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Rest Behavior

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SLEEP AS A BEHAVIOR

Most of the behavior of domesticated animals is invested in maintenance. These behaviors include feeding, drinking, body care, kinesis (or locomotion), which may comprise exploratory behavior, and, of course, sleep.

Usually defined as a period of immobility in which individuals seem unresponsive to their environment, sleep was not considered, until recently, as a behavior. The place it was alotted in most ethology textbooks exemplified this misconception. It was more usual to describe sleep as a physiologic state, alertness and sleep being commonly referred as "states of consciousness."

Fortunately, the ethogram of a given species is now generally acknowledged to include sleep as one of the components. When we look at the behavioral profiles of most of the domesticated animals, we notice that sleep always represents a significant amount of time, despite considerable variation among species (see Table 1).

Although much is known about sleep and although different species have been studied in great detail, this behavior still defies definition. No satisfactory explanation for the necessity of sleep has been offered, and no definite function has been assigned to it.

Despite the mystery concerning the function of sleep, we are aware of its importance in regard to productivity and performance in animals. The basis of productivity and performance is the aptitude of the animal to assume its self-maintenance. Sleep should be considered as important as other maintenance activities in this overall aptitude. So, a thorough knowledge of this very behavior is as necessary as the knowledge of ingestive or reproductive behaviors.

In this article, we will try to focus on sleep in Equidae and to answer some of the possible questions regarding sleep in horses: When do they sleep? How much sleep do they need? Can horses sleep standing? Do they need to lie down in order to sleep? How much do environmental factors affect horse sleep? What environmental conditions may modify sleep in horses?

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Table 1. *Time Spent (Hours) in Wakefulness and Sleep States per Day in Domesticated Species*

ANIMAL	WAKEFULNESS	DROWSINESS	SWS*	PS†	TST‡
Cat	10	2	8.5	3.5	12
Cattle	12	8	3	<1	4
Dog	11	4	6.5	2.5	9
Horse	18	2	3	<1	4
Sheep	16	4	3	<1	4
Swine	11	4	6.5	2.5	8

* SWS = Slow-wave sleep.
† PS = Paradoxical sleep.
‡ TST = Total sleep time, which excludes drowsiness.

PHYSIOLOGY OF SLEEP

Rest may be defined as a prolonged period of inactivity that can clearly be distinguished from other maintenance behaviors. Such periods of inactivity are very common in the animal kingdon,[11, 12, 14, 16] although striking differences in total duration and patterns of rest are observed. However, we must not confuse rest and sleep behavior; although closely related, they are two different things. An animal may rest without sleeping, so we must define sleep in some other way. It is here that physiology comes to the rescue of ethology.

An adequate description of sleep requires, beside the analysis of the behavioral manifestations, an electrophysiologic analysis of various organs, including the brain.

Much of our understanding of sleep has evolved from neurophysiologic studies. The introduction of the oscillograph in the 1930s to record biological potentials in animal tissues, and in the brain particularly, added the valuable and indispensable criteria of the level of alertness to behavioral observations.

For the electrophysiologic study of wakefulness and sleep in horses, the same methods and criteria are used as for man. Only three basic parameters are necessary for characterization of the different states of vigilance. These are the electroencephalogram (EEG), the electrooculogram (EOG), and the electromyogram (EMG). Depending on the purpose of the study, we may take other variables into consideration—like the electrocardiogram (ECG), for instance.

To record these electrical manifestations of organ activities, we use small electrodes connected to a polygraph. These electrodes are positioned over the cortex of the brain to obtain a recording of the spontaneous activity of cortical cells, over the extraocular muscles to measure the change in the electric fields produce by eye movements, and into a postural muscle, usually a neck muscle, to monitor variations in muscular tone.

The most obvious features of the spontaneous EEG are its frequency and amplitude. Four frequency bands are used to classify the different types of electrocortical activities: delta (low frequency, 1 to 4 cycles per sec, and high-amplitude waves), theta (low frequency, 4 to 8 cycles per sec, and medium-amplitude waves), alpha (medium frequency, 8 to 12 cycles per sec, and medium-amplitude waves), and beta (high frequency, more than 12 cycles per sec, and low-amplitude waves). The voltage of EEG may vary from only 10 μV for beta waves to as high as 250 μV for the large slow waves.

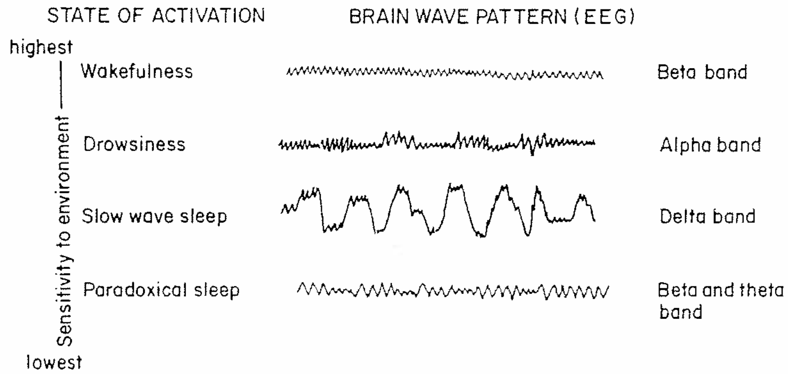

Figure 1. Brain wave pattern and level of vigilance in mammals. See text for a description of the amplitude and frequency of each wave band.

Although level of awareness or arousal exists along a continuum, we may consider subdivisions that have their typical brain-wave patterns. Figure 1 illustrates the usual associations that have been found for most mammals, and in some birds, between brain electical activity and the level of vigilance.

Usually we consider that EEG waves decrease in frequency and increase in amplitude with the lowering of alertness—that is, from wakefulness to sleep. However, since the work of Aserinsky and Kleitman in 1953, sleep is now divided into at least two different states: slow-wave sleep (SWS) and paradoxical sleep (PS), also called REM sleep (REM) or deep sleep. During this sleep state, the EEG pattern resembles that of wakefulness, despite the fact that the individual is deeply asleep. There is a slowing of the electrocortical activity of the brain from wakefulness to SWS sleep, and then, during the deepest sleep state, the EEG pattern becomes like that of the awake individual. This paradoxical situation inspired the name of this state.

PHYSIOLOGIC CHARACTERISTICS OF WAKEFULNESS AND SLEEP

In 1936, Frederic Bremer, a Belgian neurophysiologist, published his first experimental results on the EEG of the cat during wakefulness and sleep. Since that time, a large number of mammalian species have been the object of studies. In Equidae, the first recordings of EEG in relation to sleep were done some 25 years ago, by Ruckebusch, at the world's oldest school of veterinary medicine in Lyon. The first studies were done in donkeys,[21] and some years later, Ruckebusch, Barbey, and Guillemot gave a description of EEG during sleep in horses.[24]

The EEG of a horse that is involved in some activity, like eating, is not easy to study because it is mostly obscured by muscle artifacts. However, it is possible to record subjects in this situation with appropriate filtering of the signals.

During alert wakefulness, when the brain is actively processing information, the EEG characteristics of the horse are low-amplitude (10 to 30 μV) fast waves (25 to 40 cycles per sec) from the beta band, also called LVFA (low-voltage fast-activity) waves. The cortical electrical activity is said to be desynchronized. Eyes movements are frequent and irregular. Only rapid eye movements can be recorded, without any slow movements. Neck muscular tone is high with an especially large variability, depending on the position of the head.

During diffuse wakefulness, as the horse becomes drowsy, LVFA waves are partially replaced by large (up to 150 μV) slow waves (1 to 4 cycles per sec) in the delta band, alternating with alpha waves that appear in the form of spindles. As the horse falls asleep, cortical spindles alternate with more and more high-voltage slow-activity (HVSA) waves. Rapid eye movements seen in wakefulness are replaced by slow and mostly horizontal movements. Muscular tone is moderately high and very regular in amplitude.

During SWS, the EEG is mainly of the HVSA type, with large (up to 250 μV) delta waves (1 to 4 cycles per sec). The cortical electrical activity is synchronized. The EOG indicates that the eye movements are very scarce and of the slow/horizontal category. The eyelids may be partly opened, so that we can observe this relative immobility of the eyeball. The EMG still shows a persisting but reduced muscular activity; the amplitude is less than during drowsiness and may nearly disappear if the head is resting against a support.

These observations contrast with those made during paradoxical sleep, when brain electrical activity consists, for the most part, of beta waves similar to those of alert wakefulness. Muscular tone has completely disappeared. At irregular intervals during PS, we can notice bursts of rapid eye movements (REM) on the EOG, usually associated with rapid displacements of the pinna, facial and labial muscular twitching, contractions of the limbs, and even whinnying. Short trains of theta waves, very regular in amplitude and frequency, may appear on the EEG intermittently during PS. These waves usually occurred when we observed phasic ocular and somatic activities. Similar waves characterize the hippocampal electrical activity at the same time. These theta waves are also seen at this level when the animal is awake and directing its attention to something in its environment.

Figure 2 illustrates the EEG from various parts of the cerebral cortex during the state of sleep and wakefulness in a pony. Figure 3 shows the recording of the three basic parameters, EEG, EOG, and

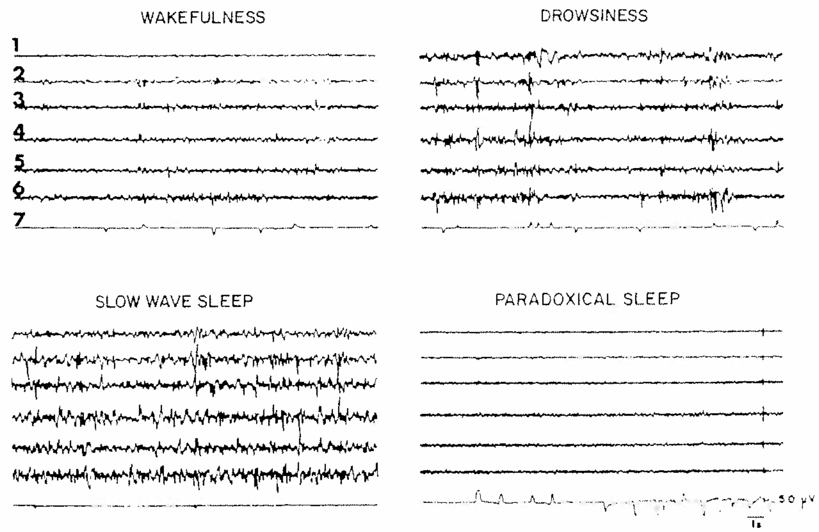

Figure 2. Recordings of cortical activity in a Pottock pony from (*1*) frontal, (*2*) parietal, (*3*) occipital, (*4*) fronto-parietal, (*5*) fronto-occipital, and (*6*) parieto-occipital views. (*7*) is EOG. (From Dallaire, A.: Recherches sur l'aternance des états de veille et de sommeil chez les Equidés. Unpublished M.Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

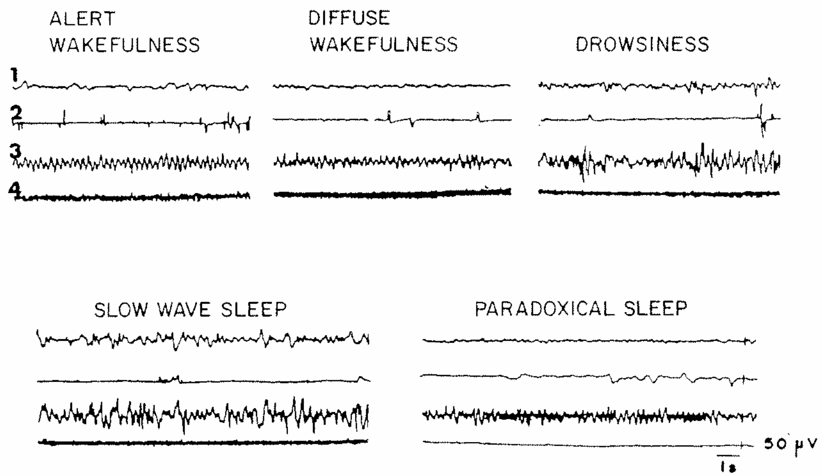

Figure 3. Recording of EEG (*1*), EOG (*2*), hippocampal EEG (*3*), and neck muscle EMG (*4*) in a pony. (From Dallaire, A.: Recherches sur l'aternance des états de veille et de sommeil chez les Equidés. Unpublished M.Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

Table 2. *Heart and Respiratory Rates during Wakefulness and Sleep in Ponies (Mean ± Standard Error in Three Subjects)*

RATE	WAKEFULNESS	DROWSINESS	SWS	PS*
Cardiac	65.5 ± 1.00/ min	56.0 ± 0.40/ min	55.9 ± 0.34/ min	55.1 ± 1.12/ min
Respiratory	31.0 ± 0.40/ min	25.8 ± 0.35/ min	26.0 ± 0.29/ min	25.2 ± 0.59/ min

* Notice the high variations in both rates during PS.

EMG, along with hippocampal activity from alert wakefulness to deep sleep.

Modifications in brain electrical activity and somatic phenomenology are accompanied by visceral or vegetative manifestations, which are also characteristic of each of the sleep states. The basic vegetative event of SWS seems to be a tonic increase in the parasympathetic outflow with a slight attenuation of sympathetic activity.[18] In particular, the cardiac and respiratory rates decrease according to this new vegative equilibrium. Table 2 presents values recorded in Pottock ponies. The reduction in rates of both activities is significant from wakefulness to SWS. We notice that the variability is also lowered.

During PS, mean respiratory and cardiac frequencies are slightly lower than those during SWS, but this is not significant. What is of interest is that variability is increased, even more than during wakefulness. This is due to the presence of arrythmias.

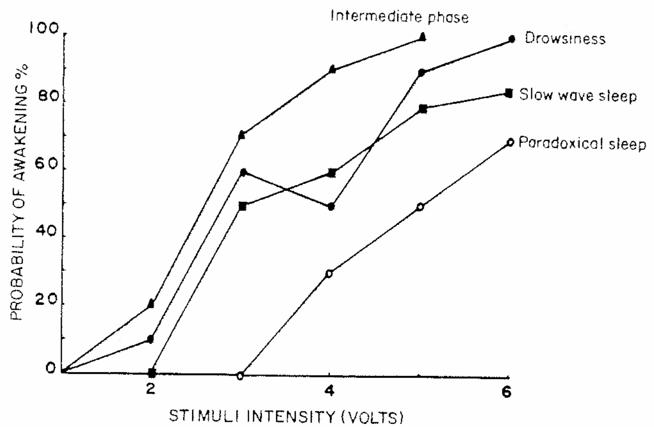

Figure 4. Intensity of an electrical stimulus applied to chest wall of a pony to produce wakefulness. (From Dallaire, A.: Recherches sur l'aternance des états de veille et de sommeil chez les Equidés. Unpublished M. Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

We can observe periods of tachycardia followed by extreme bradycardia. Respiration is characterized by sudden acceleration followed by inspiratory pauses. This vegetative phenomenology accompanies bursts of REM, as well as other somatic phasic activities. These visceral concomitants of sleep states have been described in horses and in ponies.[4, 24]

Somatosensory modifications during sleep have also been described in ponies. Figure 4 illustrates variations in arousal threshold from drowsiness to PS. Paradoxical sleep is the deepest level of sleep; arousal threshold is at its maximum.[4]

BEHAVIORAL AND TEMPORAL CHARACTERISTICS OF SLEEP

The two states of sleep, despite their obvious differences, seem to be functionally related. Paradoxical sleep never occurred without a preceding SWS episode, at least in adult animals. Episodes—that is, the individual occurrence of SWS and PS—are organized in sleep cycles. A sleep cycle (SC) is measured from the onset of one PS episode to the onset of the next, the two episodes occurring in the same sleep phase—that is, from the time the animal falls asleep to the next active waking. Figure 5 represents an hypothetical hypnogram, the circadian sleep pattern as defined by EEG and behavior, to illustrate this terminology.

Most of the animals, except man and some primates, are poly-

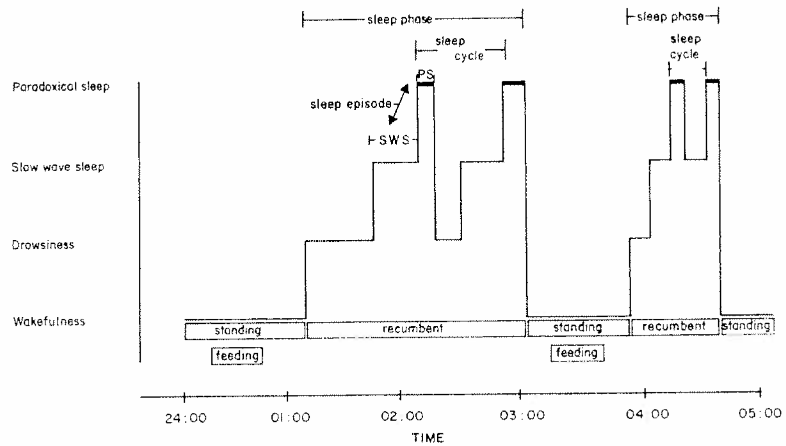

Figure 5. Hypothetical hypnogram to illustrate sleep terminology used in this article. Episodes, cycles, and phases are the temporal subdivisions of the circadian rhythm of sleep and wakefulness.

phasic, (sleep occurring in more than one phase throughout the 24-hour period). During each phase, we may observe one or more sleep cycles.

In the horse, the mean duration of sleep cycle is around 15 minutes. Mean durations for PS and SWS are 4.2 and 6.4 minutes, respectively. The difference is represented by drowsiness and by the presence of an intermediary phase, which occurs between SWS and PS in almost 30 per cent of the sleep cycles. This intermediary phase looks like drowsiness when we consider the EEG. Arousal threshold is even closer to that of diffuse wakefulness than that of drowsiness (see Fig. 4). This state may represent a partial awakening before entering in deep sleep. The fact that the animal does not enter PS directly from SWS may be regarded as a protective mechanism to avoid going into the deepest sleep without considering the security of the environment. In domesticated species other than the pony, this phenomenon is only documented in the laboratory rat.[10]

Total sleep time (TST) averages 3 to 5 hours per day—that is, 15 per cent of the total time budget. Sleep occurs during five to seven phases during the night, each one lasting 30 to 40 minutes. Paradoxical sleep represents less than 1 hour per day (45 minutes). The PS/TST ratio varies slightly from one animal to the other but usually comprises between 21 to 25 per cent. It is well known that TST and the PS/TST ratio are determined by the age of the animal. In horses, unfortunately, there is no direct study on this aspect of sleep. However, observations done on Camargue horses revealed that lying flat occupied 15 per cent of the time after birth and only 2 per cent after weaning.[2] Due to the close relationship between lateral recumbency and PS, we may assume that this change is related to a decrease in PS time.

For stabled horses, sleep is mainly nocturnal. There is also a tendency to sleep between 12:00 PM and 2:00 PM, but this does not occur regularly under stable conditions. It depends mainly on the level of activity around the horse's stall. Most often we cannot observe PS during this afternoon nap. During the night, sleep is distributed over the period from 8:00 PM to 05:00 AM; (Fig. 6); sleep phases are separated by ingestion or drowsing periods. The maximum concentration of SWS and PS is from 00:00 to 4:00 AM (Fig. 7).

Usually, horses fall asleep while standing. The drowsy horse still has its eyelids partially opened and its head hangs at a medium height from the ground (see Fig. 8). As it goes into SWS, the head will gradually go down. When the horse feels confident about its environment, it then lies down. This operation supposes awakening and takes some seconds. The horse flexes its forelegs, then its hindlegs. It first lies in sternocostal recumbency (see Fig. 8). The horse's brain enters drowsiness again and very rapidly goes into SWS. After a short time, a PS episode may occur. When it does, the horse lies in lateral recumbency (see Fig. 8). If this is not possible, the head and the body will rest against an object—the wall of the stall, for instance.

Earlier in this article, it was said that muscular tone decreased from wakefulness to SWS and disappeared during PS. In horses, how-

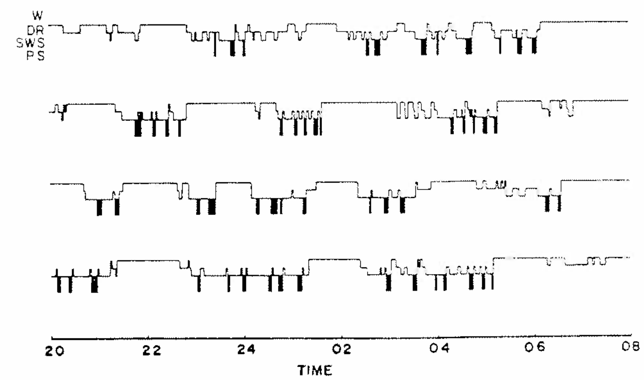

Figure 6. Occurrence of sleep phases during night time in the stabled pony. (From Dallaire, A.: Recherches sur l'aternance des états de veille et de sommeil chez les Equidés. Unpublished M.Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

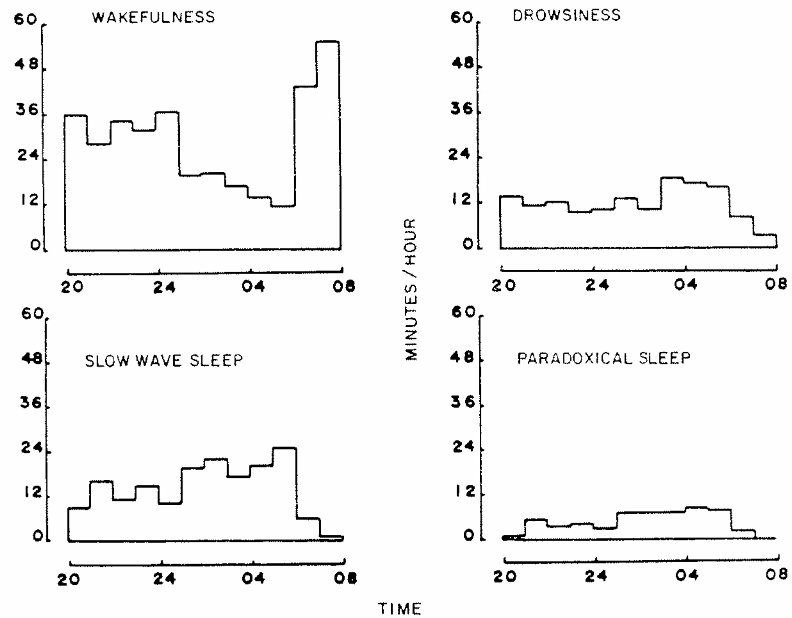

Figure 7. Hourly distribution of sleep and wakefulness during night time in stabled horses. (From Dallaire, A.,: Recherches sur l'aternance des états de veille et de sommeil chez les Equides. Unpublished M.Sc.V. Thesis. Echole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

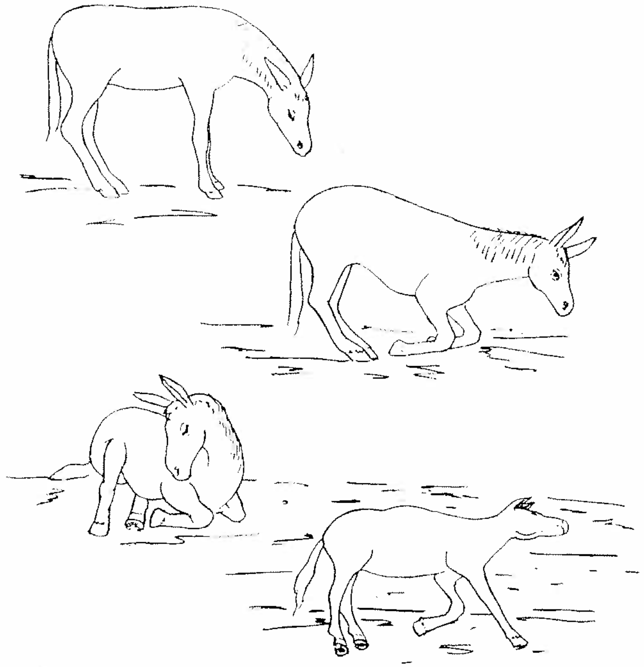

Figure 8. Drowsiness usually occurs in the standing position. The normal position for slow-wave sleep is sternal recumbency; for paradoxical sleep, it is lateral recumbency.

ever, this is a simplified view. The complete disappearance of muscular tone during PS is a fact, but during drowsiness and SWS, the intensity of neck muscular activity depends on the attitude of the animal. In a standing subject, during drowsiness, the gradual lowering of the head progressively reduces the tonic activity of the neck muscle. It may disappear almost entirely if the head comes close to the ground. In the recumbent animal, cervical muscular tone is also always present, even if the head is resting against the ground, but it may be reduced to a minimum.

During drowsiness, the horse usually stands with one hindleg partially flexed. It is possible to observe SWS in the standing animal, but if the subject is well adapted to its environment, it will take the recumbent position. Slow-wave sleep mostly occurs while in sternal recumbency. It may happen on rare occasions in lateral recumbency. Paradoxical sleep nearly always occurs in lateral recumbency.[4]

Although the horse is known for its ability to sleep while standing because of anatomic adaptations of its limbs, it is unable to complete a sleep cycle without lying down to enter PS. If a horse is put in a straight stall where it is physically impossible for it to lie down, it will

be sleep-deprived, at least of PS. In such a situation, SWS may increase in duration, but this is not a compensation for loss of PS. As soon as the animal is able to adopt the recumbent posture, there will be a rebound in total PS time. This increase in PS duration will last for two or three nights and may be twice the normal duration.[4]

The benefit of this ability to stand while sleeping may be related to the ecological niche of the Equidae; this represents a protection against predators. It is also of interest to consider that the energy cost of standing in horses during drowsiness and SWS is decreased by the presence of the suspensory and check ligaments.[29]

Even during PS, which is the deepest sleep, the horse will be aroused easily by any strange noise and will stand up very quickly. Those familiar with horses know that they must be careful when approaching a recumbent subject to avoid any risk of being hurt while the animal stands up.

In horses, sleep represents only a fraction of rest behavior. Drowsiness occupies a significant amount of time both in individuals kept under stabulation or at pasture. It accounts for 8 per cent of resting time indoors and as much as 13 to 14 per cent outdoors (Fig. 9).

When horses are put at pasture, SWS and PS time are reduced and that of drowsiness is increased. The adaptive value of these modifications is not well known. However, because drowsiness represents a light sleep or perhaps a very diffuse wakefulness state, it may be a protective mechanism against predation. When outdoors, horses are always standing when drowsy and lie down only for SWS and PS (see Fig. 9).

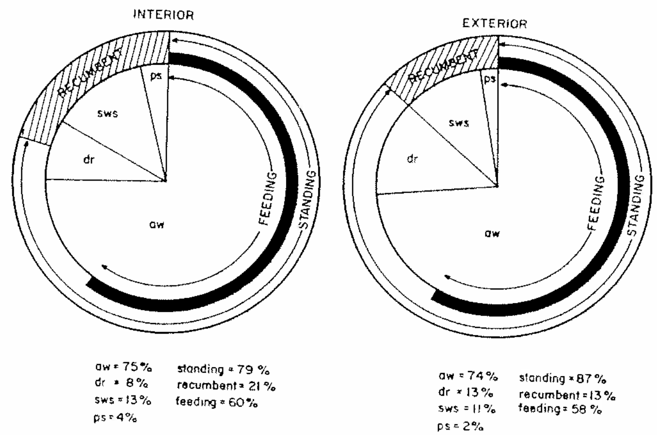

Figure 9. Average sleep and wakefulness circadian pattern in ponies. (*Interior:* n = 5, kept in separate stalls. *Exterior:* n = 2, kept in a paddock.) Outer circle indicates relative proportions of standing and recumbency; inner circle shows percentage for the relative duration of wakefulness (*aw*), drowsiness (*dr*), slow-wave sleep (*sws*), and paradoxical sleep (*ps*). Feeding duration is represented by the black strip. (Adapted from Dallaire, A.: Recherches sur l'aternance des états de Veille et de sommeil chez les Equidés. Unpublished M.Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

ENVIRONMENTAL INFLUENCES ON SLEEP

Habitat

Sleep may be altered either quantitatively or qualitatively by environmental factors. Horses will assume recumbency only in a familiar environment. When they are moved from a familiar environment to a new one, sleep may be retarded for a period of time that ranges from 1 or 2 days to several days. When subjects are put outdoors, it may be a day or two before they first lie down.[4] This habituation may be socially facilitated, in that if one horse is familiar with the new environment, it will lie down and the others will too. It is said that the dominant animal is usually the first to lie down.[22] However, this has not been thoroughly documented.

We may suspect differences in the duration and circadian rhythm of sleep when horses are put at pasture, in contrast to values observed indoors. We have seen that horses have preferred postures for the two states of sleep and for drowsiness. Although each state may occur in more than one posture, PS normally occurs in lateral recumbency, SWS in sternal recumbency, and drowsiness in the standing posture.[4] When studying free-ranging horses, time spent in these postures may be used as a correlate of time spent in the corresponding vigilance state.

In an observational study in feral ponies on Assateague Island, resting behavior was shown to occupy about 40 per cent of night time; 16 per cent of the time was spent lying down. This behavior reached a peak in the middle of the night and early morning (from 00:00 to 4:00 AM). All ponies were never seen to be lying down simultaneously.[15] This contrasts with a study in free-ranging Appaloosa horses, in which the entire herd was seen recumbent at one time during the day.[25]

A study in Camargue horses revealed almost the same figures—total rest time accounting for 30 per cent of the 24-hour period. Sternal recumbency represents 13 per cent and lying flat nearly 3 per cent of this time. The difference was for standing resting. This study also gave some indication of the effect of age on rest and sleep behavior. Lying in lateral recumbency decreased from 15 per cent in newborn foals to 2.7 per cent in preweaning foals; lying in the sternal position decreased from 17.9 per cent to 13.2 per cent and standing resting increased from 8.1 per cent to 11.8 per cent.[2, 8] We may interpret these results in the following way: time spent in PS decreased sharply after birth, time spent in SWS decreased slightly, and time spent in drowsiness increased. It seems that as the animal gets older, part of the time alloted to SWS is replaced by a similar amount of drowsiness.

In a study of rest behavior in animals kept in stalls and then placed at pasture, we obtained results that indicate the effect of free-ranging conditions on rest and sleep.[4] Total resting time was slightly increased when animals were at pasture, but this augmentation was paralleled by a decrease in time spent in sternal and lateral recumbency (Table 3). Individual duration of episodes of lying flat was not modified.

Table 3. *Comparison of Feeding and Resting Behaviors in Ponies in Stalls and at Pasture**

	FEEDING BEHAVIOR	RESTING BEHAVIOR	RECUMBENCY (TOTAL TIME)	RECUMBENCY (LATERAL)
Stable (n = 5)	867.0 ± 25.2	573.0 ± 17.8	303.9 ± 21.4	60.8 ± 10.1
Pasture (n = 2)	843.7 ± 22.2	596.3 ± 29.4	192.2 ± 11.4	29.1 ± 4.6

* Durations of each behavior in minutes (mean ± standard error) per day for total of 8 24-hour periods in each group; n is number of ponies observed. (Adapted from Dallaire, A.: Recherches sur l'aternance des états de veille et de sommeil chez les Equidés. Unpublished M.Sc.V. Thesis. Ecole Nationale Vétérinaire de Toulouse, France, 1974; with permission.)

Therefore, it is a diminution in the number of lateral recumbency episodes that is responsible for the decrease in total time spent lying flat. We may suggest that both SWS and PS decrease when animals are placed at pasture, and drowsiness increases. Ruckebush has suggested that sleep in horses kept in stables is in excess of the normal level as measured in free-ranging individuals.[23]

Diet and Sleep

Diet may influence sleep. In one study made in ponies, when the diet was changed from one of hay to one of oats, total rest time increased.[5] This was due mainly to an increase in sternal recumbency. Total sleep time was augmented, and both SWS and PS occupied a greater proportion of the 24-hour period. This modification is transitory. After 3 or 4 days, the values tend to return to their original setting. Fasting also modifies sleep time. During the first two days of fasting, SWS and PS increased by 20 and 17 per cent, respectively.

Boredom and Sleep

The level of stimuli offered by the environment of the horse may also affect sleep patterns. In an experiment on the effect of partial sensory deprivation in ponies, it was shown that the animals exibit more SWS during the deprivation period, with an increase in PS time after the perceptual deprivation.[6] These data are difficult to interpret in regard to practical management, but they draw attention to the importance of the physical milieu in which a horse is placed.

SLEEP DISORDERS

Sleep is a complex and important behavior; therefore, we must consider the possibility of any anomaly that could impair this activity. The variety of human sleep disorders is so impressive that we may suspect the existence of at least some of these problems in domestic animals.

Unfortunately, this is not well documented in horses. Only one disease, narcolepsy, has been identified in this species. This disease consists of excessive sleepiness and sudden onset of PS, or something similar to it. There may be muscular atonia or weakness, and the animal may fall down. This may occur with a loss of consciousness.

One case had been reported in a 15-year-old Quarter Horse by Sweeney and colleagues.[27] According to Foutz and colleagues, at least four cases of narcolepsy have been observed in ponies.[9] We also had such a case in a 6-month-old Belgium colt in the school of veterinary medicine in St-Hyacinthe. Cataplectic attacks were easily observed when we tried to move the animal outside its stall. Shaking its head or trying to haul it forward by pulling at its halter was sufficient to induce such attacks. Everything that excited the animal also induced sudden sleep episodes.

The clinical diagnosis of this condition is aided by pharmacologic testing. Imipramine given intavenously prevents cataleptic attacks. This condition seems to occur infrequently in horses; however, the clinical cases reported in the literature suggest that it may exist in a variety of equine species.

ANATOMIC AND BIOCHEMICAL BASIS OF SLEEP

Most of the research on sleep mechanisms has been done in laboratory rats and cats; large domesticated animals, except for goats, have rarely, if ever, been used. We must extrapolate by analogy, knowing that the horse brain is not exactly identical to that of the rat or the cat.

When animals are awakened every time an episode of REM-sleep commences, to produce a sleep deficit, the subjects may become irritable and anxious. Subsequently, when allowed to sleep "ad libitum," PS-deficient animals spend a greater amount of time in PS. This is true for most species, including horses. These studies, initiated by the French physiologist Pieron at the turn of the century, have led to the conclusion that a deficiency of paradoxical sleep causes a build-up of some biochemical factor that normally would be utilized or eliminated during periods of deep sleep.

If sleep scientists now agree on the anatomic structures governing sleep and wakefulness, there is no such agreement on a single neurochemical theory. Numerous controversies still exist about the exact contributions of various neurotransmitters that are actually known to be involved in the control of the sleep-wakefulness cycle. Moreover, there is evidence that humoral mechanisms, the agents of which are not identical to the chemical mediators of nerve transmissions, play an important part in the sleep phenomenon.

Michel Jouvet, one of the leaders in sleep research, has suggested that arousal is associated with activity in noradrenergic fibers, and deep sleep is mediated by serotonergic cells of the brain-stem raphe nuclei. Destruction of these nuclei produces an animal that cannot sleep. A pharmacologic experiment using an inhibitor of serotonin synthesis, the drug parachlorophenylalanine (PCPA), which inhibits tryptophan hydroxylase, duplicates the results of ablation. In this second experiment, insomnia is alleviated by injection of a 5-hydroxytryptophan (5HTP), which is a serotonin precursor.[13]

A second brain-stem region involved in sleep control is the nucleus of the solitary tract. This nucleus receives inputs from taste buds and many other viscera. Electrical stimulation of this region promotes a synchronization of EEG—that is, the appearance of delta HVSA waves. A related region is the area postrema. Serotonin applied to this neural region modulates the influence of the nucleus solitarius on sleep. It is not known exactly how these two regions act to produce sleep, but they may mediate some of the effects of feeding, metabolism, and visceral activities in inducing sleep.

Finally, when electrically stimulated, the preoptic region of the basal forebrain induces EEG synchronization and drowsiness, which lead to SWS. Inversely, lesions of this region produce insomnia.

In the actual situation, it is difficult to describe the anatomic and biochemical basis of sleep and wakefulness. There are too many controversies to determine the contributions of each of these regions and of each of the neurotransmitters that seem to be involved. Recently, the research of Monnier and colleagues in Switzerland demonstrated the release of a nonapeptide with a significant hypnogenic effect after cerebral intraventricular injection.[17] This peptide was obtained from sleeping rabbits by extraction from venous blood.[17]

Arousal and sleeping are behaviors involving the whole animal. Such behaviors require a central system with widespread connections. We can say that the regions mentioned previously form just such an extensive system controlling wake-sleep alterations. Each center uses specific transmitters and seems of special importance. However, the coordination of these centers could be accomplished by the release of a neurohumoral factor, like the nonapeptide suggested by Monnier.

FUNCTION OF SLEEP

As soon as one knows that the mammalian brain creates its own sleep, the notion of a function of the hypnotic phenomenon cannot be doubted. One must acknowledge, however, that the exact nature of this function remains obscure.

That sleep serves a restorative purpose is still of current interest; it is probably the only role that comes to the mind of most people. Many physiologists refer to SWS as the sleep of the mind, because the brain seems to be "relaxed" at that time, and to PS as the sleep of the body, because muscular tone is absent. Because of the great variety of functions that have been proposed, we can only summarize the most important and refer the reader to the excellent book, "*The Sleep Instinct*," by Ray Meddis.[16]

Since its discovery, PS received the most theoretical attention; by comparison, SWS received little attention. The latter inherited the recuperation or restorative function, which was previously assigned to sleep in general. There are arguments in favor of the role of SWS in growth or repair of body tissues. The link between this state of sleep and the release of growth hormone suggests such a function. Unfortunately, this link has been investigated mainly in human beings, so this hypothesis is debatable.

The functions to be attributed to PS may be grouped into two categories: the psychologic and the biologic theories. The first group of theories states that some form of memory consolidation occurs at that time. This hypothesis relies on evidence that information memorized before going to sleep is better recalled on arousal if PS is present during the interval before waking. This has been demonstrated in human beings and rats. It is also believed by some that deep sleep permits the reworking of old memories.

Biologic theories of PS function emphasize either neural stimulation or repair functions. The activated nature of PS may serve to exercise the brain, mainly the ocular area of the cortex, as well as the tiny muscles that control the eyes movements. Deep sleep may also serve to stimulate the growth of brain cells in the fetus and the young animal; this is why sleep is represented almost exclusively by PS at the beginning of the life. According to some authorities in sleep research, PS would serve to increase protein metabolism in the brain and enable nervous tissue repair.[16]

These views do not explain the basic organization into an ultradian rhythm, the sleep cycle, and they do not take into consideration the circadian pattern of sleep cycles. To explain the role of sleep, we must consider SWS and PS as a whole, not separately. Sleep cycle must be regarded as the basic unit of the sleeping behavior.

The view that sleep, particularly PS, is involved in learning and memory is supported by numerous experimental observations. We must also pay attention to the fact that phylogenetic evolution of PS parallels that of play behavior. Most ethologists agree that play serves a learning purpose. This may also be true for sleep behavior. The sleep cycles may be involved in learning and memory consolidation.

We can make an analogy with a computer and a database. When we are concerned with the use of a database, we must enter information each day or so. Deleting, packing, and sorting of this information must be done on a regular basis. This is necessary to ensure efficiency when a particular piece of information is needed. Slow-wave sleep and paradoxical sleep may accomplish these functions. Slow-wave sleep may be regarded as the time when one is deleting unnecessary information and packing (that is, the definite elimination of deleted records); sorting is done during paradoxical sleep. Sorting involves comparison between records (memories), and this may be the source of dreams. The nature of dreams in humans suggests this function.

Analysis of the electrical activity at the level of the hippocampus may support this. We observe the same theta waves during alert wakefulness (gathering of information) and PS. The hippocampus is known to be involved in memory. In the future, we will have to investigate these correlations more closely.

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