

The subjects were ten adult, laboratory-reared cactus mice, *Peromyscus eremicus*, from the colony maintained at the University of Florida (4). Stock originally were trapped near the Rillito River in Arizona. The females were mated with 12 males from the same colony.

An attempt was made to complete six tests with each female—two tests in each of three conditions. In the first condition (1E), the female was introduced into the male's home cage and the pair was permitted to copulate until the completion of one ejaculatory series. The female was then returned to her home cage. In the second condition (SAT), copulation was permitted until attainment of a satiety criterion of 30 minutes without copulation. The 30-minute criterion is the standard, if somewhat arbitrary, criterion for regarding a male as sexually satiated. The female was then removed. Tests in the third and final condition (SAT + ON) were identical to those in the SAT condition, except that after attaining the satiety criterion, the female was permitted to remain unobserved in the male's home cage overnight. (One of the scheduled 60 tests could not be conducted because of the death of the female.)

Animals were housed individually and maintained on a reversed light-dark cycle. Vaginal smears were taken each morning with a thin wire loop. Tests were conducted on the first day of disappearance of leukocytes from the vaginal smear, provided the female had shown a stable baseline of at least two successive cycles of 7 days or less. Following copulation, a female could show any of three possible responses: (i) continue to cycle (display a proestrous or estrous vaginal smear in 7 days or less), (ii) pseudopregnancy (a 10- to 15-day diestrus), or (iii) pregnancy. All females classed as pregnant delivered litters after 28 to 32 days, except one which suffered an apparent spontaneous abortion on day 19.

Estrous cyclicity was altered in only 10 percent of the cases in which just a single ejaculatory series was permitted (see Table 1). Thus in cactus mice, in contrast to laboratory rats and mice, a single ejaculatory series with sperm transfer does not usually suffice to initiate neuroendocrine responses essential for pregnancy. By contrast, after 80 percent of the tests in the SAT and SAT + ON conditions females became pseudopregnant or pregnant.

Table 1. Number of mice that continued to cycle, became pseudopregnant, or became pregnant as a function of condition, expressed as the number positive/the number of tests, as well as in percentages.

Category	Condition		
	1E*	SAT†	SAT + ON‡
Continue cycle (3 to 7 days)	18/20 (90%)	4/19 (21%)	4/20 (20%)
Pseudopregnant (diestrus, 10 to 15 days)	1/20 (5%)	6/19 (32%)	4/20 (20%)
Pregnant (gestation, 28 to 32 days)	1/20 (5%)	9/19 (47%)	12/20 (60%)

* Completion of one ejaculatory series. † Satiety criterion attained and then the female was removed from the cage. ‡ SAT condition, except the female remained in male's cage overnight. (See text for details of these three conditions.)

There were no substantial differences between the latter two groups.

Measures of copulatory behavior in the first series were quite similar across groups and resembled the values reported earlier for this population (4). Copulation beyond the first ejaculation occurred in all tests in the SAT and SAT + ON conditions with a mean of 28.2 postejaculatory intromissions in the former condition and 22.0 in the latter. This is somewhat higher than the value reported for females in hormone-induced estrus (4). However, on no test was a second ejaculation observed to occur. Thus the copulations that were critical in initiating neuroendocrine responses of pregnancy were not accompanied by additional sperm transfer.

In both the SAT and SAT + ON

conditions, the females becoming pregnant received significantly more postejaculatory intromissions than the females becoming only pseudopregnant (16.0 versus 36.8 in the SAT condition and 5.5 versus 29.5 during observation in the SAT + ON condition) (5). This suggests that in addition to a copulation-sensitive mechanism for the initiation of a functional luteal phase, a second mechanism, critical for true pregnancy, may exist. This mechanism might resemble that through which preejaculatory intromissions facilitate sperm transport in rats (2).

Many species continue to copulate after attaining ejaculation and have short estrous cycles in which pseudopregnancy is copulation-dependent (1, 6). We believe this to be the first demonstration that postejaculatory copulations without sperm transfer can be critical to the initiation of the neuroendocrine responses that halt the estrous cycles and trigger a functional luteal phase.

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5. Mann-Whitney U tests: $U = 10$; $P < .05$ (two-tailed) in SAT condition and $U = 2$; $P < .02$ (two-tailed) in SAT + ON condition.
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7. Supported by grant GB-33837X from the National Science Foundation.

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Sleep and Cardiac Rhythm in the Gray Seal

Abstract. *Telemetric studies of electroencephalograms, electrocardiograms, and electrooculograms and concurrent observations of behavior revealed that seals can sleep underwater, on the surface, or while hauled out. Rapid eye movement preceded slow wave sleep and was accompanied by increased respiratory rate and rhythmic tachycardia. While slow wave sleep occurred under all sleep conditions, rapid eye movement occurred only when a seal was hanging at the water surface or hauled out, never underwater.*

Although many investigators (1) have observed seals sleeping in various ways, there have been no neurophysiological investigations of sleep in pinnipeds. We were interested to learn if seals do sleep in or under the water and, if so, whether sleep in the water differs from sleep observed in terrestrial mammals (2).

Sleeping pinnipeds have been ob-

served hauled out on land (3), on the sea surface (1, 4), and underwater (4, 5). Waking cardiac arrhythmia (bradycardia during apnea and tachycardia during breathing) in pinnipeds is eliminated by anesthesia (6). Since pinnipeds have been observed underwater, apparently asleep, for up to 23 minutes (7), we wanted to know if bradycardia oc-

curred during this apparent sleep state.

Radiotelemetry devices (8) were implanted in the hypodermis of the back and neck in gray seals (*Halichoerus grypus*) 12 to 18 months old (9). Initially a single-channel transmitter was used to record the electroencephalogram (EEG). Later a three-channel multiplex unit was built to transmit the EEG and the electrooculogram (EOG). One EEG lead was placed over the dura about 1.0 cm off the midline and 0.5 cm from the posterior margin of the parietal bone. The second lead was placed through the parietal bone about 1.5 cm from its ventral margin and 1.5 cm from the posterior margin of the frontal bone. The EOG lead was dorsal to the orbit midway between the zygomatic process of the temporal bone and the frontal bone. Another transmitter, which broadcast the electrocardiogram (ECG), was placed in the back with a lead extending across the thorax. All the transmitters broadcast in the frequency modulation (FM) range, around 102 Mhz, and were tuned to separate the signals (10). A magnetic switch turned the transmitters on and off. This allowed recordings (11) from each seal over a period of up to 6 months.

Seals were housed in three ways: (i)

in a large community tank with a raft moored in the center, (ii) in individual tanks with an adjacent haul-out area, and (iii) in a glass tank with a Plexiglas lid so that the seal could not climb out. The area was under continuous illumination before and throughout the study.

On 12 occasions, four seals were observed and recorded continuously from 6 p.m. one evening until 8 a.m. the next morning. Only one seal was observed at a time. Of the 12 all-night observations, one was of a seal in the community tank, four were of seals in the glass tank, and seven were of seals in the individual tanks.

In the water, the most common sleeping position was a semifloating one; the nostrils were at the surface, usually just clear. The body sloped down at an angle of about 30° and the rear flippers occasionally made swimming movements. At other times a seal would bob up and down slowly, taking several breaths at the surface and then sinking below for a minute or so before rising to breathe. In a more extreme version of this behavior, a seal took 10 to 20 breaths at the surface and sank for as long as 4 minutes.

In another sleep position, the seals

appeared to be resting against a corner of the tank, as if sitting back in a comfortable chair. The head was often thrown back with the snout pointed directly overhead. At other times the seals would rest their chins on the edge of the tank.

There were long periods when a seal was inactive, but apparently awake, resting in the water with its eyes open. It would breathe one to five times with its nose just clear of the surface and then sink. It would hang in midwater for 20 seconds to a minute or more, with the rear flippers languorously moving from side to side, before slowly emerging. We called this state quiescent waking (QW). An animal in QW responded immediately to an observer approaching the tank or to a noise in the area.

Quiescent waking preceded sleep and lasted from about 20 minutes to 3 hours. Respirations were three to seven per minute and always irregular. With each breath there was a brief tachycardia equivalent to 90 to 160 beats per minute lasting for three to six heartbeats (Fig. 1). As a seal sank, the heart rate decreased to 20 to 60 beats per minute and remained low until the next breath. Quiescent waking was followed by an interval that we first called "rapid heartbeat" sleep. Later we determined that rapid heartbeat sleep and rapid eye movement (REM) sleep were synonymous. During this state, the heartbeat became regular and fast (110 to 170 per minute). The respiration was also regular and increased to 12 to 16 per minute. The REM state was observed both in and out of the water, but seals in the water exhibited REM only when floating with the nostrils just clear of the surface. Periods of REM were as long as 63 minutes and as short as 5 minutes.

Whisker twitches were frequently observed during REM. Myoclonic twitches and other body movements were also seen, especially when the seal was out of the water. A seal was difficult to arouse during REM and in some cases could actually be touched without behavioral arousal. There were no instances of spontaneous arousal from REM.

The EEG during the rapid heartbeat phase progressed to high-voltage slow wave activity (Fig. 1). Soon after slow waves began to appear, the respiration reverted to the arrhythmic style. The seal took 1 to 20 breaths in succession,

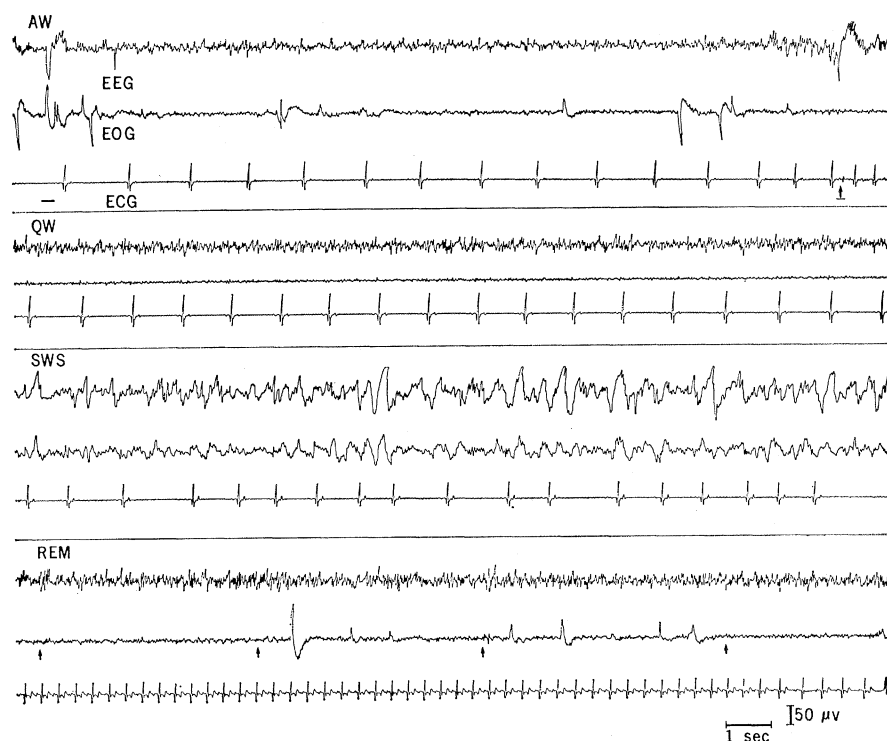


Fig. 1. Recordings from a seal in water. Abbreviations: EEG, electroencephalogram; EOG, electrooculogram; ECG, electrocardiogram; AW, active waking; QW, quiescent waking; SWS, slow wave sleep; and REM, rapid eye movement (sleep). Arrows indicate breaths, and dashes (—) indicate gross body movements. The 50- μ v calibration mark refers to the EEG channel only.

attended by tachycardia (90 to 160 beats per minute); this was followed by a breath hold for 20 seconds to 4 minutes, during which the heart rate slowed to 30 to 70 beats per minute. In some animals the transition between REM and slow wave sleep (SWS) was abrupt, taking 1 minute or less; in others, REM and SWS alternated (along with heart and breathing rates) for up to 30 minutes before SWS became dominant and sustained.

Slow wave sleep that lasted for 20 minutes to 4 hours was observed whether the seal was completely out of the water, in the water with just the tip of the nose clear during breathing, in the water bobbing up and down, or in the water with the head out. The observer could approach the seal and speak quietly without inducing behavioral arousal. If the observer touched the seal, or if a seal in another tank nearby vocalized, behavioral arousal followed.

During the 12 all-night sessions an average of 2.8 ± 1.5 hours was spent in active waking (AW), 5.0 ± 2.3 hours in QW, 4.7 ± 2.2 hours in SWS, and 1.5 ± 1.1 hours in REM (12). When seals awoke spontaneously and became active during the night, a return to behavioral quiescence always followed the sequence QW to REM to SWS. When seals awoke momentarily from SWS they returned to that state.

The sleep of gray seals was distinctive from that of man and other terrestrial mammals that have been similarly studied in that (i) it took place in water as well as out; (ii) REM sleep was accompanied by a rapid, regular heart rate, whereas in other mammals studied it is accompanied by the lowest and most irregular heart rate (13); (iii) respiration was regular during REM sleep, whereas in terrestrial mammals it is irregular; and (iv) REM sleep in the seal appeared first, whereas in other mammals it normally follows SWS. The gray seal, and perhaps other pinnipeds as well, may have evolved a unique sleep mechanism to cope with the necessity for sleeping in water.

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9. Six gray seals obtained in Iceland were employed in these experiments. Electrophysiological observations were made on four of the seals. The seals were acquired in November 1970, shortly after they were weaned and had begun taking dead fish in captivity. The experiments were conducted during late 1971 and early 1972, when the seals weighed 70 to 100 kg and were well adapted to captivity. All experiments were conducted at the University of Cambridge under a license from the British Home Office.
10. Since FM telemetry is virtually useless in sea water, we kept the seals in fresh water. Gray seals have been maintained for long periods of time in fresh water in various zoos. Each seal was kept in an individual tank to which salt was added for a few days after each implant.
11. A portable FM radio receiver (Sony, model 7F-74DL) was placed within 5 m of the implanted seal. The output of the radio was connected by an electrical lead to a decoder and displayed on an oscilloscope (Tektronix, model 564B) and a polygraph (Grass, model 78). The transmitters and the decoders were constructed in our laboratory.
12. Averages were rounded off to the nearest tenth of an hour.
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14. We thank Derek Thurlborn and Andrew Greenwood for technical assistance and William F. Flanagan for reviewing the manuscript.

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Student Evaluation

Gessner (1) and Frey (2) appear to contradict our finding (3) of a substantial inverse correlation between amount learned by students and evaluation of the instructor. However, methodological and substantive aspects of both their studies undercut the superficial contradiction.

Gessner reports a positive correlation between rating of instructor and amount learned and concludes that student ratings are a good measure of teaching performance. However, instructor and subject matter are confounded in the Gessner study. Assume for a moment an acceptable measure of amount learned. The different instructors taught different subject matters. One could just as reasonably conclude from the positive correlation between instructor rating and amount learned that students perform better in subject matters they like better, quite independently of who is teaching or how.

The preceding assumption of an acceptable measure of amount learned is not, however, warranted. Gessner's assertion that little could be concluded from student performance on departmental examinations is clearly correct. Since the various instructors taught different subject matters and each prepared his own questions, it would have been impossible to tell whether students did well in a subject area because the instructor's teaching was

superior or because his questions were easier. Gessner rejected student performance on departmental exams as a measure of student learning for rather different reasons: they did not correlate positively with student ratings and they were uncorrelated with student performance on a national exam (the National Medical Board Examination). He therefore used performance on the national exam as his measure of amount learned. More precisely, he measured student learning by how well his sample of students performed relative to the national sample. Gessner's use of this measure presents several problems.

Gessner takes the performance of the national sample on a given question as a measure of the difficulty of the question. However, he found no relationship between performance of the national sample and performance of his sample in the individual questions of the national exam [reference 18 in (1)]. The finding that his measure of item difficulty is unrelated to actual item difficulty for his sample would seem to invalidate his measure. Performance on the national exam is a good measure of item difficulty only on the assumption of standardized course content. Otherwise, unusually high or low scores obtained by a student sample may simply reflect unusual content emphasis relative to the norm.