captive zoo elephants. The opportunity cost difference sheds light on why elephants in the wild sleep less than elephants in captivity.

Table 2: Model Parameters, Predicted and Actual Sleep for Elephants

parameter	description	captive	wild	ratio
q	periods per day	144		
ν_W	decay half-life while awake	8 hours		
$ u_S$	decay half-life while asleep	8 hours		
κ	curvature of circadian penalty	2.0		
μ_W	waking asymptote	1.0		
μ_S	sleeping asymptote	-1.5		
λ	wake-sleep switching cost	0.2		
χ	utility weight on circadian cycle	10.0		
$\mid \eta \mid$	curvature of foraging production	1.0		
γ	curvature of foraging utility	.8		
ρ	autoregressive component of z_t	.9		
ξ	multiplicative factor in foraging	.8	6.4	8
σ	standard deviation of innovations to z_t	0.01	0.13	13
\bar{S}	steady state hours of sleep	6.29	2.21	0.35
σ_S	standard deviation of hours of sleep	0.22	0.94	4.30
	observed mean hours of sleep	6.28	2.20	0.35
	observed standard deviation	0.21	1.03	4.90

Figure 6: Stylized Elephant Sleep Patterns



3.2 Three-Toed Sloth Behavior

We next apply our model to three-toed sloths. Rattenborg et al. (2008) conducted a study of wild Three-Toed Sloths. Their sample was three wild females who were captured and fitted with electroencephalogram (EEG) and electromyogram (EMG) recorders. A total of 12.8 days of essentially continuous recording were obtained. A second study examined two sloths over a 7-month period using radio collars and the automated radio-telemetry system (ARTS). They found that sloths in the wild sleep 9.63 hours per day on average with a standard deviation of 0.5 hours. Sloths are highly polyphasic sleepers with a tendency "to be awake and feeding during the first two-thirds of the night, and sleeping during the last." A typical sleep cycle of REM and non-REM sleep lasted 46 minutes.

In contrast, Galvao de Moura Filho et al. (1983) examined a group of 24 captive sloths using similar EEG equipment. Sleep patterns were observed over a period of two months. They found an average sleep time of 15.85 hours per day. They also document a great deal of polyphasic sleep.

As with elephants, we hypothesize differences in opportunity costs between wild and captive sloths drives the observed differences in sleep patterns. Again we calibrate our model first using data on captive sloths and then determine the level of opportunity cost needed to generate observed sleep patterns in the wild. We use the same calibrated parameters as with elephants except for the values shown in Table 3. The table shows that opportunity cost for wild sloths is about five time higher than that for captive sloths. We have no data on the standard deviation of sleep time for captive sloths, so we hold the value of σ the same over both groups. In a follow-up study to Rattenborg et al. (2008), Voirin et al. (2014) show that

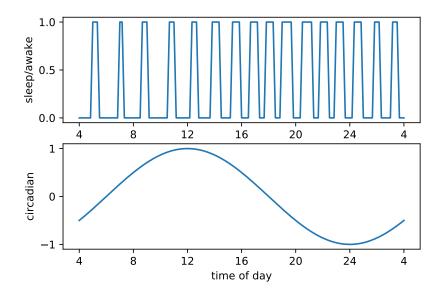
differences in wild versus captive sleep patterns cannot be due to predation risk. They examine two groups of sloths, one on the mainland with natural predators and the other on an island with no predators present. They find no statistical difference in hours slept between these two groups. Hence, we conclude that all sleep differences are driven by foraging opportunity costs.

We are also able to generate sleep patterns over the day that match those of wild sloths. Figure 7 shows the timing of sleep for a stylized day with no random shocks to opportunity cost. There are 16 sleep episodes with shorter duration as the circadian cycle rises and longer duration as it falls. The switching cost in our calibration is $\lambda = .5$ and the difference between high and low utility over the full 24-hour day is 69.32.

Table 3: Model Parameters, Predicted and Actual Sleep for Sloths

parameter	description	captive	wild	ratio	
μ_W	waking asymptote		5.5		
μ_S	sleeping asymptote		1.0		
λ	wake-sleep switching cost		0.5		
ξ	multiplicative factor in foraging	1.0	4.9	4.9	
σ	standard deviation of innovations to z_t	0.025	0.025	1	
\bar{S}	steady state hours of sleep	15.77	9.64	0.61	
σ_S	standard deviation of hours of sleep	0.39	0.53		
	observed mean hours of sleep	15.83	9.63	0.61	
	observed standard deviation	n/a	0.50		

Figure 7: Stylized Sloth Sleep Patterns



In sum, we find that our model fits the difference between wild and captive sloths quite well. We find that the opportunity cost of sleep for wild sloths is five times greater than for captive sloths, which explains why sloths in captivity sleep more than sloths in the wild.

4 Conclusions

This paper introduces a new model of sleep for mammals. It extends the classic two-process model of sleep to account for differences in external circumstances. We apply this model to previously-collected data on elephants and sloths, comparing sleep patterns in the wild with sleep patterns in captivity. We find that the model does very well in explaining sleeping patterns for both types of animals, in both the captive state and in the wild state.

The model is sufficiently flexible that it can be applied to all life forms, including humans. The key insight is that sleep is not purely a biological function, but is also a function of the immediate environment and circumstances of the animal. The direct inference from this is that sleep is a dynamic process; it will vary depending on whether an animal is in captivity or in the wild, but it will also likely vary across the year, depending on the external circumstances the animal faces. Therefore, any measurement of sleep will be conditional on the particular conditions.

APPENDIX

A1 Fixed Opportunity Cost is Implicit in the Two-Process Model

With a small switching cost, the subject will sleep and H_t will fall until it reaches the lower bound. Then the subject will wake and H_t will rise until it reaches the upper bound. If $\mu_W = -\mu_S$ and $\nu_W = \nu_S$. Then the subject will sleep exactly half the time as the homeostatic process moving upward while awake is perfectly symmetric with the process moving downward during sleep.

Now suppose we add an opportunity cost of sleeping. We can think of circadian utility as some measure of the distance between H_t and y_t , i.e. $u = u(H_t - y_t)$. We are now adding an additional amount of utility that derives simply from being awake. Suppose this is a constant, \bar{u} . If sleeping the subject will remain sleeping until the disutility from H_t falling below y_t plus the opportunity cost is greater than the cost of waking up. In the two-process model this would be achieved by increasing the value of μ_S , so that the lower bound is reached sooner. Similarly, if waking the subject remains awake until the circadian cost of waking plus \bar{u} is less than the switching cost, amd the upper bound is reached later. This is achieved by raising the value of μ_W .

Raising μ_W and μ_S will result in less sleep and more time awake. Hence, the value of the homeostatic process asymptotes relative to the peaks and troughs of the circadian cycle (normalized to 1 and -1) are what reflects the implicit opportunity cost in the two-process model.

References

- Borbély, Alexander A, "A two process model of sleep regulation," *Human Neurobiology*, 1982, 1 (3), 195–204.
- _ and Peter Achermann, "Sleep homeostasis and models of sleep regulation," Journal of biological rhythms, 1999, 14 (6), 559–570.
- Campbell, Scott S. and Irene Tobler, "Animal Sleep: A Review of Sleep Duration Across Phylogeny," *Neuroscience and Behavioral Reviews*, 1984, 8, 269–300.
- Carskadon, M.A. and W.C. Dement, "Monitoring and staging human sleep," in M.H. Kryger, T. Roth, and W.C. Dement, eds., *Principles and practice of sleep medicine*, 5th ed., Elsevier, 2011, pp. 16–26.
- Galvao de Moura Filho, A. G., S. E. Huggins, and S. G. Lines, "Sleep and waking in the three-toed sloth, Bradypus tridactylus.," *Comparative Biochemistry and Physiology Part A: Physiology*, 1983, 76 (2), 345–355.
- Gravett, Nadine, Adhil Bhagwandin, Robert Sutcliffe, Kelly Landen, Michael J. Chase, Oleg I. Lyamin, Jerome M. Siegel, and Paul R. Manger, "Inactivity/sleep in two wild free-roaming African elephant matriarchs Does large bodysize make elephants the shortest mammalian sleepers?," *PLOS ONE*, 2017.
- **Hediger, H.**, "Comparative Observations on Sleep," *Proceedings of the Royal Society of Medicine*, 1969, 62, 153–156.
- Phillips, Andrew JK, Peter A Robinson, David J Kedziora, and Romesh G Abeysuriya, "Mammalian sleep dynamics: how diverse features arise from a common physiological framework," *PLoS computational biology*, 2010, 6 (6), e1000826.
- Rattenborg, NC, B Voirin, AL Vyssotski, RW Kays, K Spoelstra, and F Kuemmeth, "Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest," *Biology Letters*, 2008, 4, 402–405.
- Rempe, Michael J, Janet Best, and David Terman, "A mathematical model of the sleep/wake cycle," *Journal of mathematical biology*, 2010, 60 (5), 615–644.

- Siegel, Jerome M., ""Do all Animals Sleep?"," Trends in Neurosciences, 2008, 31 (4), 208–213.
- Skeldon, Anne C., Derk-Jan Dijk, and Gianne Derks, "Mathematical Models for Sleep-Wake Dynamics: Comparison of the Two-Process Model and a Mutual Inhibition Neuronal Model," *PLOS ONE*, 2014, 9 (0), 1–16.
- **Tobler, I.**, "Is sleep fundamentally different between mammalian species?," Behavioural Brain Research, 1995, 69, 35–41.
- Voirin, Bryson, Madeleine F. Scriba, Dolores Martinez-Gonzalez, Alexei L. Vyssotski, Martin Wikelski, and Niels C. Rattenborg, "Ecology and Neurophysiology of Sleep in Two Wild Sloth Species," *Sleep*, 2014, 37 (4), 753761.