discharge per unit width, θ is the inclination of water surface, and v is mean runoff velocity.
15. Spatially and temporally averaged runoff power per unit area is $P = \tau_0 v = \rho g q(\sin\theta)$, where τ_0 is mean bed shear stress and ρ is fluid density. R. A. Bagnold [*Water Resour. Res.* **13**, 303 (1977)] discussed the general relation between flow power and sediment transport. M. Kilinc and E. V. Richardson [*Colo. State Univ. (Fort Collins) Hydrol. Pap. 63* (1973)] found that the rate of sediment transport by artificially generated shallow flows was closely related to flow power. See also (*11*).
16. Energy-intensity for these experiments is equal to the average intensity of the rainfall during 20 minutes multiplied by the total kinetic energy released.
17. R. H. Webb and H. G. Wilshire (*J. Arid Envir.*, in press) determined soil property and vegetation recovery rates through measurements of areas undisturbed for known times since their initial severe disturbance. The Wahmonie site offers this unique opportunity because it is located on the Nevada Military Test Site, which is closed to the public.
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Photoperiodic Control and Effects of Melatonin on Nonshivering Thermogenesis and Brown Adipose Tissue

Abstract. *Exposure to a short photoperiod improved the thermogenic capacity, and cold resistance of Djungarian hamsters and increased the respiratory power of their brown adipose tissue. Exposure to a long photoperiod caused a decrease in thermogenic measurements. This thermotropic action of the short photoperiod was detectable only during late summer and fall. A similar thermotropic response could be elicited by implanting hamsters with melatonin, indicating that the pineal may be involved in photoperiodic control of thermoregulatory effectors.*

At thermoneutrality, most small mammals have only a small capacity for nonshivering thermogenesis (NST); full capacity is developed after a few weeks of cold adaptation (*1*). This thermogenic improvement is always accompanied by an increase in mass or by structural changes improving the metabolic capacity of brown adipose tissue (BAT), which is the most important site of NST (*2*). The uniformity and intensity of thermogenic improvements during cold adaptation in the laboratory suggest that seasonal changes of NST in field populations of small mammals living in temperate latitudes are simply a consequence of seasonal changes in ambient temperature (T_a). However, there is evidence that nonthermal stimuli, such as the photoperiod, may also affect the development of NST and BAT (*3*). Furthermore, seasonal changes of NST were observed in Djungarian hamsters living in a seasonally changing photoperiod at constant thermoneutral T_a (*4*). To test whether this seasonality was the result of photoperiodic control, we exposed Djungarian hamsters to long or short photoperiods at different times of the year and measured the changes in their thermogenic capacity as well as in the oxidative capacity of BAT.

Djungarian hamsters, *Phodopus s. sungorus*, were bred and raised in the laboratory under naturally changing photoperiodic conditions, at a constant T_a of 23°C. At different times of the year (Fig. 1), hamsters were transferred from the natural photoperiod to either a long (16 hours of light per day) or short (8 hours of light) photoperiod at the same T_a of 23°C. After 2 months, the hamsters were subjected to a cold resistance test (*5*), and their capacity for NST was estimated from the thermogenic response to noradrenaline (NA) (0.8 mg per kilogram of body weight) in the nonanesthetized animals. After analysis of thermogenic measurements, BAT was removed for preparation of mitochondria (*6*). The specific amount of mitochondria was determined from the activity of four mitochondrial marker enzymes measured in the tissue homogenates and in the isolated mitochondrial fraction (*7*). In addition, the DNA content of BAT was determined in order to evaluate changes in the mitochondrial portion per cell of BAT.

Djungarian hamsters responded to the short photoperiod by an increase in thermogenic capacity in comparison with hamsters kept at the long photoperiod (Table 1). Maximum cold-induced oxygen consumption ($\dot{V}O_2$) and NST were both elevated by about 2.5 ml of oxygen per gram per hour (29 percent and 36 percent, respectively), which enabled these hamsters to maintain normothermia down to a T_a of −41°C during the cold resistance test. The effect of the short photoperiod was even more exaggerated when respiratory capacities of BAT were compared. Cytochrome oxidase activity was increased by 116 percent, and mitochondrial protein was increased by 76 percent in the short photoperiod. These biochemical changes indicate an improvement of thermogenic capability for BAT, as expected for an enhanced NST capacity. Cytochrome oxidase and mitochondrial protein were evaluated per unit of fresh weight of BAT as well as per unit weight of DNA in BAT. The two modes of expression gave similar changes due to photoperiodic stimulation, indicating that intracellular respiratory capability of single BAT cells was affected by the photoperiod.

Similar photoperiodic treatments were

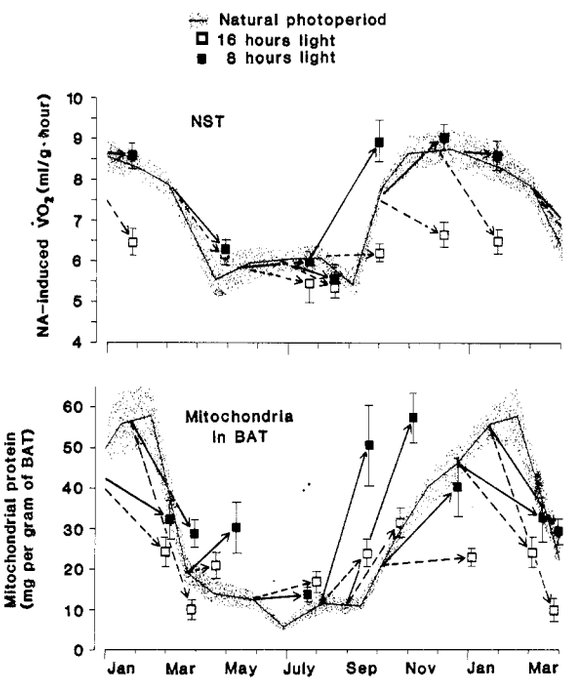

Fig. 1. Seasonal variation of photoperiodic effects on NST and on BAT mitochondria. The solid line surrounded by a dotted area shows the seasonal development of both parameters when hamsters were kept in a seasonally changing photoperiod but at constant T_a of 23°C. The arrows indicate the changes induced by exposure to short (■) or long (□) photoperiods at that particular time of the year. Values are means ± standard error (S.E.).

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Table 1. Effect of photoperiod and melatonin on thermogenesis and properties of brown adipose tissue in *Phodopus* from 3 October to 10 December 1979. For treatment with melatonin, each hamster received two implants of crystalline melatonin in Silastic capsules (*18*) at the beginning of the photoperiod exposure. Values are means ± S.E.; $N = 8$ for biochemical data; $N = 9$ for physiological data.

	Long photoperiod		Short photoperiod	
	Control	Melatonin-implanted	Control	Melatonin-implanted
Maximum cold-induced $\dot{V}O_2$ (ml/g · hour)	8.94 ± 0.17	12.35 ± 0.23†	11.53 ± 0.51‡	11.57 ± 0.43
Cold limit (°C)	−37.2 ± 1.7	−44.0 ± 1.7†	−41.0 ± 0.3‡	−41.0 ± 1.0
Maximum NA-induced $\dot{V}O_2$ (ml/g · hour)	6.65 ± 0.29	9.45 ± 0.27†	9.05 ± 0.4‡	8.85 ± 0.35
NST capacity (mW/g)*	27.5	48.9	40.1	39.4
Mitochondrial protein in BAT				
Per weight unit of BAT (mg/g)	18.9 ± 1.96	47.8 ± 3.8†	35.6 ± 5.82§	23.8 ± 1.7
Per milligram of DNA (mg/mg)	15.1 ± 1.58	28.2 ± 2.08†	21.3 ± 1.85	18.2 ± 0.96
Cytochrome oxidase activity				
Per weight unit of BAT (U/g)	50.3 ± 5.5	113.4 ± 10.0†	108.9 ± 21.4§	68.0 ± 6.4
Per milligram of DNA (U/mg)	38.1 ± 4.5	67.7 ± 7.4†	75.4 ± 10.7‡	52.5 ± 5.0

*Increase of maximum NA-induced heat production above basal heat production at thermoneutrality. †Differs from control group, $P < .01$. Short photoperiod differs from long photoperiod. ‡$P < .01$. §$P < .02$.

repeated at different seasons for 2 years, during which we observed a seasonal pattern of responsiveness to long and short photoperiods (Fig. 1). This indicates that the thermotropic response to short days was not simply a static physiological response, but was dependent on the prior photoperiodic treatment of the animals. A thermotropic action of short days was detectable only during late summer and autumn. During winter, artificial short days did not produce any changes in NST beyond the values obtained in the natural photoperiod. At the end of winter and during spring, when NST capacity was gradually reduced in the natural photoperiod, a prolonged exposure to short days could not prevent this development toward a low summer level of NST. This refractoriness of the thermotropic response continued during late spring and early summer, when hamsters maintained minimum values of NST in the natural photoperiod and any artificial photoperiod.

The inhibitory action of a long photoperiod on NST capacity was detectable during late summer, fall, winter, and spring, with each exposure to long days causing the hamsters to reduce their NST capacity close to the minimal values observed during summer. This inhibitory action of long days was even observable during the transition period from winter to summer when hamsters did not respond to the stimulatory action of a short photoperiod.

Our findings on photoperiodic control agree well with photoperiodic control of reproduction in the same species (*8*), except that the stimulatory and inhibitory roles of the different photoperiods were inverted. A short photoperiod stimulated development of NST but inhibited reproductive activity (*8*), whereby responsiveness in both functions was limited to summer and fall. Hamsters did not respond to the short photoperiod during the rest of the year, and we found spontaneous regression of thermogenesis in late winter, just as Hoffmann had found spontaneous recrudescence of gonads (*8*), despite prolonged exposure to a short photoperiod. Exposure to long days reduced the thermogenic capacity to the summer minimum at any time of the year, and there was an unlimited gonadotropic responsiveness to the long photoperiod (*8*). The inverse relation between thermogenesis and reproduction becomes clear if one visualizes the seasonal occurrence of both functions in the Djungarian hamster. Reproduction is limited to summer months to assure that breeding occurs during the season with optimum food supply and most favorable climate in the Siberian steppe, whereas maximum thermogenic capacity is required in the Siberian winter.

The NST capacity and the mitochondrial content of BAT show a similar seasonal variation in responsiveness to photoperiod (Fig. 1), indicating that the same mechanism may be responsible for seasonal changes in respiratory capacity of BAT and for the physiological availability of thermoregulatory NST. The endocrine or neural nature of this mechanism is unknown. However, the coincidence between photoperiodicity of reproduction and thermogenesis suggests that both functions depend on a common mechanism for photoperiodic time measurement. For photoperiodic control of gonadal activity in golden hamsters, photoperiodic light perception occurs through the retina, and retinal information is conveyed through fibers of the retinohypothalamic tract (*9*) in conjunction with the suprachiasmatic nucleus (*9, 10*) to the superior cervical ganglion, which in turn sends fibers back into the brain, innervating the pineal gland (*11*). The synthesis and release of various pineal compounds can be controlled by this pathway, as has been described for melatonin (*12*). Because of this apparent complexity and the fact that seasonal fluctuations in body weight, torpor, and molt (*4, 8, 13*) are closely linked to photoperiodic control of reproduction, it is unlikely that there is a different pathway for photoperiodic control of thermogenic functions.

The differentiation between the stimulatory action of a short photoperiod on thermogenesis and its inhibitory action on gonadal activity most likely occurs at or after the level of pineal endocrine hormonal control. One of the compounds released by the pineal is melatonin, and repeated treatment with melatonin can inhibit reproductive activity in hamsters (*8, 14*). By analogy, treatment with melatonin should induce thermogenic improvements in hamsters that have been kept in a long photoperiod, mimicking the thermotropic effect of a short photoperiod. In fact, melatonin enhanced the capacity for NST, improved cold resistance, and increased the amount of mitochondrial proteins and activity of cytochrome oxidase in BAT in comparison with untreated hamsters kept in a long photoperiod (Table 1). The effect of melatonin on thermogenic measurements was quantitatively similar to thermogenic improvements caused by exposure to a short photoperiod. When hamsters kept in a short photoperiod are treated with melatonin, no further stimulation beyond the prevailing NST capacity is observed. This supports our expectation that melatonin mimics the thermotropic effect of a short photoperiod.

The annual pattern of photoperiodic sensitivity in Djungarian hamsters offers a suitable basis for perfect seasonal control of thermogenic functions, since thermotropic responsiveness to short days is limited to late summer and fall; that is, to

those times of year when such stimulation is required under natural conditions. Shortening of the photoperiod in the fall is a much more reliable cue for seasonal phasing than are changes in T_a. Therefore, photoperiodic control allows thermogenic improvement well in advance of the lowering T_a, actually demanding greater thermogenic efficiency.

The physiological background of photoperiodic control of thermogenesis seems to be closely related to photoperiodic control of other seasonally varying functions, such as reproduction and molt (*8, 13*). This suggests that there is a common neural pathway for photoperiodic time measurement, terminating at the pineal as the "neurochemical transducer" (*15*). Such a function of the pineal has been suggested for photoperiodic control of gonadotropic activity of the hypothalamopituitary system (*15, 16*). Our results suggest that this action of the pineal may be extended to control of thermoregulatory functions and corroborates conclusions about the significance of the pineal complex for thermoregulation in vertebrates (*17*). The chemical nature and the pathway of information transmission from the pineal to thermoregulatory effectors are still unclear.

GERHARD HELDMAIER
STEPHAN STEINLECHNER
Zoological Institute,
University of Frankfurt,
D-6000 Frankfurt,
Federal Republic of Germany
JOHANNES RAFAEL
PAVEL VSIANSKY
Biochemical Institute I,
University of Heidelberg,
D-6900 Heidelberg,
Federal Republic of Germany

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Cystinuria in the Maned Wolf of South America

Abstract. *Of 42 maned wolves in zoos or live-trapped in Brazil, 34 had excessive cystine in their urine. Renal clearance studies of five of the affected wolves revealed a variable defect for the reabsorption of cystine and dibasic amino acids. The renal tubular handling of other solutes including glucose, phosphate, sodium, potassium, and uric acid was considered normal. Urinary calculi composed of cystine were found in four wolves and proved fatal in three of them. With the exception of the high incidence in this species, this hereditary disease resembles the disorder described in dogs and humans.*

In recent years, considerable attention has been given to metabolic diseases in domestic and wild animals which resemble those in humans (*1*). Such diseases provide comparisons with diseases of humans and, possibly, models for studying basic disease mechanisms. Cystinuria, an inherited metabolic disease associated with excessive urinary excretion of cystine and other amino acids, has been reported in man (*2*) and dog (*3, 4*). Alteration of kidney cell transport of cystine and dibasic amino acids has been proposed as the underlying mechanism. The major clinical manifestation of cystinuria is the presence of urinary calculi composed primarily of cystine, which is highly insoluble in urine.

We previously reported the occurrence of cystine calculi in one maned wolf (*Chrysocyon brachyurus*) from a zoo (*5*). We now report the incidence and nature of this disease in a much larger number of maned wolves, both captive and wild. This rare South American canid (Fig. 1) inhabits Brazil and Argentina and is uncommonly found in zoos. Due to alteration of habitat, maned wolves are listed as vulnerable to extinction by the International Union for the Conservation of Nature Resources.

To determine the incidence of the disease we used paper chromatography, a sensitive and reliable test for detecting excessive aminoaciduria in wolves and dogs. The results were confirmed by renal clearance studies. Urine specimens were collected from adult maned wolves in zoos in six countries and from live-trapped wolves in Brazil. Of the 42 wolves tested, 34 had excessive cystine and dibasic amino acids in their urine. Nearly equal numbers of males and females were affected. Six of the eight live-trapped wolves and 28 of the 34 captive wolves were positive for cystinuria. (The captive wolves had themselves been trapped in Brazil or were their offspring.) Thus, despite the differences in diet and habitat between captive wolves and those in the natural state, the incidence of cystinuria appears to be the same for both groups. Four of the wolves had cystine stones, as determined at necropsy or by the presence of urinary obstruction. (Clinical signs of cystinuria include urinary straining, frequent urination, and urinary obstruction.) Three of the wolves died from such obstruction. Crystallographic analysis of the calculi showed them to be more than 95 percent cystine. The incidence of calculi in the other cystinuric wolves is unknown, since most of them were not radiographed.

Renal clearance studies were performed on five of the affected wolves. The wolves were deprived of food for 18 hours prior to study and were immobilized with appropriate pharmacological agents (*5, 6*). Since normal wolves were not available as controls, three normal

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