A Continuum of Sleep and Shallow Torpor in Fasting Doves

Abstract. *Fasting doves entered shallow torpor during nocturnal sleep. Body temperature dropped lower each successive night by 1° to 3° in parallel with diminished rapid-eye-movement sleep until torpor was composed almost entirely of slow-wave sleep at a body temperature of 30° to 32°C. Shallow torpor in doves, as in mammals, thus appears to lie on a metabolic continuum with sleep.*

Shallow torpor and hibernation in mammals appear to lie on a physiological continuum with sleep, conserving increased amounts of energy through progressive reductions in metabolism and body temperature (T_b)—1° or 2°C for sleep, 5° to 20°C for shallow torpor, and 15° to 35°C for hibernation (*1*).

Marmots and ground squirrels enter hibernation and round-tailed ground squirrels and pocket mice enter shallow torpor for the most part while asleep (*1*–*4*). Rapid-eye-movement (REM) sleep progressively diminishes as T_b declines and eventually disappears at about 25°C, leaving slow-wave sleep (SWS) as the predominant electrophysiological pattern of shallow torpor. Thermoregulatory adjustments during entrance into hibernation appear to be an extension of those initiated at the onset of SWS (*5*).

Several hummingbird species enter torpor at night when their energy reserves are depleted but revert to nocturnal euthermia (normal body temperature) when reserves are restored (*6*). We found that the much larger dove, when fasting, also enters shallow torpor while asleep. Thus sleep and torpor may be homologous processes in both mammals and birds, lying on a continuum of decreasing metabolism.

Four adult ringed turtle doves (*Streptopelia risoria*) had implanted cortical electroencephalogram (EEG), electrooculogram (EOG), and neck electromyogram (EMG) electrodes and fine-gauge thermocouple wire in the interscapular region to measure subcutaneous temperature (T_s). In one of these doves additional thermocouples were implanted into the pectoral muscles and the hyperstriatum to measure body and brain temperature (T_{br}), respectively. In four others, implantations were limited to T_s and T_b thermocouples. A strain gauge attached to the cable connecting the electrodes to a mercury slip-ring assembly registered body movements. Each individual was studied in winter in a 50 by 60 by 35 cm cage within an electrically shielded incubator at an ambient temperature (T_a) of 23° ± 1°C (12 hours of light and 12 hours of dark, with lights on at 8 a.m.). Electrophysiological activity, body movement, T_s, and T_b were continuously recorded on a polygraph (Grass model 7; speed, 6 mm/sec); T_s and T_b were also recorded on a dynograph (Beckman type R411; speed, 0.1 mm/sec).

Following adaptation (1 week minimum) to the recording chamber, baseline patterns of undisturbed sleep, wakefulness, T_b, and T_s were established during two consecutive 24-hour periods with food and water freely available. Food was then removed at 8 a.m. and withheld until each dove lost 20 to 22 percent of its baseline body weight. This took from 3 to 8 days in direct proportion to initial weight (range, 102 to 164 g). Both T_b and T_s were measured from the records at 30-minute intervals. The beginning of an entrance into shallow torpor was defined as the point at which T_s progressively declined below 38.5°C, the baseline mean minimum nocturnal T_s. Coded electrophysiological recordings were scored blind by 25-second epochs for wakefulness and SWS and by 2.5-second epochs for REM sleep. The sleep stage data were then averaged for the hourly epochs.

When fasting, the doves entered shallow torpor each evening soon after the onset of sleep, about 30 minutes before dark. Both T_s and T_b during torpor dropped progressively each night by 1° to 3°C, unlike the temperatures of most hibernating mammals which remain constant (*3*). Decreases in T_s ranged from 9°C on the third night of fasting in one dove (Fig. 1) to 5°C in another on its sixth fasting night. The mean maximum decreases in T_b and T_s for the eight birds during their last fasting nights were about twice those of baseline nights (Table 1, $P < .005$ and $P < .001$, respectively). Their T_b (nearly always 1° to 2°C higher than T_s) returned to baseline levels when they awoke each day (last fasting day maximum T_b, 41.3° ± 0.2°C), and they remained euthermic throughout sleep the night after food was returned (night minimum T_b, 38.8° ± 0.2°C). The entrances into shallow torpor took approximately 2 hours; 90 percent of this time was scored as SWS (range 86 to 99 percent) with intermittent periods of brief wakefulness (mean, 1.1 minutes; range 0.6 to 1.9 minutes). T_{br} in the one dove followed the same pattern as T_b and T_s, but the progressive drops on successive fasting nights were smaller. There were always sufficient energy reserves to enable the spontaneous daily return of T_s, T_b, and T_{br} to euthermic levels. Similar nocturnal decreases in T_b occur in fasting sparrows (*7*) and Inca doves (*8*).

Although EEG amplitude decreased together with T_s during shallow torpor, states of sleep and wakefulness could be identified according to conventional criteria (*9*) at even the lowest T_s of 30°C, when the record displayed almost continuous SWS. Wakefulness was characterized by a low-voltage (< 50 μV) and high-frequency (10 to 12 cycles per second) EEG, a high tonic EMG with phasic activity accompanying head and body movements, and EOG potentials generated by eye and nictitating membrane movements. Bursts of slow-wave EEG activity (< 6 cycles per second) occasionally accompanied head and eye movements. Transitions to SWS were distinguished by sustained EEG slow waves of high amplitude (200 to 300 μV) and behavioral quiescence, represented by decreased tonic activity and disappearance of phasic activity in the EMG, and absence of eye movements and few-

Table 1. Body temperature (T_b) for five doves, subcutaneous temperature (T_s) for eight doves, and percentages of sleeping times for four doves. Day temperatures are maximums and night, minimums. Values are means ± standard error. Statistical comparisons (analysis of variance and Duncan's multiple range test) were made between baseline and first fasting period and between baseline and last fasting period. Abbreviations: TRT, total recording time (24 hours); TST, total sleep time; REM, rapid-eye-movement sleep.

Period (24 hours)	T_b (°C)			T_s (°C)			Time (%)	
	Day	Night	Difference	Day	Night	Difference	TST/TRT	REM/TST
Baseline	42.4 ± 0.1	38.8 ± 0.2	3.6 ± 0.2	41.0 ± 0.2	38.4 ± 0.3	2.6 ± 0.2	71.1 ± 3.2	4.9 ± 0.8
First fasting	42.3 ± 0.3	37.8 ± 0.7	4.5 ± 0.9	41.0 ± 0.3	36.9* ± 0.7	4.1* ± 0.6	68.2 ± 3.0	5.5 ± 0.6
Last fasting	41.3† ± 0.2	35.0‡ ± 0.3	6.3† ± 0.2	40.0† ± 0.2	33.3‡ ± 0.6	6.7‡ ± 0.5	67.7 ± 5.5	2.1* ± 0.5

*$P < .05$. †$P < .005$. ‡$P < .001$.

er nictitating membrane potentials in the EOG. REM sleep was defined by low voltage (< 50 μV), fast (> 10 cycles per second) EEG activity, eye movements occurring singly and in bursts, and tonic EMG activity equal or lower in amplitude to that of preceding SWS. Transitions from SWS to wakefulness were invariably associated with increased EMG activity.

There were no statistically significant changes in total sleep time throughout the fast (Table 1). However, the nocturnal minimum T_s was lower in the two doves that slept the most (30° and 32°C) than in the two that slept the least (35° and 34°C). Regardless of how much they slept, all four doves spent less of their total sleep time in REM sleep on the last fasting night than on baseline nights ($P < .05$, Table 1).

There are striking similarities between these sleep and T_b patterns of doves and those of mammals during torpor (*1–3*). Like ground squirrels and pocket mice, doves enter shallow torpor while asleep, displaying reduced amounts of REM sleep as T_b falls (*10*). Cooling the hypothalamus of kangaroo rats also reduces REM sleep (*11*). Since thermoregulatory processes are switched off during REM sleep (*12*), T_b related reductions in REM sleep may be a kind of homeostatic adjustment bringing about almost continuous regulation of T_b during torpor.

In the marmot, SWS was also associated with declines in brain temperature during entrance into hibernation (*4*). Although intermittent periods of wakefulness tended to be longer and behaviorally more active than in the ground squirrel (*2*), extended active episodes were accompanied by a decrease in the rate of decline of brain temperature or even an increase [figure 3 in (*4*)], as in squirrels. Episodes of intermittent wakefulness were shorter during entrance into torpor in the dove than in mammals (*2, 4*) and did not affect the course of the decline in T_b.

The decreased EEG amplitude associated with the decline in T_b points to the temperature dependence of neural activity. Similar EEG attentuation occurs in reptiles exposed to low T_a's (*13*) and in hypothermic nonhibernating mammals (*14*). In other respects, the EEG characteristics of SWS, REM sleep, and wakefulness during shallow torpor were essentially unaltered.

The doves always entered shallow torpor at times corresponding to their usual sleep-associated circadian decrease in T_b immediately following the onset of darkness (Fig. 1), unlike ground squirrels and pocket mice which sometimes enter torpor at times remote from their normal circadian decreases in T_b (*1, 3*). However, shallow torpor and hibernation are polyphyletic phenomena (*15*) and their temporal occurrence, duration, and depth are linked with several factors, such as T_a, body size, food availability, and amount of adipose tissue. Nevertheless, the correlation between shallow torpor and sleep in doves provides support for the suggestion that SWS and torpor in birds and mammals are homologous processes varying in depth along a continuum of decreasing T_b and metabolism. The ubiquity of drops of 1° or 2°C in T_b during sleep, with further drops into shallow torpor being contingent on negative energy balances, is to be expected if the positive curvilinear relation between metabolic rate and body-T_a differential shown for bats at T_a's below thermoneutrality (*16*) applies to most endotherms. Thus initial drops in T_b of 1° or 2°C during sleep yield greater energy savings (and would, therefore, be under greater evolutionary selective pressure) than subsequent reductions in T_b of equal magnitude during shallow torpor.

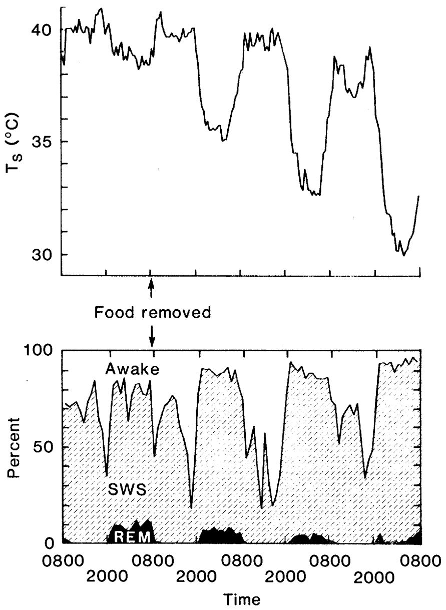

Fig. 1. Skin temperature (T_s) and percentages of time awake and in slow-wave sleep (*SWS*) or rapid-eye-movement sleep (*REM*) for a dove before and throughout a 3-day fast. Note the 9° drop in T_s and virtual disappearance of REM sleep during the last 24 hours of the fast.

LARRY E. WALKER
JAMES M. WALKER
JOSEPH W. PALCA
RALPH J. BERGER

Department of Biology, University of California, Santa Cruz 95064

References and Notes

1. J. M. Walker and R. J. Berger, *Prog. Brain Res.* **53**, 255 (1980); R. J. Berger, *Biol. Psychol.*, in press.
2. J. M. Walker, S. F. Glotzbach, R. J. Berger, H. C. Heller, *Am. J. Physiol.* **233**, R213 (1977).
3. J. M. Walker, A. Garber, R. J. Berger, H. C. Heller, *Science* **204**, 1098 (1979).
4. V. M. Miller and F. E. South, *Physiol. Behav.* **27**, 989 (1981).
5. S. F. Glotzbach and H. C. Heller, *Science* **194**, 537 (1976); G. L. Florant, B. Turner, H. C. Heller, *Am. J. Physiol.* **235**, R82 (1978).
6. R. C. Lasiewski, *Physiol. Zool.* **36**, 122 (1963).
7. E. D. Ketterson and J. R. King, *ibid.* **50**, 115 (1977).
8. R. C. MacMillen and C. H. Trost, *Comp. Biochem. Physiol.* **23**, 243 (1967).
9. J. M. Walker and R. J. Berger, *Behav. Biol.* **7**, 195 (1972).
10. J. M. Walker, E. H. Haskell, R. J. Berger, H. C. Heller, *Experientia* **37**, 726 (1981).
11. S. Sakaguchi, S. F. Glotzbach, H. C. Heller, *Am. J. Physiol.* **237**, R80 (1979).
12. P. L. Parmeggiani and C. Rabini, *Arch. Ital. Biol.* **108**, 369 (1970); H. C. Heller and S. F. Glotzbach, *Int. Rev. Physiol.* **15**, 147 (1977); P. L. Parmeggiani, in *Physiology in Sleep*, J. Orem and D. Barnes, Eds. (Academic Press, New York, 1980), p. 97.
13. J. M. Walker and R. J. Berger, *Brain Behav. Evol.* **8**, 453 (1973).
14. J. ten Cate, G. P. M. Horsten, L. J. Koopman, *Electroencephalogr. Clin. Neurophysiol.* **1**, 231 (1949); W. P. Koella and H. M. Ballin, *Arch. Int. Physiol.* **62**, 369 (1954); J. W. Scott, *Electroencephalogr. Clin. Neurophysiol.* **7**, 466 (1955).
15. G. A. Bartholomew, in *Hibernation and Hypothermia, Perspectives and Challenges*, F. E. South, J. P. Hannon, J. R. Willis, E. T. Pengelley, N. R. Alpert, Eds. (Elsevier, Amsterdam, 1972), p. 663; C. P. Lyman, in *Strategies in Cold: Natural Torpidity and Thermogenesis*, L. C. H. Wang and J. W. Hudson, Eds. (Academic Press, New York, 1978), p. 9.
16. E. H. Studier, *Comp. Biochem. Physiol.* **70A**, 537 (1981).
17. Supported by NIH grant GM23694 and a University of California, Santa Cruz, faculty research grant to R.J.B.

20 October 1982; revised 14 March 1983

Circumglobal Transport of the El Chichón Volcanic Dust Cloud

Abstract. *The stratospheric dust cloud from the 4 April 1982 eruption of El Chichón volcano in southern Mexico was observed to travel completely around the world in a 3-week period. Images from satellites operated by the National Oceanic and Atmospheric Administration were used to prepare daily maps of the location of the volcanic dust cloud, which is the largest and longest-lasting one so far observed with satellite imagery.*

On 4 April 1982, after one eruption on 28 March and two on 3 April, El Chichón volcano in southern Mexico erupted violently, sending a dense cloud of dust into the stratosphere. Lidar observations on 10 and 11 April from Hawaii, made as the densest part of the cloud passed over, showed that the highest concentration of dust was at an altitude of approximately 26 km, well above the tropopause, which