HIBERNATION IN MAMMALS

By GEORGE E. JOHNSON

Kansas State Agricultural College

(Contribution 133 from the Department of Zoology, Kansas State Agricultural Experiment Station, Manhattan, Kansas)

HIBERNATION is often referred to as "winter-sleep" in English, *"Winterschlaf"* in German and *"sommeil-hivernal"* in French. It is also called "torpor," "lethargy," and, in Italian, *"letargo."* These terms may be considered essentially synonymous. They involve an inactive state in which the metabolism is so greatly lowered that the body temperature is only a little higher than that of the surroundings. A limitation of the term hibernation to this condition and not applying it in the older more literary sense of "spending the winter" would make the meaning of the word clearer.

It should be stressed that hibernation is not ordinary sleep occurring in the winter. This was recognized long ago by Horvath (1881), who repeated a statement of the botanist, Ferd. Cohn, that *"Winterschlaf"* is not sleep and has nothing to do with winter. In this way he emphasized that hibernation may occur even in the summer and that the insensibility is far deeper than in ordinary sleep. If such a meaning can be given *"Winterschlaf"* there should be little difficulty in limiting the term "hibernation" to actual states of torpor and also in having it include all such states, not excepting those that occur in summer in the field or laboratory. There is no evidence that mammals ever become insensitive or partly torpid because of warm surroundings, all reported cases of lowered metabolism apparently having occurred when the surrounding temperature was considerably below that of the normal animal. For this reason the term "aestivation" appears inappropriate for summer torpor in mammals, although it may be proper for inactivity actually produced by surrounding high temperatures. Aestivation might be used for the denning up of the animals following a drying of the vegetation by the heat in the summer, but since any known cases of semi-torpor at this season are produced by cold such conditions should, it would seem, be called partial hibernation.

ANIMALS THAT HIBERNATE

Hibernation is common in such invertebrates as the snails in the Mollusca and the crustaceans, insects, arachnids and myriapods in the Arthropoda. It is the usual winter condition of most amphibians in colder climates and of terrestrial reptiles such as the tortoises, lizards and snakes. Invertebrates and the lower vertebrates are generally considered as having no heat-regulating mechanism, and since their temperature varies chiefly with that of the surroundings they are said to be poikilothermal or cold blooded. Recently, however, evidence has been produced that the turtle has some power to regulate the temperature of its body (Baldwin, 1925). All birds and most mammals maintain a relatively high and almost con-

439

stant body temperature regardless of the environment, and are said to be homoiothermal or warm blooded. Hibernating mammals do not appear to maintain a very constant temperature and at times definitely assume the poikilothermal state, so that their temperature is only a little higher than that of the surrounding atmosphere or soil.

Hibernation has been studied by various workers in monotremes, insectivores (hedgehogs), bats, and in several genera of rodents (woodchucks, dormice, ground squirrels, prairie dogs, some chipmunks and certain jumping and pocket mice). Mills (1892) says the porcupine, a large spiny rodent, hibernates but Pratt (1923) and Anthony (1928) state that this animal does not hibernate. According to Pratt (1923) and Bailey (1926) some northern species of carnivores (raccoons, skunks and badgers) hibernate. Anthony (1928) states that raccoons hibernate and skunks and badgers "den up" during very cold weather. All three of these writers state that some bears hibernate. Other workers (e.g. Merzbacher, 1904) deny that bears enter into a real state of hibernation and call attention to the fact that the young, usually two in number, are born in late winter and that the body temperature of the mother could not be low at that time. Dubois (1896) calls attention to the vapors emerging from the winter den of the bear, and he and Adler (1926) each state that bears and badgers maintain a high temperature. Seton (1928) states that the raccoon, skunk and bear are partial hibernators in the northern regions, but that they do not assume a death-like torpor.

It may be noted that the hibernating animals do not belong to any one order but that most of them live in the ground and have no access to their usual food during the time the ground is frozen. Horvath (1874, 1881) sought some test whereby one could determine whether a given species could hibernate or not. He found that animals that were known not to hibernate would die when immersed to the neck in cold water if the body temperature fell below 19°C. (essentially confirmed by Britton, 1922), whereas known hibernators would survive at body temperatures a few degrees above the freez-

ing point of water. The latter finding was confirmed by Tait and Britton (1923), who found that a woodchuck would recover if its body was cooled even to 3°C. by the immersion method. The author has observed that ground squirrels, caught by "drowning out" methods become very torpid while wet in cold air, but recover when warmed. It seems probable that this test developed by Horvath may help in distinguishing between hibernators and non-hibernators. However, placing several animals of a species in a cold environment in the fall and winter probably would be the safer practice.

PLACE OF HIBERNATION

Barkow (1846) states that bats hibernate in stone walls, cellars, and hollow trees. Dormice hibernate in dry holes under rocks, roots or garden walls, depending on the species, and the hedgehog hibernates under roots of trees and shrubs and under garden walls. He also states that the hamster hibernates 5–10 feet and the marmot 3–7 feet underground in a nest lined with vegetation and that it closes its burrow in the winter. North American bats hibernate largely in caves (Bailey, 1924; Hahn, 1908). Ground squirrels hibernate in nests made of dry vegetation in hollowed-out underground chambers connected with their burrows. The chambers vary as to depth and size with the species. In the thirteen-lined ground squirrel, with which the author has worked, 24 nests studied varied from 4 to 10 inches in diameter and from about 3 to 27 inches below the surface (Johnson, 1917). In this and other species these nests may be connected with a drain and the entrance to the burrow is always plugged with soil before hibernation (Johnson, 1917; Shaw, 1925a). Prairie dogs hibernate in larger nests 10 or more feet below the surface (Merriam, 1901; Swenk, 1915). Their nests may be above the main tunnel as a protection against the burrow being filled with water; the entrance is not closed, possibly because the animals hibernate less than ground squirrels. Other American rodents hibernate under ground or in nests under stones. Apparently raccoons hibernate in hollow logs. If skunks and badgers hibernate they would do so in underground chambers where they normally sleep.

Food stores are sometimes found in the nests of rodents. An unusual case was observed by the author. A ground squirrel, *Citellus tridecemlineatus tridecemlineatus*, had stored about 24,000 kernels of oats

in one underground chamber and about 4,000 in another (Johnson, 1917). Oats, wheat, corn and weed seeds were frequently found in the excavations in which the hibernation nests were made, but in decreasing quantities with the advance of autumn (Johnson, 1917), suggesting that this food is eaten chiefly before entrance into hibernation. However, storage of grain was not found to be universal in this species (Johnson, 1917; Fitzpatrick, 1925). Bailey (1926) reports that there is storage of seeds and grains in the pocket mice and some of the chipmunks which are not very fat when they hibernate but apparently wake at intervals to eat.

Whether animals store food or not probably depends partly on its abundance preceding the hibernation period. While different species do not hibernate at the same time or become equally torpid, it is generally agreed by most writers that hibernation serves to conserve the life of the species that hibernate and that torpor is associated primarily with a cold season when food is impossible to secure. Whether every such species would perish if it should not be able to become torpid is difficult to determine, but this appears probable.

HIBERNATION IN THE SUMMER

That hibernation is not a condition which can occur only in the winter has been shown by a number of workers. Forel (1887) found that two dormice hibernated first in the spring after becoming fat and remained lethargic most of the summer. Horvath (1881) observed hibernation in ground squirrels in the laboratory at 22°C. Polimanti (1912) refers to summer torpor observed by Brown-Sequard in dormice lasting a week at external temperatures of 15° to 20°C., and also in marmots (European woodchucks) in June at external temperatures of 21.5° to 23°C. Bats may hibernate in June at 15°–16°C. according to Koennick (Adler, 1926). Summer torpor in thirteen-lined ground squirrels has been observed by the author to take place in a refrigerator each summer since 1924 (Johnson, 1925, 1930). In fact, hibernation was found more commonly in the summer than in the spring (Johnson, 1930). Many cases of partial hibernation have been observed in the animal house on cool mornings in August and also during later fall and winter months when the temperature fell to about 21°C. With what may be considered typical summer temperatures of about 24°C. or above no hibernation

was observed. Cases of partial hibernation on cool summer days have been reported in the Townsend ground squirrel by Shaw (1925b) and in the thirteen-lined form by Wade (1930).

The tenrec of Madagascar has often been cited as an animal that hibernates in summer, but Milne-Edwards (1857) has pointed out that several workers have reported this animal hibernating during the cold season.

Since hibernation may occur in the summer in the laboratory it would be expected that it may also occur in the field, as Horvath (1881) suggested, at temperatures below 22°C. A "drowsy" Columbian ground squirrel was dug out of its burrow in August, but all efforts to find a torpid animal prior to December 13 failed (Shaw, 1925a). Seeking for this condition in the thirteen-lined ground squirrel Wade (1930) procured his earliest record of hibernation on October 16. If the animals are partly torpid in the early fall, they must be so slightly torpid that they are aroused by the sounds of the digging and are fully active when found.

Indirect evidence that such a condition may occur in nature is produced by Shaw (1925a), who found that the Columbian ground squirrels had almost all retired to their burrows by August 10 one year and in another drier summer all had disappeared by August 7 (1925c). Similar observations that hot dry weather and a consequent drying of vegetation send ground squirrels (related to our prairie dogs) of Turkestan into their burrows by June 1 is given by Kashkarov and Lein (1927). Wade (1930) mentions the disappearance of wild thirteen-lined ground squirrels one year in eastern Nebraska in hot weather early in September. He also found that of 22 animals transferred to outdoor pens in the spring nine plugged the entrance to their burrows, one in May, two in July, five in August and one in September. Wade also states that the individuals at large in the fields in late September were young or lean ones.

It has been the experience of the author that it is more difficult to secure ground squirrels from boys in western Kansas in August and September than in April to July, a fact which would support Wade's statement. However, many animals have been secured in the fall in the Dakotas, in Illinois and in Kansas, even as late as September and October.

LENGTH OF HIBERNATION

Two things make it difficult to state how long a given species hibernates. One of these is the apparent tendency of torpid mammals to wake up at intervals and the other is the possibility of some individuals of a species hibernating in the early fall when others are still at large. The waking of hibernating

mammals every few days has been observed by Barkow (1846) in ziesels or ground squirrels after one to seven days of torpor, and in hedgehogs; by Horvath (1878) in ground squirrels after torpor for four days; by Mangili (1807), Valentin (1857) and Dubois (1896) in marmots, after periods of torpor varying from a few days to three or four weeks; and by Shaw (1925a, b) in the Columbian and Townsend ground squirrels.

The author has found in many experiments, each involving 20 animals kept in the refrigerator for two weeks, that some of the animals will usually hibernate within one to three days and then awaken from one to ten days later, remaining active for a day or more. In cases where animals were in the refrigerator for long periods, castrated males were in continuous hibernation as long as 15, 16, 18 and 33 days and normal males for 13, 14 and 15 days, as judged by daily observations and their lack of feeding.

To avoid any possibility of animals waking between daily observations unbeknown to the observer, further records were taken for over four months on eight *C. t. pallidus* ground squirrels which had already been in the refrigerator 25 days. Three or four grains of oats were dropped gently on the back of the torpid animal, which would fall off only when the animal woke or moved about. The food placed in the cages consisted of dry oats and a small amount of green grass at first, but later carrots and a few kernels of oats were placed in the cages. The animals were seldom handled as previous observations had confirmed Dubois' (1896) statement that taking temperatures, etc., caused more frequent awakening. The grains of oats appeared not to stimulate waking. The range of continuous hibernation was from one to eighteen days with an average of approximately six days. One record each of 18, 17, 14 and 13 days of continuous hibernation was made, but four records of 11 days and six records of 10 days were made. There appeared to be some tendency towards a lengthening of the periods of hibernation from an average of about four at first to about eight days after a few weeks in the refrigerator. This may indicate that the torpor is more prolonged after the first few periods, although it is probably partly accounted for by the lowering of the refrigerator temperature from about 11° to about 3°C. during the course of the experiment. The average time during which the animals remained awake between periods of torpor was approximately one day. The faeces voided by each animal during the first two months of this experiment were proportional to the time spent awake. On the 62nd day of the experiment the animals were carefully transferred to clean cages and in a total of over 80 observations the animals, almost without exception, were found to void an appreciable amount of urine and faeces each time they were awake. In some cases as many as 20 or 25 faecal masses and large amounts of urine were seen. Apparently when such surprising amounts were found the animal had eaten more freely than usual. It appeared probable that most of the food passed through the animal before it became torpid again. These observations support the statements of others that these short periods of waking are caused by the stimuli produced by the urine in the bladder and faeces in the rectum.

Carrots and apples fed at different times in the experiment usually showed tooth marks after an animal had been awake for a few hours, but in several instances no food appeared to have been eaten. A few grains of oats were sometimes hulled and eaten, but most of the oats were left untouched. While the quantities of food taken at any one time were as a rule small, it should be stated that near the end of the experiment and to a less extent at other times an animal which was thin might consume large quantities of carrots in one or two days and then go back into hibernation. In general, these observations confirm those of Horvath (1878), who found that ground squirrels ate when awake more than a few hours.

It is not known whether animals wake at intervals in their burrows. One of the author's animals, which had built its nest within six inches of the surface in an outdoor cage in Chicago, came out of its burrow in late December and in late January when the weather was warm. It seems quite probable that waking occurs at intervals throughout the winter in nature, for the ground squirrels continued to do so in the refrigerator even at 2°–3°C. Waking may be more frequent in the fall because at that time the soil temperature and therefore the metabolism is higher than in mid-winter and there will be formed more urine and faeces.

Different individuals of a single species may not spend the same amount of time in hibernation. Old hedgehogs may hibernate earlier than young ones (Barkow, 1846). Old ground squirrels den up first and the females go in before the males and appear several days later in the spring (Shaw, 1925b; Wade, 1930; Johnson, unpublished data), so that the average period spent underground by the Columbian ground squirrel is 220 days in the female and 204 days in the male (Shaw, 1925b). The fact that these animals are doubtless not torpid all of this time, together with the other variations also presented, will make it clear that only approximate figures can be given for the length of hibernation in different species.

According to Barkow (1846) the hedgehog is underground four to five months, from November or December to March or April. Merzbacher (1904) gives this period as three or four months for the

hedgehog and Lapland marmot, and two or three months for German marmots, badgers, dormice and ground squirrels. Howell (1915) states that woodchucks hibernate four to six months. Raccoons hibernate nearly four months in the Red River Valley (Seton, 1928) and three to four months in Ohio (Williams, 1909). Thirteen-lined ground squirrels have been seen as late as October in Illinois (Corey, 1912; Johnson, 1917), in South Dakota (Hahn, 1914; Johnson, 1917) and in Nebraska (Wade, 1930), and on November 9 in Colorado (Burnett, 1914). They appear again in March, sometimes early (Hahn, 1914, in South Dakota) but more often late in the month (Burnett, 1914, Colorado; Corey, 1912, Illinois). In Kansas both the typical variety and the paler variety from the western part have generally been procured in fairly good numbers late in March.

POSITION IN HIBERNATION

In hibernation rodents are rolled up in their nests in the ordinary sleeping position. Striped ground squirrels sit on the posterior surface of the hind legs, the back strongly arched above, the nose tucked into the fur of the posterior part of the abdomen so that the top of the head rests partly against the pelvic girdle and partly on the bottom of the nest. The weight of the animal appears to be divided between the hind legs, the posterior dorsal part of the sacrum and the posterior dorsal part of the head. The Townsend species is illustrated in this position by Shaw (1925b), but the Columbian rests on the sacrum alone (Shaw, 1925a) as does also the *Callospermophilus* form. The fore legs are held close at the sides of the head. The eyes and mouth are tightly closed. The outside curvature of the body describes nearly a circle and it lacks only a little width in the middle to form a perfect sphere. This position doubtless tends to conserve body heat.

IMPERFECT TEMPERATURE CONTROL OF HIBERNATING MAMMALS

That the temperature of hibernating mammals, even when not torpid, may be lower than in mammals which do not hibernate was observed long ago by Saissy (1815) and others. Saissy gave records of 25°–30°R. (32.2°–37.5°C.) for woodchucks, hedgehogs, dormice and bats. Barkow (1846) observed a drop in temperature in hedgehogs and bats in ordinary sleep, in sickness and in starvation, but concluded that they are ordinarily warm blooded when awake, bats even having temperatures as high as 41.0° and 41.6°C. Dubois (1896) also found no fluctuation in the temperatures of hibernators except in the fall. According to Merzbacher (1904), Hall found a drop in

temperature in a bat during its day sleep. Marked fluctuations in temperature in *Citellus tridecemlineatus tridecemlineatus* and also in *C. t. pallidus* have been observed at all times of the year (Johnson, 1928). The temperatures of ground squirrels when not in hibernation ranged from about 32° to about 41°C., but a range of 35° to 39°C. was common in a warm room and of 31° to 36°C. in a cold room. The lower normal temperatures grade into those of slight torpor at about 29°–32°C. The highest animal temperature recorded, 42.3°C., in a heated chamber was probably very close to the highest the animal can endure. The fluctuations in body temperature appear to be produced largely by changes in the surrounding temperature, but partly by the animal's activity and its rather poorly adjusted heat regulating mechanism. Vigorous exercise or confinement in a heated environment may cause a marked rise in body temperature (Johnson, 1928).

That this lack of temperature regulation and the accompanying power to hibernate is not a recent acquisition is indicated by the work of Martin (1901) on the spiny ant eater (*Aechidna*) and duckbill (*Ornithorhyncus*). These egg-laying animals are the lowest living representatives of the mammals. In *Aechidna* there was a fluctuation of 10°C. in the body temperature when the environment varied from 5° to 35°C. In *Ornithorhynchus* the temperature was low but more constant than in *Aechidna*. Martin found evidence for modification of both heat production and heat loss in *Ornithorhynchus*, and still greater heat control in marsupials.

Rectal temperature records (unpublished) taken almost daily on an adult male opossum, mostly in December, 1926, showed temperature variations in five readings ranging between 33.6° and 35.5° when taken in a room of between 25° and 29°C. The same animal removed to a refrigerator temperature of 4° to 6°C. showed a range of temperature varying from 33.5° to 34.7°C. A young opossum in a room temperature of 14° to 19°C. in February, 1925, showed a range of rectal temperature varying from 33.2° to 35.0°C. Two other opossums under the same conditions gave single temperature readings of 36.0°C. No hibernation was observed in four opossums in a cool cave nor in one kept at about 5°C. in a refrigerator.

Four pocket gophers (*Geomys bursarius*) kept in a cold room of about 4°C. for five days showed only slight temperature fluctuation, in one case 33.8° to 35.2°C. and in another case 35.2° to 35.8°C. The four died in a few days and like others kept in the refrigerator at other times never hibernated. A dying animal showed a rise of body temperature from 19.5° to 23.0°C. with a rise in heart beat from 40 to 124, on

removal to a warm room. As the animal died this was probably only a temporary rise in metabolism produced by the warming of the animal, and the lowered temperature cannot be considered hibernation.

Since prairie dogs (*Cynomys ludovicianus*) have been reported to hibernate only for short periods in nature it was felt that a study of their temperatures would be interesting. Forty-six daily records on seven animals in the cold room ranged chiefly between 32° and 36°C., whereas 57 daily records on five animals in the warm room showed a relatively stable temperature at 36°–37°C. (Table 1).

Three prairie dogs in a refrigerator had temperatures of 27°, 28° and 28°C. and were therefore on the verge of torpidity. Among several prairie dogs kept in a refrigerator temperature of about 5°–12°C. for several weeks at a time only three cases of normal hibernation were observed. These animals were not

TABLE 1

Temperatures of Normal Prairie Dogs

	ANIMAL TEMPERATURES						
	31*	32	33	34	35	36	37
Number of records at refrigerator temperature 3°–10°C.................	1	5	8	9	7	14	2
Number of records in warm room, range about 22°–29°C........	0	0	0	2	7	31	17

* Each degree given includes the decimals of that degree, thus 31 = 31.0° − 31.9°C.

completely torpid, but could move very stiffly and trembled like ground squirrels in the later stages of a disturbed awaking from hibernation. The rectal temperature of one was 21.5°C. at a room temperature of 9.5°C. The second had a rectal temperature of 19.4° in a room of 9.5°C. A third was found, partly torpid, at a room temperature of 4.4°C. In breathing it made a wheezing noise, but this stopped as it gradually recovered its normal temperature. A fourth animal was considered as in abnormal hibernation. It was partly torpid at 22.0°C. cheek pouch and rectal temperatures. This animal seemed to have much difficulty in breathing, and in the quarter hour it was observed its temperature fluctuated a little with exertions but showed no real rise. The next day, however, it had a rectal temperature of 30.0°C. and was more active, although somewhat sluggish. Again 13 days later this animal was slightly torpid at rectal and pouch temperatures of 29.5° and 29.3°C. respec-

tively. At this time it had difficulty getting air and its heart beat was somewhat irregular, showing pauses between a series of regular beats.

Incidentally, from these temperature studies it may be concluded that the opossum may possibly hibernate to a slight extent, that the pocket gopher does not hibernate, and that the prairie dog hibernates only for short periods in the coldest weather. In this connection also, it is of interest to note that young mice and rats do not regulate their own temperatures well until they are ten days old (Pembrey, 1895), and even a group of adults may have a range of 1.0° to 2.0°C. (Sumner, 1913). According to Bierens de Haan (1922) a rise of 5.0°C. in external temperature produced an average rise of 0.70°C. in the body temperature of 3½ week old rats.

TEMPERATURE IN HIBERNATION

Body temperatures lower than or equal to those of the surroundings have been reported in torpid bats by Hall (1832), in marmots by Valentin, according to Barkow (1846), and by Monti and Monti (1900). In torpid ground squirrels Horvath (1872a) reported a body temperature of 2°C. in a room of 2°C., (1878) of 11.8°C. in a room of 13°C., of 11.5°C. in a room of 12°C., and of 4.6°C. in a room of 5.8°C. Barkow (1846) made similar findings but like Valentin considers that body temperatures are usually a little higher than those of the surroundings. Saissy (1815) and others found the temperatures of torpid marmots, hedgehogs, dormice and bats to be higher than those of the room, the difference being 1° to 2°C. (Quincke, 1881), i.e., 0.5° to 0.8°C. in bats in a cave of 6.4° to 7.7°C. (Delsaux, 1887); 0.25° to 2.0°C. in bats (Pembrey and White, 1896); a few tenths of a degree in the marmot (Dubois, 1896); and 1.1° in ground squirrels in a box of 2.2°C. (Shaw, 1925b).

That serious errors could be made in the study of animal temperatures in relation to room temperatures became evident to the writer in the progress of his work. The causes of these errors were eliminated by meeting the following conditions: constant room temperature, room temperature taken at the level of and near the animal, animal not in contact with a floor that was colder or warmer than rest of room, complete corrections applied to thermometers, animal and room temperatures taken immediately upon entering the room, animals disturbed as little as possible, light not used intermittently, and quietness in the hibernating room.

In a cold room (Johnson, 1928) when the temperature had become fairly constant after a gradual fall, three temperature curves of *C. t. pallidus* ground squirrels remained about 0.5° to 1.0°C. higher than the room temperature curves in three animals. Thermo-

couples placed in the bottoms of thick corkboard nests indicated body temperatures of a little less than 1.0°C. (0.5° to 1.2°C. in 92 per cent of 144 records) above that of the surroundings in ground squirrels long in deep hibernation. Of 25 records obtained by removing torpid ground squirrels from a refrigerator and immediately taking their pouch temperatures thermoelectrically, 40 per cent were less than 1.0° higher, 68 per cent were less than 2.0° higher and all the records were less than 4.0° higher than the refrigerator temperature, which ranged from 4.9° to 8.4°C. Torpid ground squirrels appear, then, to be usually about 1.0° to 3.0°C. warmer than their surroundings, but they are often less than 1.0°C. above, and may be rarely only 0.3°C. above the surrounding temperature. That Horvath and Monti and Monti and some other workers failed to observe proper precautions seems evident. The metabolism of the animal is sufficient to keep its temperature slightly above a constant surrounding temperature.

The lowest temperature in a torpid woodchuck observed by Dubois was 4.6°C. He states that the temperature of bats may fall to 5.0°C. or even to 1.2°C. in hibernation. Horvath (1872a) gives the lower temperatures of hibernating ziesels as 2.0° and later (1881) as varying between 1.8° and −0.2°C. The animal with a temperature of −0.2°C. woke up as a result of an external temperature of −0.5°C. As has already been pointed out, some of Horvath's temperatures were possibly not reliable; hence these may not be either. The lowest temperature given by Horvath was recorded during a falling outside temperature and may have been taken near the surface of the body; the emergent stem may have slightly lowered the reading, or the thermometer may not have been accurate. Dubois (1896) states that Brehm found temperatures of bats as low as 1.2°C. Adler (1926) states that if bats are cooled carefully and are not disturbed by touching or noise, their temperature may be lowered to 0.5°C., but that this temperature usually starts the awakening process.

That animals in hibernation may approach the freezing point of water was evidenced in my work (Johnson, 1928) in which a *C. t. tridecemlineatus* was observed with a food pouch temperature of 2.0°C. in a room of 1.0°C. This animal woke in a normal manner. That death results somewhere between 2.0° and 0.0°C. was indicated by the fact that one *C. t. pallidus*, which was almost dead, had a temperature of 0.2°C. (Johnson, 1928). It did not respire for an hour and had a very slow and abnormal awakening. An animal with a temperature of 0.0°C. breathed very slightly after 22 minutes but did not wake up. In several instances where the refrigerator temperature fell to 0.0° or slightly below, the torpid ground squirrels died. Semper (1881) reviews some reported cases of survival of frogs and other animals when frozen, but concludes that there is insufficient evidence especially that the tissues, blood, etc., were actually frozen even though the external temperature may have been much below freezing.

The death of torpid animals at freezing temperatures in this and other laboratories (e.g., Hunter, 1837) casts doubts upon the conclusions of Barkow (1846), Valentin (1857), Horvath (1881), Dubois (1896) and others that such temperatures always produce waking of a torpid mammal. Experiments have been reported (Johnson, 1929b) which showed that a lowering of the external temperature from about 3° or 4°C., to 1°C., woke some of the ground squirrels (*C. t. pallidus*) but not all, and those which woke usually went back into normal hibernation with the air temperature at 1.0°C. These animals were observed frequently, so it was not possible that any woke and went back into hibernation without being observed. Wade (1930) found that a rapid drop in room temperature to −1.0° or −2.2°C. woke most but not all his ground squirrels, some dying without awakening.

RESPIRATION IN NORMAL ANIMALS

Saissy (1815) reported respiration rates of 30, 16, 45 and 7 respectively per minute for the marmot, hedgehog, dormouse and bat at 16°R. (20°C.) in August. Barkow (1846) counted 20 to 40 respirations in sleeping hedgehogs. A surprising range has been found in ground squirrels (Johnson, 1928). Among 48 *C. t. tridecemlineatus*, there was a range of 45 to 340 inspirations a minute, with an average of 187. In 37 awake and quiet *C. t. pallidus*, respiration varied from 20 to 360, with an average of 126 a minute, while a group of 12 others, after moving or feeding averaged 213 a minute, individuals varying from 140 to 320. A rate of 100 to 200 has been considered as most common in either variety of ground squirrel. Hoy's (1875) rate of 50 a minute for ground squirrels was probably from an inactive or semi-sleeping animal, since my observations on sleeping animals gave a range of 7 to 68, with an average of about 25 a minute in the two varieties of squirrels. In addition to degree of excitation, the variation in respiration rate in ground squirrels may be largely accounted for by the existence of a slow type of inspiration, involving a great but slow expansion of the whole thorax when the animal is quiet, and of a rapid shallow expansion of the abdomen and posterior thorax seen when the animal is excited or very active.

RESPIRATION IN HIBERNATION

Mangili (1807) found respiration to be very irregular in hibernation. He reported a 15 minute pause in the respiration of the hedgehog followed by 30 to 35 slow respirations. In dormice at 1°C. he recorded 147 inspirations in 42 minutes but with pauses of 3 to 8 minutes. In other series of records the pauses ranged between 2 and 13 minutes and between 3 and 5.5 minutes.

Some correlation between temperature and frequency of respiration in hibernation was seen by Saissy (1815). In hibernation that he considered was not very deep the respiration counts per minute were 7–8 for the marmot, 4–5 for the hedgehog, 9–10 for the dormouse, and either 0 or 4–5 for the bat. In deep hibernation he saw no breathing in the bat and considered this to be the general rule with other animals in deep hibernation. Hall (1832) and Delsaux (1887) observed no respiration in very torpid bats but the latter found that they gave off 394–615 mgm. CO_2 per kgm. per hour. It must be admitted there is a greater possibility of absorption of oxygen through the thin skin of the wings of a bat than through the skin of other mammals. Ziesels at 2.5°C. body temperature and undisturbed torpid hedgehogs had no visible respiration according to Barkow (1846). Dubois (1896) observed 1–4 very feeble respiratory movements a minute in profoundly torpid marmots.

While pauses in respiration have been noted in torpid ground squirrels, absence of respiration for several minutes is probably abnormal (Johnson, 1928), for two animals that showed no respiration until 14 and 25 minutes respectively after removal to a warm room died after a slight breathing for a few minutes. Two others which respired only after 19 and 22 minutes recovered abnormally. A fifth, which showed no respiration for an hour, recovered very slowly with the aid of artificial respiration. From careful observations, it was concluded that in deeply torpid ground squirrels in a room below 10°C., inspirations may average from one-half to four a minute normally, but that they may fall somewhat lower in thin animals long in hibernation.

To determine the ability of poikilothermal mammals to endure the lack of air while in the active state Carlisle (1805) kept a hedgehog under water of 8.8°C. for 30 minutes, but apparently the animal had its nose to the surface a number of times. It recovered in two hours, whereas another kept under water of 34.4°C. died in 10 minutes, due possibly to the higher rate of metabolism when warmer. Barkow (1846) states that the normal hedgehog may sometimes endure total immersion for eight minutes, but others died in 3, 4 and 5 minutes. Hall (1832) also states that normal bats and hedgehogs drown in about 3 minutes, but two torpid bats were under water 11 and 16 minutes and a hedgehog 22.5 minutes without injury. Poisonous gases did not injure torpid bats and marmots according to Spallanzani (1803) and a hedgehog could endure nitrogen gas for 15 minutes, whereas the mouse, rat and sparrow died respectively in 2.5, 2.5 and 0.5 minutes (Saissy, 1811). Saissy also found that a hibernating animal could use up all the oxygen in a closed chamber before suffocating, whereas the rabbit absorbs only 75 per cent, the rat only 62.5 per cent, the sparrow only 42.5 per cent before dying. Delsaux (1887) showed that normal bats placed in a chamber in which the air was rarified by means of a vacuum pump to 50 mm. of mercury appeared asphyxiated, but could remain in this condition for half an hour and still recover when removed.

Delsaux (1887) reported Regnault and Reiset as finding that a marmot used only one-thirtieth as much oxygen when torpid as when awake. According to Dubois (1896) Valentin reported that a torpid animal used one-forty-first as much oxygen and eliminated one-seventy-fifth as much carbon dioxide as a normal animal. Pembrey (1903) found that the relation of the carbon dioxide excreted in hibernation (body temperature 12° to 16°C.) and in activity was about 1 : 100 in the dormouse and 1 : 10 or 1 : 20 in the hedgehog. Gorer (1930) points out that the highest metabolic rates of hibernating mammals were reported by Pembrey for the dormouse, about 300 cc. oxygen per kgm. per hour being absorbed when torpid at 10°C. as compared to about 8,000 cc., about 27 times as much, when awake. For the marmot the amounts were about 35 and 550 cc., about 1 : 16 at 10°C. and awake, respectively. Stockard (1930) gives the carbon dioxide output of a white tailed prairie dog (*Cynomys leucurus*), in hibernation November 15 at a body temperature of about 21°C., as less than one-eighth that of the same animal two and three days later when sleeping or awake but quiet at a body temperature of about 32°C. (The date and temperatures have been kindly provided by Mr. Stockard in a letter to the author.)

In studying the effect of hibernation upon the respiratory quotient $\left(\dfrac{CO_2}{O_2}\right)$ Dubois (1896) found that more O_2 was absorbed than was represented in the CO_2 given off and the respiratory quotient approached 0.5, and he states that Regnault and Reiset found it to be as low as 0.4, whereas in the animal awake or in the process of waking it approached unity and even exceeded unity at the very beginning of waking. Pembrey (1903) found a respiratory quotient as low as 0.23 and 0.50 in torpid dormice and hedgehogs, re-

spectively. According to Gorer (1930) several work-
ers object to low quotients, but he concludes that the
real quotient must be below 0.7 and believes that it
ranges from 0.3 to 0.5. A low respiratory quotient
according to Pembrey (1903) and Bayliss (1918, p.
278) indicates that there is a conversion of fat, which
contains a small amount of oxygen, into carbohy-
drate, which contains more oxygen. Gorer (1930)
considers the significance of the respiratory quotient
at some length but concludes that direct evidence on
the metabolism is needed and would help to deter-
mine the quotient.

HEART BEAT IN THE NORMAL AND
HIBERNATING STATES

In active bats a pulse rate of 200 a minute was re-
ported by Prunelle (Barkow, 1846). Rates of 90 a
minute in a room of 19°C. and of 30 a minute just be-
fore hibernating in a room of 6°C. were found by

From the slight bleeding when a vessel was cut
and from the lack of enlargement when vessels were
tied in the neck and legs, Saissy (1815) concluded that
there was no peripheral circulation in deep hiberna-
tion, but merely a slight ebb and flow in the vessels
near the heart. He was supported in this by Brown
(1847), who also agreed with Mangili (1807) that
little blood reached the brain in torpor. Dubois
(1896) maintained that a very slow circulation is pres-
ent in hibernation, a view shared by the present
writer.

Instances of heart-block, or the independent beat-
ing of auricles and ventricles, have been cited by
Buchanan (1911) as occurring in the partly torpid
dormouse. A complete missing of beats of the heart
has been shown in an electro-cardiogram from a
ground squirrel which had begun to awake from hi-
bernation (Johnson, 1929b).

The rate of heart beat in normal ground squirrels
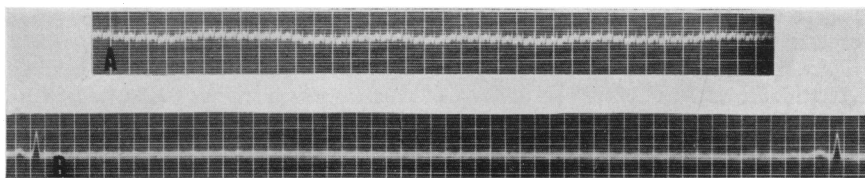varies greatly (Johnson, 1928). In both varieties

FIG. 1, A. ELECTROCARDIOGRAM OF CITELLUS TRIDECEMLINEATUS PALLIDUS, No. 947, STRUGGLING AND BITING,
SHOWING 506 BEATS A MINUTE. LEAD 1, TWO ARMS. B. ELECTROCARDIOGRAM OF C. T. PALLIDUS, No. 938, IN
DEEP HIBERNATION, SHOWING 1 BEAT IN 10.32 SECONDS OR 5.53 BEATS A MINUTE. LEAD 1, TWO ARMS.
TIME 3:03.

Saissy (1815), and of 28 a minute in hibernation by
Hall (1832).

In active dormice Reeve (1809) states that the rate
is too rapid to count but falls to 88 a minute in be-
ginning torpor, or to 105 at 19°C. and 88 a minute at
6°C. (Saissy, 1815). In deep torpor it falls to 16-20
(Reeve, 1809), 20-25 (Saissy, 1815), or 10-12 a minute
(Spallanzani, by Barkow, 1846).

In hamsters pulsation rates of 150-200 (Sulzer, by
Barkow, 1846) in activity or of 100-150 when irri-
tated (Reeve, 1809), fall to about 60 before hiberna-
tion and as low as 12-15 in deep torpor (Reeve, 1809;
Sulzer, by Barkow, 1846; Dubois, 1896).

Hedgehogs may have a pulse rate of 75 a minute in
a room of 19°C., falling to 25 at 6°C. At these tem-
peratures a marmot had 90 and 70 beats a minute
respectively (Saissy, 1815). In torpor the marmot
was found to have a pulse rate of 27-28 a minute
(Mangili, 1807), but this rate may have been raised
by the decapitation and opening of the thorax, for
Saissy (1815) gives a rate of 10-12, and Dubois (1896)
has made some cardiograms with a rate as low as 3-4
a minute in torpid marmots.

the range was found to be about 100 to 200 in animals
just awakened from normal sleep, but rose to 200 to
350 in animals held, some quiet and some struggling.
In excited struggling animals the rate often rose above
350, rates of approximately 400 being sometimes re-
corded by counting the beats in an abbreviated man-
ner with a stethoscope. That the rate may go still
higher is shown in Figure 1a, an electro-cardiogram of
a C. t. pallidus ground squirrel biting and struggling
violently while it was held showing 8.43 beats in
one second or 506 beats a minute. This is 100 times
as fast as the lowest rate (5 a minute) recorded in two
very torpid animals (a cardiogram of 5.53 beats a
minute is shown in Figure 1b). It is 29 times faster
than the average (17.4 beats) of the 22 lowest records
of animals whose temperatures were below 10°C.

SURVIVAL OF THE HEART

Several workers have observed the persistence of
reflexes in decapitated hibernating mammals (Merz-
bacher, 1904) and the continued beating of the heart
three hours after decapitation in a torpid marmot

(Mangili, 1807). A ground squirrel, *C. t. tridecem-lineatus*, was dug out of its underground nest in the winter by the author and its heart beat observed within 8 minutes by cutting open the thorax ventrally. The heart beat was 13.5 a minute at first, the body temperature, 2.0°C., respiration rate, 2 a minute, and air temperature, 4.0°C. After 18 minutes the heart beat rate was 14 and the animal was taken into an air temperature of 0.0°C. After 47 minutes the heart beat had fallen to 6.5, with a body temperature of 5.5°C. and attempted respirations of 2.4 a minute. From 1:52 to 6:00 (taking the beginning of the experiment as 0:00 hour) the heart beat was irregular at about 2 to 4 a minute and attempted respiration stopped before 3:38. When removed to a temperature of 18°C. at 6:28 its heart beat rose to 9.2, 18 and 28 respectively at 6:38, 6:56 and 7:05. It was necessary to leave the laboratory, so the animal was then skinned. By 7:21 its heart beat rose to 61 a minute. The body was placed in 10 per cent formalin. The heart stopped beating in 30 minutes, which was seven and one-half hours after it was exposed. Another torpid ground squirrel, a *C. t. pallidus*, had a heart beat of 17 a minute when cut open, but this decreased to 6 in one hour and to 3 in two hours and ten minutes. At first the attempts at respiration were deep and frequent; the last slow and feeble attempts were noted one hour and 24 minutes after opening the thorax. The heart ceased beating sometime between two hours and ten minutes and four hours and 31 minutes after exposure. A second torpid *C. t. pallidus*, with a heart beat of 15 a minute when the thorax was cut open, showed great efforts to expand the thorax and the heart beat increased to 17 in 7 minutes, but by 23 minutes the expansion of the thorax was slight and the heart beat 10 a minute. The heart beat fell to 7 in one hour, 6 in 2 hours, 3 in 5.5 hours and stopped before 8 hours. In the last two experiments the room temperature averaged about 4°C.

The beating of the heart of the torpid animal several minutes after isolation and placing in warm Ringer's or salt solution has also been confirmed by the author. Merzbacher (1904) states that the heart of a hibernating mammal will beat for hours if excised and kept cold and moist.

Death in hibernation appears to be produced by cessation of respiration rather than of heart beat, for the heart was still beating in five ground squirrels in which no respiration was seen for respectively 14, 19, 22, 25 and 60 minutes after the animals had been removed from the cold to a warm room. The first and fourth of these died after respiring slightly for a few minutes. The others recovered very slowly, were very weak and the last one would probably have died

if artificial respiration had not been resorted to (Johnson, 1928).

RESISTANCE OF TORPID MAMMALS TO TOXIC SUBSTANCES

Injected poisons produced little or no effect on torpid animals (Merzbacher, 1904). Hibernating bats were found resistant to pilocarpin, apomorphine and strychnine by Koennick, according to Adler (1926), who compares this resistance when the animal is not awakened to that of cold blooded animals. Blanchard (1903) found that torpid marmots were sensitive to inoculations of trypanosomes and to toxins of tetanus and diphtheria as well as to venom of the cobra. Hibernation merely slowed up the action of the toxins, for they were nearly as deadly to the torpid as to the normal animals.

IRRITABILITY IN HIBERNATION

While the nervous system of a torpid mammal functions to maintain a low rate of heart beat and of respiration, it becomes progressively less sensitive to stimuli as its temperature falls. Before this falls to about 30°C. thirteen-lined ground squirrels can move and respond to stimuli in practically the normal way. When it has fallen to about 20–30°C. they may move forward in a dazed manner or merely raise up stiffly and try sluggishly to bite when touched. At about 10°–15°C. the animals are more inert and are likely only to raise the head slightly or give other weak responses. If the body temperature falls to about 2°–5°C. there is usually no response even to strong mechanical stimuli such as inserting a thermometer bulb into its food pouch or pricking the animal with a needle. At low body temperatures Franklin, Richardson and *Callospermophilus* ground squirrels have been observed by the author to be as unresponsive as the thirteen-lined species. Hatt (1927) made similar observations on the *Callospermophilus* and Shaw (1925c) on the Columbian ground squirrels. Touching a torpid hedgehog caused it to breathe eight to twenty times, the respirations gradually becoming shorter and slower and the animal did not wake unless the stimulation was continued or the animal taken to a warm room.

While the immediate responses may not be made to such severe stimuli as falling from a table and breaking a collar bone or by having the nose cut open to expose nerves and blood vessels as in a young marmot (Valentin, 1857), stimuli of this strength would invariably wake a ground squirrel in due course of time. However, it is often possible to gently lift a deeply torpid ground squirrel out of the nest and

carefully insert a thermocouple into its food pouch without causing it to wake (Johnson, 1928).

Horvath (1881) states that conditions in hibernation may vary somewhat in different groups of mammals. In *Myoxus drias* he found that the eyes were not closed as in ground squirrels, and the hamster might give forth loud cries, or more probably, draw in deep sonorous inspirations when disturbed as stated by Cleghorn (1910). The degree of immobility in bats may vary with the temperature, time of year and the species according to Dubois (1896) and others. Black tailed prairie dogs and a pocket mouse in partial hibernation with a body temperature somewhat above 20°C. were observed by the author to straighten out and make feeble attempts to crawl when held in the hand. If the temperature in these two forms can fall to 2°-5°C. it is probable they would be as inert as ground squirrels.

Electrical stimuli produced no effect on woodchucks and hedgehogs but caused slight movement on the part of dormice and bats (Saissy, 1815). Marmots were not roused by an electric spark and they were excited only for a short time by a shock from a Leyden jar according to Reeve (1809) and earlier workers quoted by him. If the electrodes were placed directly on the exposed muscles or nerves that go to them, Horvath (1872b) found that the cold muscles responded even to weak induction stimuli. Electrical stimulation of the exposed cerebral hemispheres of torpid bats produced no effect on one bat, but on another strong stimulation (coil at 6 cm.) caused inhibition of respiration for ten minutes (Merzbacher, 1903a). By stimulation of torpid ground squirrels by means of shocks from an induction coil (Harvard inductorium) the author has produced movements, such as raising of the body or even the turning of the head, which had not been produced by mechanical stimuli at the same temperature.

While considerable variation has been seen both in the tendency to hibernate and in the irritability in hibernation among large numbers of the same species of ground squirrels observed, it nevertheless appears that there is a marked general relation between body temperature and activity. This is especially evident in the regaining of powers of motion as a torpid animal wakes, observed by many authors. Britton (1922) has shown that even in a cat cooled to the point of lethargy the muscular activities return in a certain order and at somewhat definite body temperatures as the animal recovers, although such non-hibernating animals lose their power to respond to stimuli at a higher body temperature when that is lowered artificially. The production of immobility, whenever an animal's body temperature falls, suggests that the bear and possibly the raccoon do not actually become torpid, for Dubois (1896) and Bailey (1926) state that they are easily aroused, which could hardly be the case if the body temperature is very low.

EFFECT OF HIBERNATION ON WEIGHT

All workers have recognized that loss of weight in hibernation is small as compared to that in starvation and have pointed to this conserving action of lethargy as its chief function. While it is also generally recognized that there is a considerable loss in body weight in an extended period of hibernation, there is no marked agreement as to the exact loss. Bailey (1926) believed there was "only slight loss of fatty tissues." He considered the lack of food after waking and during the breeding season as drawing heavily upon the stored fat. In pocket mice and some chipmunks he observed no accumulation of fat but called attention to their stores of seeds and grains which he believed they consume at intervals of awakening. Earlier workers have generally considered that animals are fat in the fall and wake up lean in the spring, as reported for the dormouse by Murray (1826) and several others.

Marmots lost one-fourth to one-sixth of their body weight in about 130–150 days of hibernation and in two animals even in 56 and 59 days respectively, and two hedgehogs lost one-fourth of their weight in 26 and 50 days respectively (Valentin, 1857). Wade (1930) has estimated that one-half of the weight may be lost by ground squirrels which den up in late summer, and some of his records (p. 173) show losses of 59 and 61 per cent in 207 and 228 days in which the animals burrows were closed.

The weight losses of five *C. t. tridecemlineatus* which hibernated outdoors have been studied by the author. Estimating that they changed little in weight in the four to six weeks before hibernating (they were fed well, but they also exercised considerably in digging burrows and building nests) the losses from the time of closing their burrows till they were dug out in the torpid state were: 19 per cent in 65 days; 21 per cent in 83 days; 18 per cent in 106 days; 32 and 39 per cent in 100 days. A *C. t. pallidus* lost 38 per cent in 79 days. As none of these animals hibernated as long as animals would in nature, this average loss of 28 per cent is probably lower than occurs in nature. The average daily loss was 0.32 per cent. A comparison of average weight (93 grams) of 120 *C. t. pallidus* received early in the spring with that (157 grams) of 45 adult laboratory animals which were not excessively fat in the fall would indicate an average loss of about 41 per cent from fall to spring (Johnson, 1928).

Ground squirrels which refused to hibernate when placed in a refrigerator showed marked losses if fed sparingly, but lost less or even gained slightly when fed well (Johnson, 1928). Where two or more weight records were obtained within a period of hibernation in which waking was believed not to occur, the average daily loss in eight records of 14 to 17 days was 0.57 per cent. If the loss were computed on this basis, calculating it on the reduced weight each 15 days, the animal would lose 45 per cent of its original weight in 100 days, and 59 per cent of its original weight in 150 days. Five other animals whose periods of hibernation averaged 28 days lost 0.43 per cent daily. If the successive reductions in weight are used and the losses computed in periods of 25 days each, an animal in 100 days of hibernation would lose 36 per cent, and in 150 days, 49 per cent of its original weight.

Seven *C. t. pallidus* ground squirrels were placed in a refrigerator August 5 and removed January 8, 156 days later. They were in hibernation an average of 83 per cent of this time. Five of these animals which were in good condition, weighing 147–185 gm., when placed in the refrigerator, were taken out somewhat thin, having lost 37 to 49 per cent (average 45 per cent) in weight. Two which had been very fat lost respectively 40 and 39 per cent of their original weights of 226 and 250 gm., but were still somewhat fat. Considering that the loss in hibernation in a closed underground burrow may be less than in a refrigerator, the data presented would appear to indicate that ground squirrels commonly lose 30 to 45 per cent of their weight in five months of hibernation in nature.

The loss in weight during hibernation is accounted for chiefly by the using up of the thick layers of fat under the skin, in the mesenteries, and in the mesovaria or mesorchia. In the fall the latter may be 4 mm. in thickness, their appearance suggesting thick pieces of bed quilts, but in the spring the fat may be reduced to streaks along the blood vessels which course through the epithelium to the reproductive organs (Johnson, 1928). Williams (1909) has called attention to the localization of "a heavy fat blanket" on the more exposed hind quarters and back in the hibernating raccoon. He found more than one-fourth of the body weight to be fat.

Slight temporary increases in weight have been reported by Horvath (1878), Dubois, (1896) and others, but this condition was attributed by Valentin (1857) to absorption of moisture by the fur rather than to fixation of oxygen with retention of carbon dioxide as mentioned by Pembrey and White (1896) and others. Valentin (1857) also discovered gains in weight in animals that had awakened between weighings.

THE PROCESS OF WAKING FROM HIBERNATION

Types of awaking

Two types of awakening from hibernation have been described (Johnson, 1929a): (a) A relatively rapid awakening accompanied by trembling and shaking of the head and shoulders, following a disturbing of the animal by removing it from the nest and laying it on the side or back, and either taking it to a warm room or leaving it in the cold room; (b) A more gradual awakening, usually without trembling or shaking, after removal without disturbance to a warm room, or following some handling at first after which it was placed back in the rolled up position in the nest and left in the cold room.

In the first type of awakening the breathing increased in rate, the body showed some movement of forefeet or head or of both, then more marked movements such as trembling, shivering, shaking the head sideways or jerking it up and down. These movements were accompanied by a gradual straightening of the body from the rolled up position and were

usually followed by deep, rapid and con-vulsive respirations, and later by the rais-ing of the head, the getting up on the fore-feet, and still later by standing on all fours. Before or at this time they became very irritable and could fight in a drunken but determined manner. Soon the eyes would open and if disturbed they would move forward, awkwardly for a few minutes. If the animal was transferred to a warm room in addition to being stimulated by being laid on its side and having its temperature taken, the steps mentioned were crowded together and the stages given might occur two at a time. This type of waking has been described in various forms by Pembrey and Pitts (1899), Hahn (1914), Dubois (1896), Shaw (1925b), Hatt (1927) and others. Merz-bacher (1903) has described four stages in the return of activity in a bat waking from hibernation. These were: (1) rigid-ity, with only reflexes of the spinal cord; (2) hanging on, with reflexes of the medulla oblongata; (3) beginning of cere-bral activity with loss of sub-cortical re-flexes and accompanied by the opening of the eyes; (4) fully awake, with cortical control of sub-cortical reflexes.

In the second or relatively undisturbed type of awakening there was much abbre-viation and elimination of the steps given for the first type. Increased respiration or a raising or humping of the rolled up body was often followed by a working out of the head from underneath, then by raising the head and opening the eyes accompanied by standing on the forefeet. While this type of awakening is probably typical of that in nature, the disturbed type has been the one usually described.

The opening of the eyes occurred usually in the disturbed awakening between 20° and 34°C. in 12 *C. t. pallidus* and 15 *C. t. tridecemlineatus*, and in the un-disturbed type it occurred between 21° and 37°C. in 45 *C. t. pallidus*. The difference in temperature at

waking therefore was not great. However, the 27 disturbed animals woke in 63 minutes on the average, whereas the undisturbed animals woke in an average of 114 minutes.

Effect of stimulation during waking

While strong stimulation at first is al-most certain to produce complete awaken-ing even in the cold, showing that irri-tability is not completely lost in deep torpor, even if no quick response is seen, it is interesting to note that continued stimulation during the waking by drop-ping small weights on the animal or by applying electrical shocks with an induc-torium did not hasten the process very much and sometimes caused inhibition of the heart beat and respiration for a short time.

Mid-brain necessary for waking

Dubois (1896) found that destruction of the cerebrum and corpora quadrigemina did not prevent waking from hibernation, but a destruction of the mid-brain pre-vented waking. With only the medulla oblongata left the torpid marmot would live 8 to 9 hours or more but could not awake automatically and died while tor-pid.

The rise in respiration, heart beat and temperature

When waking from hibernation is started by some external stimulus the heart beat seems usually to take a slight lead over respiration in producing a warm-ing of the animal (Johnson, 1929b). Figure 2 illustrates the increases in respira-tion, heart beat and temperature in dis-turbed waking in a cold room (Ia, IIa, IIIa), in a moderately warm room (Ib, IIb, IIIb), and in an unusually warm room (Ic, IIc, IIIc). It is seen that the rise in metabolism is slow at first in the cold room (a) but speeds up considerably at about 60 minutes. In the moderately

warm room (b) the rate is rather steady throughout, the respiration and heart beat showing a very great increase after 35 or 40 minutes. In the warmest room (c) the temperature rise is very pronounced as soon as the animal is removed from the cold to the warm room, indicated by the

animal is fully awake, as was stated by Dubois (1896). In about 35 minutes after the animals, I, J, K and L, were taken to the very warm room (Ic) the respiration rate rose from about 8 a minute to about 150, the heart beat rose from 28 to 375 a minute, and the food pouch temperature
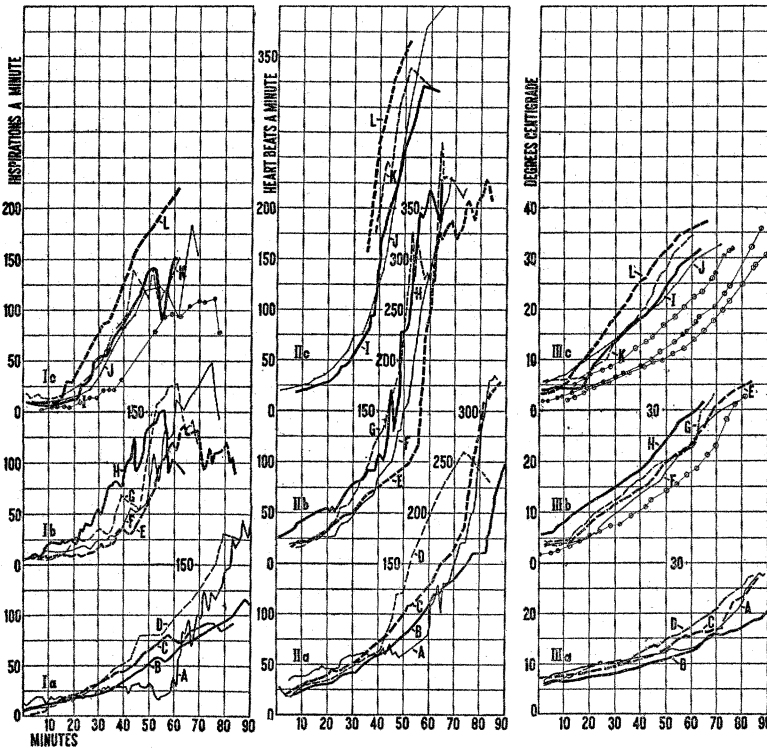
Fig. 2. Graphs of Increase in Respiration (I), in Heart Beat (II) and in Temperature (III), in a Cold Room of About 2° to 10°C. (a), in a Room of About 15° to 22°C. (b), in a Warm Room of About 25° to 35°C. (c)

The curves belonging to one animal are designated by the same capital letter, thus I a A, II a A and III a A represent the respiration, heart beat and temperature increases respectively in one waking process in the cold room of the animal A. The fine lines connecting the rings in I c, III b and III c are graphs of animals waking relatively undisturbed (thermocouple gently placed in the food pouch and the animal replaced rolled up in the nest). In the other graphs the animals were disturbed by being straightened out and by taking of heart beat in addition to temperature.

abrupt rise in the temperature curves at 5 to 10 minutes in the graphs. There is the same rate of increase in heart beat at about 25 or 30 minutes in the warmest room that was observed in the medium warm room ten minutes later. Heart beat may be more rapid at this time than when the

from about 7° to about 27°, or 20° in 35 minutes, or 0.57°C. a minute. In the undisturbed awakening of two animals (Fig. 2, fine lines connecting the rings in IIIc) the rate of rise of temperature was about 19° or 20°C. in 40 minutes, about 0.5°C. a minute, after the rise was well begun.

Dubois (1896) gives some graphs of respiratory movements showing a rising rate as waking progresses. Other graphs of the waking dormouse showing pauses followed by a series of inhalations (Biot's type) and pauses followed by increasing depth of inspirations then decreasing again to another pause (Cheyne-Stokes respiration) were shown by Pembrey and Pitts (1899).

Several references to rate of temperature rise in waking were found in the literature. From these records the average rise has been calculated and is substituted here. For a portion of its waking period the bat may warm up about 1.1°–1.6°C. a minute (Pembrey and White, 1896; Pembrey, 1898). Ground squirrels (ziesels) may warm up 0.26° and 0.38°C. (Horvath, 1872a), 0.40°–0.45°C. (Horvath, 1878), or 0.30°C. (Mares, 1892) a minute. Dormice may warm up 0.37° (Pembrey, 1898) or 0.95°C. (Pembrey and White, 1896) a minute. Hedgehogs, which are larger, warm more slowly, 0.17° a minute (Pembrey, 1903), while the still larger marmots require three or four hours to warm from about 5° to 30°C., a rate of about 0.10° to 0.14°C. a minute. Most of these records were based on rectal temperatures and it has been shown that this lags far behind the esophageal, mouth or pouch temperatures (Quincke, 1881; Dubois, 1896; Mares, 1892; Shaw, 1925c; Johnson, 1929b; and others) and apparently catches up with the esophageal and pouch temperatures late in the waking process (Dubois, 1896; Johnson, 1929a, p. 179) especially in the cold room. This late rapid rise in rectal temperature appears to be produced largely by a sudden increase of circulation to that region after the anterior region has gradually warmed up from the beginning of waking, for Mares (1892) showed that jugular injection of indigo-carmine in a torpid ziesel quickly produced intense blue staining in the skin and mucous membrane anteriorly but not posteriorly. For the reasons given rectal temperatures are not reliable indicators of the rate of rise of metabolism but have been included here because they have some value in comparison between species.

The time required for waking from complete torpor depends somewhat on the size of the species. The following observations of waking time have been reported: (1) for the bat, 14 or more minutes (Pembrey and White, 1896; Pembrey, 1898), "a few minutes" (Adler, 1926), a half to one hour on the snow (Mangili, 1807), and three or four hours (Saissy, 1815; Quincke, 1881); (2) for the hedgehog, five to six hours (Saissy, 1815; Quincke, 1881); (3) for the marmot, three to four hours (Dubois, 1896), five to six hours (Quincke, 1881), and eight to nine hours (Saissy, 1815). These rates would probably be less variable if the observations had always begun at a certain body temperature and ended with the return of voluntary activity, and also if esophageal or food pouch temperatures had been taken.

The energy consumed in a unit time in waking ziesels has been stated to be 70 per cent greater than in the normal state (Mares, 1892). Mares found that during waking 5.9 gm. of oxygen per kilogram per hour were absorbed as opposed to 3.8 gm. in the normal state, and 6.0 gm. carbon dioxide are exhaled in waking compared to 3.9 gm. in the normal state. Pembrey and White (1896) noted the sudden increase in temperature just at the point of waking in bats, and this was observed to be accompanied by a much greater rate of heart beat and respiration at about the time of opening the eyes in ground squirrels (Johnson, 1929b) than was found after the animal was fully awake but not excited. The contraction of the heart, the movement of the thoracic muscles and the trembling, which may be present, appeared to account for the rapid rise in temperature in the latter part of waking. Mares (1892) considered that burning of fat produced this, but Dubois (1896) considered that glycogen in the liver was converted into sugar and this was burned. Further evidence of a great increase of sugar in the blood early in awakening has been submitted by Dworkin and Finney (1927). In waking there appears to be a vicious cycle. As the heart beat increases because of stimulation it is accompanied by more rapid respiration, both processes producing heat. Increased heat and greater muscle contraction both demand more oxygen. The excessive increase in metabolism in waking suggests to the author that the heat regulating mechanism is rather sharply brought into play after waking has progressed somewhat, for once the waking process is well started, placing the animal back in the cold and leaving it undisturbed almost never prevent complete awakening.

GOING INTO HIBERNATION

While the literature contains references to going into hibernation no exact data have been presented as to the physiological changes that occur, probably because study at this time almost invariably awakens the partly torpid animals. Dubois (1896) states that a marmot may wake in 3–4 hours, but requires 4–5 times as long to go into hibernation. Hatt (1927) states that a *Callospermophilus* might go into hibernation in 6 hours. Hibernation is always entered from a condition of normal sleep. The author took a great many food pouch temperatures of *C. t. pallidus* ground squirrels at intervals of one or two to several hours after the animals were placed in a refrigerator. The gentle picking up of the animal and careful insertion of the thermocouple in some cases did not prevent the

entrance into hibernation and the pouch temperature dropped from 1° to 3° an hour (Johnson, 1929c). Further work showed that it might drop 5°C. or even more an hour.

By taking temperatures thermo-electrically (illustrated in Johnson, 1929a) without disturbing the animal at all at the time the record was taken, drops of 6° to 7°C. an hour were observed for short periods in partly torpid animals in a rapidly falling room temperature, but the pouch temperature remained 1° to 2° C. above that of the room (Johnson, 1929c) even remaining 1°C. or more above when the room temperature stopped falling. From these data it was concluded that a fall in animal temperatures of 4°C. or more an hour was not uncommon.

The drop of 1° to 5°C. an hour in the early part of becoming torpid and up to 6° or 7°C in short periods in the later stages is very much slower than the rise of 20° in 35 minutes in rapid awakening in a very warm room.

CONDITIONS IN HUMANS RESEMBLING HIBERNATION

A considerable lowering of temperature in a hysterical person sleeping after being hypnotized was reported by Mares (1892). Fakirs in India have been often reported to be revived after months of burial underground (Busk, 1885; Mills, 1893, and others), but, while attested to by English officials, the possibility of deception by the fakirs has been raised (Hulk, 1885, and others). According to Claparède (1905), Cleghorn (1910) and other writers, in times of famine in some parts of Russia the peasants may conserve food by voluntarily sleeping for four or five months, doing only the necessary things and eating very sparingly. While metabolism is probably lowered in this way, it seems doubtful if there is much lowering of body temperature. Cushing and Goetsch (1915) have described symptoms of slightly lowered temperature and excessive adiposity in humans with deficient pituitaries and have considered this state related to hibernation. Mills (1892) also reported cases of excessive sleeping in two feeble minded men and in a woman who was tuberculous and had many adhesions of organs. Lowered temperature and drowsiness might, it would seem, be the effects of the illness rather than a condition resembling hibernation. Cases of lowered temperature in dying pocket gophers could easily be mistaken for real hibernation.

A CONSIDERATION OF THE POSSIBLE CAUSES OF HIBERNATION

There are certain outstanding facts regarding causes of hibernation. One is the existence of a large number of theories, summarized by Rasmussen (1916a). Another is the tendency of some writers to go to extremes in denying the causative influence of some possible factors. Thus cold has been declared not to be a cause of hibernation (Merzbacher, 1904, and others). A fact which must be kept in mind is that a poorly developed heat regulating mechanism is a prerequisite to the ability of a mammal to hibernate, and since this is essentially a pre-mammalian characteristic, we may consider hibernation as something retained rather than acquired by hibernating mammals.

Many authors have sought for a single cause for hibernation, but many conditions, both internal and external, may influence entrance into it. The possible external factors in hibernation will be considered first, and then the internal conditions which may influence it.

Temperature

Among the external conditions a low temperature has been considered a cause by many (Brown, 1847; Quincke, 1881; Adler, 1926), but many others have pointed out that only moderate cold is favorable for hibernation and animals may die below freezing temperatures (Mangili, 1807; Adler, 1926); or they may be awakened at first at about the freezing point of water (Dubois, 1896; Mangili, 1807; Pflüger, according to Merzbacher, 1904), or hibernation may even be prevented sometimes (Valentin, 1857). Sudden severe cold may irritate and finally kill the animal (Dubois, 1896; Johnson, unpublished). Others have shown that animals in captivity may fail to hibernate in winter, even if in a cold place (Mangili, 1807) but may hibernate in the summer or early fall in cool but not cold surroundings (Horvath, 1881; Wade, 1930; and others). Some dormice kept over winter by Forel (1887) failed to hibernate until May, but as they did not become fat until that time their failure to hibernate earlier may have been caused by a poor physical condition. Simpson (1911-12) considered that woodchucks wake in the spring without a higher surrounding temperature.

Perhaps no investigator who has had a large number of animals under observation at one time would deny that animals hibernate more in a room of about 5°-10°C. than in one of 20°-25°C., or even of 15°-20°C.

This has been the experience of the author, who recognizes, however, that cold is not the only cause, and that internal causes may aid hibernation in ground squirrels in cool weather (20°–22°C.) in the late summer, or hinder hibernation in cold weather (0°–10°C.) almost any time of year but especially in the spring. In outdoor pens in Chicago ground squirrels kept their burrows open until periods of cold weather and snow in December, 1915. Hahn (1914) observed this in nature.

The idea that heat may be a cause of hibernation (Brown, 1847; Merzbacher, 1904, quoting Cuvier and Buffon as authorities) in mammals appears to the author to be erroneous. It has previously been mentioned that no cases of hibernation have been seen in surrounding temperatures much above 20°—22°C., which must be considered low in comparison with the usual body temperature. The tenrec (*Ctentes ecaudatus*) of Madagascar has often been cited as an animal that hibernates in the warm season but Milne-Edwards (1857–1863) cites evidences that it actually hibernates during the colder season.

Precooling

Koelsch (1925) and others have stated that animals cannot be made to hibernate in the summer by artificial cold and therefore the phenomenon is produced by internal factors only. While the work in this laboratory has shown conclusively that hibernation can be produced any time of the year, it must be admitted that there is less tendency to hibernate and greater mortality in the spring and early summer than in late summer (August), fall and winter. This is doubtless caused in part by internal factors but some evidence has been seen that it may be partly attributed to the previous season of hibernation, the poor conditions and greater excitability of new animals caught just before spring or summer study. It was also found that precooling ground squirrels nightly, as usually happens in the fall in animal quarters before the heat is turned on, caused them to go into hibernation significantly sooner when taken to a cold room than those which had not been precooled (Johnson, 1927, 1930). While precooling probably has facilitated the production of hibernation in the fall by various workers, it should not perhaps be considered a necessary cause in nature. However, intermittent or gradual cooling of the ground in the fall doubtless aids somewhat in preparing the animal for hibernation.

Food

Several authors consider starvation a cause of hibernation (e.g., Mangili, 1807; Hall, 1832; Forel, 1887; Simpson, 1912; Mann, 1916; Shaw, 1925c), but most of these men and others (e.g. Valentin, 1857) state that little food is eaten before hibernation even if it is present. The latter has not been borne out in ground squirrels in this laboratory. While the presence of food has often not prevented hibernation (Saissy, 1815; Mills, 1892; Wade, 1930) starvation has been found to make ground squirrels hibernate sooner than feeding (Johnson, 1925, 1930). Nineteen experiments in each of which six were fed and six starved and kept in the cold room from 7 to 23 days showed 13 per cent hibernation in the fed groups and 42.4 per cent in the starved groups. The fed groups showed an average of 78.5 per cent days before hibernation while the starved group went into hibernation after an average of only 42 per cent of their days in the refrigerator.

Dry Food

In order to test the theory advanced by Shaw (1925b) and Kashkarov and Lein (1927) that desiccation of vegetation produces aestivation 44 dry feed experiments were run by Kalaboukhov (1929) on 28 *Citellus pygmaeus* Pall. and 2 *Citellus fulvus* Licht. In these experiments there were 11 cases of hibernation in animals given dry feed but none in those given the same food soaked in water. Room temperatures during these experiments were from 12° to 22°C. No torpor occurred at temperatures above 22°C. Kalaboukhov remarks that the lethargy was identical to hibernation, which has also been the author's observation in numerous cases of torpor in the summer. Since no difference was noted no particular mention has been made of summer hibernation in the papers from this laboratory. Returning to Kalaboukhov's statement that no hibernation took place in the animals that had soaked food, it may be remarked that the author has had numerous cases of hibernation in July and August in a room of about 10°C. (a little colder than Kalaboukhov's temperature) among animals given green alfalfa or grass in addition to dry feed. For incidental evidences of this see Johnson (1930, Table I) and Johnson and Hanawalt (1930, Table II). The author has had numerous cases of partial hibernation following drops in room temperature for a night or for a few days in September. These animals hibernated in spite of water kept before them. A *C. t. tridecemlineatus* with a temperature of 31.0°C. in a room of 28.0°C. was only slightly torpid and could walk. Two *C. t. pallidus* at 28.0° and 20.2°C. in a room of 22.0° and 19.0°C. respectively could hardly move when taken up.

Wade (1930) performed some experiments on four *C. t. tridecemlineatus* outdoors and three indoors from July to October in which the animals had access only

to dry feed. His results would not support the conclusions of Kalaboukhov, for Wade's animals did not hibernate, although they lost much in weight. Since Wade's animals were doubtless at a higher temperature and mine were usually at a lower temperature than Kalaboukhov's, his results at temperatures of 12° to 22°C. are not contradicted by Wade's and mine. Furthermore, in a single experiment at 10°–15°C. nine *C. t. pallidus* ground squirrels fed only dry oats went into hibernation in an average of 3.8 days whereas ten fed soaked oats went in at 8.3 days.

Present data would seem to warrant a conclusion that dry food, as compared with moist, may serve as a weak cause of torpor. There is no question, of course, that dry hot weather followed by a drying up of the vegetation tends to drive the ground squirrels (Shaw, 1925b) and prairie dogs (Kashkarov and Lein, 1927) into their burrows, but once there it would seem that the quietness and coolness must aid in the production of torpor, if torpor is common in these animals in the summer.

Light

While many investigators have placed their animals in the dark to hibernate (Mann, 1916), light has not prevented hibernation (Wade, 1930, and others), and no influence on hibernation was found in 19 controlled experiments involving 12 animals each (Johnson, 1925, 1930b). It should be noted that the rolled up position of the animal in sleep and hibernation tends to shut out the light from the eyes even if it is present.

Confined Air

There appears to be no agreement as to the rôle of confined air in the production of hibernation. Mangili (1807) declared that it has no effect, but Bert (1868, 1870) produced a fall in temperature to 12°C. in dormice confined in a bell jar in the cold and Claparède (1905) considered that confined air would lower metabolism, aiding the change from sleep to torpidity. Brown (1847), Wade (1930) and others have mentioned hibernation in open air, but the former considers the lack of oxygen as a cause of hibernation.

In experiments involving 108 animals each in a half gallon can closed tight except for four nail holes about 3.0 mm. in diameter in the lid, the ground squirrels went into hibernation on the average after 19 per cent of their total days in the refrigerator had elapsed, whereas a similar number of controls in open cages hibernated only after 49 per cent of their stay in the refrigerator (Johnson, 1930). That this earlier entrance into hibernation was not produced by the more

limited space of the half-gallon cans was shown by the fact that other controls in similar cans but with the tops highly perforated hibernated practically at the time and to the extent of those in the open cages.

In this connection we may consider Dubois' (1895, 1896) autonarcosis theory, which involves both external and internal conditions. He maintained that an excess of carbon dioxide in the blood is a cause of torpor. Torpid marmots to which he supplied a mixture of 12 per cent oxygen, 43 per cent air and 45 per cent carbon dioxide continued torpid until pure carbon dioxide was added at the beginning of the fifth hour, which caused the respiration rate of 3–5 a minute to double in ten minutes (1895). He concluded that a certain proportion of carbon dioxide would cause torpidity but that a greater proportion of it was responsible for waking. He also found that he could anaesthetize a dog in a mixture of air containing 17.3 per cent carbon dioxide (1901b). Rasmussen (1915, 1916b) found that the carbon dioxide content in the blood of the woodchuck was increased in hibernation, especially in the latter part of this state, but decreased again in waking. He also found that the difference in amounts of gases in the venous and in the arterial blood is greater in the torpid than in the normal animal. In two torpid woodchucks he found no increase in amount of carbon dioxide in the blood, indicating that Dubois' "autonarcosis" theory would not account for all cases of hibernation.

Obesity

Of the internal conditions, fatness has been agreed upon as a cause by practically all who have studied it as a possible factor (e.g., Horvath, 1881; Brown, 1847; Claparède, 1905; Mangili, 1807; Mills, 1892, 1893; Mann, 1916; Johnson, 1930; Wade, 1930). Lack of fatness has probably kept captive animals awake in the winter in some cases. Forel's (1887) dormice, for instance, did not hibernate until they became very fat in May, but from then until August they hibernated at a body temperature of 20°–22°C. A significantly greater amount of hibernation was found by the author in 38 heavy ground squirrels than in 118 light animals (Johnson, 1930) and the greater tendency of fat animals to hibernate has been observed in many animals in other experiments. Sometimes it would appear that very thin animals went into hibernation sooner than those of medium weight but closer study revealed the fact that such animals very frequently died after two or three days in torpor, so that their hibernation is not normal. Probably deaths reported by others as occurring when animals have been cooled in the summer have been due to thinness of the animals, and possibly also to the sudden transfer from hot to cold atmospheres.

Loss of Body Moisture

Loss of body water may be considered a possible internal cause, although it may be caused in turn by a dry food diet, which has already been found slightly conducive to hibernation. Since desiccation has been found to favor hibernation in the potato beetle (Tower, 1906; Breitenbecher, 1918; Fink, 1925) and also to produce cold hardiness in insects (Bodine, 1923; Payne, 1927) it is interesting to note that Dubois (1895, 1909) found that the blood of torpid marmots was somewhat desiccated. Rasmussen (1915, 1916c) found an increase of 5 per cent in erythrocytes in hibernation and a 20 per cent decrease after the woodchucks had eaten and drunk, indicating a tendency to desiccation in hibernation. It is concluded by Gorer (1930), however, that the water balance is not uniform in hibernating mammals.

Hypofunction of the Thyroid Gland

Histological work on the thyroid of ground squirrels, *C. t. tridecemlineatus*, (Mann, 1916; and Peiser, 1906, according to Gorer, 1930) led to no evidence of a relationship to hibernation, but did show a flattening of the cells and a great diminishing of colloid in the fall. Adler (1920a) found histological changes in thyroids of bats and hedgehogs that indicated excessive secretion of colloid just after waking in the spring and this was later confirmed by Coninx-Girardet (1927). Subcutaneous injections of extracts of thyroid and also of thymus and suprarenals were found usually to produce waking in the hedgehog by Adler (1920a, 1926). From other experiments in which the heat regulating center had been removed and the sympathetic nervous system deadened with ergotoxin he concluded that these substances produced waking by increasing oxidative processes at the periphery and not wholly by action on the heat regulating center or on the sympathetic nervous system (Adler, 1920b, 1926). Schenk (1922) also found the same extracts produced a rise in metabolism and sometimes a waking in torpid hedgehogs. Zondek (1924), however, produced waking not only with Adler's extracts but also with others including physiological salt solution of a temperature of 8°C. or more above the rectal temperature of the animal and concluded that the warmth and not the specific nature of Adler's extracts produced waking.

Intra-peritoneal injections of very large doses of thyroxin (31 to 52 times the human dose considering comparative body weights) in 66 *C. t. pallidus* and feeding of thyroid substances to 23 produced no inhibition of hibernation over that of the controls (Johnson and Hanawalt, 1926, 1930). From these experiments it appears that the thyroid does not prevent hibernation and that the increased activity of the gland in the spring, shown by Adler (1920a) and Coninx-Girardet (1927) is not the cause of waking but accompanies it, possibly as a result.

Adrenal Glands

Adler's (1920a) work indicating an inhibitory effect of an adrenal extract as well as thyroid and thymus extracts and Zondek's (1924) refutation of it have already been mentioned. Enlargement of the adrenals of *C. t. tridecemlineatus* in the spring was reported by Mann (1916), but little change except an enlargement of the blood vessels was found in these glands in the winter (Coninx-Girardet, 1927). Britton (1928) has shown that in artificially cooled cats the presence of the adrenals is necessary for spontaneous awakening from this condition of torpor and suggests that waking from hibernation is produced by increased "sympatico-adrenal" activities, whereas entrance into hibernation is caused by decreased activity.

The Pituitary Gland

Gemelli (1906) observed no change in the posterior lobe but in the anterior he found a great decrease in number of "*cianofile*" cells in hibernation in the marmot. Cushing and Goetsch (1915) observed drowsiness and a lowering of temperature, respiration and heart beat in humans with diseased pituitaries. They also found reduction in size of the ductless glands, especially of the anterior pituitary, in hibernating marmots and a production of fatness and drowsiness in a young hypophysectomized dog. Mann (1916) found no constant change in the pituitary associated with seasons in the ground squirrel. Rasmussen (1921) found no changes from fall to winter in woodchucks but found indications of increased activity in the spring. Coninx-Girardet (1927) found an increase in number of basophile cells in the woodchucks in the spring including the breeding season, which also indicated increased activity of the pituitary at that time. In the winter decreased activity was indicated by a reduction in number of basophile cells and by a more open grouping of the cells of the pituitary.

While the histological appearance of the anterior pituitary indicates renewed activity in the spring it should be noted that this might be a result and not a cause of waking and only physiological experiments can give conclusive evidence. Experiments in this laboratory with a weak extract by B. R. Coonfield and the author showed no effect on hibernation. More recently a stronger alkaline extract has shown some inhibitory action and subcutaneous injection of cut

pieces of the pituitary into 20 ground squirrels has shown marked inhibitory effects on entrance into hibernation.

No evidence has been produced which indicates that the posterior pituitary has any influence on hibernation; on the contrary, the injection of pituitrin by Johnson and Hanawalt (1926, 1930) gives definite evidence that it has neither an inhibitory nor a causative action on hibernation.

Gonads

Gonadal enlargement in hibernating forms in the spring has been found by Mann (1916), Drips (1919), Rasmussen (1917, 1918), Shaw (1926) and Johnson (1930). Mann showed that castration did not prevent hibernation in C. t. tridecemlineatus. That gonadal activity tends to prevent hibernation in the spring but not at other times of the year has been shown by Johnson (1927, 1930) in C. t. pallidus, for castrated animals hibernated to a significantly greater extent than did normal animals during the breeding season. It was also recognized that this activity is probably caused by increased secretion of the anterior pituitary.

Other Possible Causes Investigated

Removal of the spleen was found to show no effect on hibernation by Mann and Drips (1917), although they found the vessels much congested. Extracts of the thymus used by Adler (1920a) produced waking from hibernation, but this work was questioned by Zondek (1924), and other work seems to raise the question whether this structure is an endocrine organ. Structural differences between hibernators and other animals were sought by Mangili (1807), who considered that the arterial blood supply to the brain was small in hibernating forms, and by Saissy (1815), who stressed the large blood vessels of the thorax and abdomen, small peripheral vessels, large nerves to the head, and limited blood supply to the brain as characteristic features in hibernating forms. While many authors have noted the lack of peripheral bleeding when a hibernating animal is cut and have seen the congestion in the chief blood vessels, it would not seem that these can have a causative relation to hibernation.

Injection of insulin sufficient to produce hypoglycemia caused woodchucks, dogs and cats to pass temporarily into a state of torpor (Cassidy, Dworkin and Finney, 1925a, b; Dworkin and Finney, 1927), in which the respiratory quotient fell in the dogs as if they were in true hibernation (Finney, Dworkin and Cassidy, 1927). Injection of adrenalin and pituitrin brought back the shivering reflexes in partly torpid animals that had ceased to shiver (Cassidy, Dworkin and Finney, 1926). Whether these observations reveal any internal causes of hibernation it is difficult to say. It would be interesting to know whether the blood sugar level of an animal that falls into hibernation very readily is different from that of one that shows great resistance to hibernation in a cold room.

The inhibiting effect on hibernation of external stimuli has long been recognized. Thus Dubois (1896) found that the taking of temperatures of the marmot tended to shorten its hibernating period and Brown (1847) found that excitability kept animals awake.

LIST OF LITERATURE

ADLER, L. 1920a. Schilddrüse und Wärmeregulation (Untersuchungen an Winterschläfern). Arch. exper. Path., 86: 159–224.

———. 1920b. Über den Angriffspunkt der Blutdrüsenhormone bei der Wärmeregulation. Weitere Untersuchungen an Winterschläfern. Arch. exper. Path., 87: 406–423.

———. 1926. Der Winterschlaf. Handbuch der Normalen und Pathologischen Physiologie, 17: 105–133.

ANTHONY, H. E. 1928. Field Book of North American Mammals. Putnam, New York.

BAILEY, V. 1926. Hibernation good for mankind too. New York Times, July 4, p. 6.

———. 1928. Animal Life of the Carlsbad Cavern. Williams and Wilkins, Baltimore.

BALDWIN, F. M. 1925. Body temperature changes in turtles and their physiological interpretations. Amer. Jour. Physiol., 72: 210–211.

BARKOW, H. C. L. 1846. Der Winterschlaf nach seinen Erscheinungen im Thierreich. Hirschwald, Berlin.

BAYLISS, W. M. 1918. Principles of General Physiology. Longmans, London.

BERT, P. 1868. Hibernation artificielle des lérots dans une atmosphère lentement appauvrie en oxygène. Comp. rend. Soc. biol., Sér. 4, 5: 13.

———. 1870. Leçons sur la physiologie comparée de la respiration. Paris.

BIERENS DE HAAN, J. A. 1922. Die Körpertemperatur junger Wanderratten (Mus decumanus) und ihre Beeinflussung durch die Temperatur der Aussenwelt. Archiv f. Entw.-Mech. der Organismen, 50: 1–12.

BLANCHARD, R. 1903. Expériences et observations sur la marmotte en hibernation. Comp. rend. Soc. biol., 55: 734–741; 1120–1126.

BODINE, S. H. 1923. Hibernation in Orthoptera. I. Physiological changes during hibernation in certain Orthoptera. Jour. Exp. Zool., 37: 457–476.

BREITENBECHER, J. K. 1918. The relation of water to the behavior of the potato beetle in a desert. Carnegie Inst. Wash., Pub. No. 263: 341–384.

BRITTON, S. W. 1922. Effects of lowering the temperature of homoiothermic animals. Quart. Jour. Exp. Physiol., 13: 55–68.

———. 1928. Studies on the conditions of activity in endocrine glands. XXII. Adrenin secretion on exposure to cold, together with a possible explanation of hibernation. Amer. Jour. Physiol., 84: 119–131.

BROWN, P. A. 1847. An Attempt to Discover Some of the Laws Which Govern Animal Torpidity and Hibernation. Philadelphia.

BUCHANAN, F. 1911. Dissociation of auricles and ventricles in hibernating dormice. Proc. Physiol. Soc. (Jour. Physiol., 42: xix–xx).

BURNETT, W. L. 1914. The striped ground squirrels of Colorado. Office of State Entomologist, Fort Collins, Colo., Circ. 14.

BUSK, K. 1885. Hibernation. Nature, 31: 316–317 and 482.

CARLISLE, A. 1805. The Croonian lecture on muscular motion. Phil. Trans. (Lond.), 95: 1–30.

CASSIDY, G. J., DWORKIN, S., and FINNEY, W. H. 1925a. The rate of action of insulin in artificially cooled mammals. Amer. Jour. Physiol., 73: 413–416.

———. 1925b. Insulin and the mechanism of hibernation. Amer. Jour. Physiol., 73: 416–428.

———. 1926. The effect of various sugars (and of adrenalin and pituitrin) in restoring the shivering reflex. Amer. Jour. Physiol., 77: 211–218.

CLAPARÈDE, E. 1905. Théorie biologique du sommeil. Arch. d. Psychol., 4: 245–349.

CLEGHORN, A. 1910. Natural history and physiology of hibernation. Pop. Sci. Mo., 77: 356–364.

CONINX-GIRARDET, B. 1927. Beiträge zur Kenntnis innersekretorischer Organe des Murmeltieres (*Arctomys marmota* L.) und ihrer Beziehungen zum Problem des Winterschlafes. Acta Zoologica, 8: 161–224.

CORY, C. E. 1912. The mammals of Illinois and Wisconsin. Field Mus. of Nat. Hist. Pub., Zool. Ser., 11.

CUSHING, H., and GOETSCH, E. 1915. Hibernation and the pituitary body. Jour. Exp. Med., 22: 25–47.

DELSAUX, E. 1887. Sur la respiration des Chauves-Souris pendant leur sommeil hibernal. Arch. de Biol., 7: 207–215.

DRIPS, D. 1919. Studies of the ovary of the spermophile. Amer. Jour. Anat., 25: 117–184.

DUBOIS, R. 1895. (Three short articles on autonarcosis). Comp. rend. Soc. biol., 47: 149–151; 814–815; 830–831.

———. 1896. Étude sur le méchanisme de la thermogenèse et du sommeil chez les mammifères. Physiologie comparée de la marmotte. Annales de l'Université de Lyon. Paris.

———. 1901a. Le centre du sommeil. Comp. rend. Soc. biol., 53: 229–230.

———. 1901b. Sommeil naturel par autonarcose carbonique provoqué expérimentalement. Comp. rend. Soc. biol., 53: 231–232.

DWORKIN, S., and FINNEY, W. H. 1927. Artificial hibernation in the woodchuck (Arctomys monax). Amer. Jour. Physiol., 80: 75–81.

FINK, D. E. 1925. Physiological studies on hibernation in the potato beetle, Leptinotarsa decemlineata Say. Biol. Bull., 49; 381–406.

FINNEY, W. H., DWORKIN, S., and CASSIDY, G. J. 1927. The effects of lowered body temperatures and of insulin on the respiratory quotients of dogs. Amer. Jour. Physiol., 80: 301–310.

FITZPATRICK, F. L. 1925. The ecology and economic status of Citellus tridecemlineatus. University of Iowa Studies in Nat. Hist., 11: 1–40.

FOREL, A. 1887. Observations sur le sommeil du loir (*Myoxis glis*). Revue de l'hypnot. exp., 1: 318–319. (Also in Centralbl. f. Physiol., 1: 208–209).

GEMELLI, A. 1906. Su l'ipofisi delle marmotte durante il letargo e nella stagione estiva. Archivo per le Scienze Mediche, 30: 341–349.

GORER, P. A. 1930. The physiology of hibernation. Biol. Rev. (Camb.), 5: 213–230.

HAHN, W. L. 1908. Some habits and sensory adaptations of cave-inhabiting bats. Biol. Bull., 15: 135–193.

———. 1914. Hibernation of certain animals. Pop. Sci. Mo., 84: 147–157.

HALL, M. 1832. On hibernation. Phil. Trans. (Lond.), Pt. I: 335–360.

HATT, R. T. 1927. Notes on the ground-squirrel, Callospermophilus. Occas. papers, Mus. Zool., Univ. of Michigan, 185: 1–22.

HORVATH, A. 1872a. Zur Physiologie der tierischen Wärme. Zentralbl. f. med. Wissensch., pp. 706–708; 721–724; 734–739.

———. 1872b. Zur Lehre vom Winterschlafe. Zentralbl. f. med. Wissensch., pp. 865–866.

———. 1874. Zur Abkühlung der Warmblüter. Pflüger's Archiv f. Physiol., 12: 278–282.

———. 1878. Beitrag zur Lehre über den Winterschlaf. Verh. d. Phys.-Med., N. F., 12: 139–198.

HORVATH, A. 1880. Ueber die Respiration des Winterschläfer. Verh. d. Phys.-Med., N. F., 14: 55–120; 15: 177–186.

———. 1881. Einfluss verschiedener Temperaturen auf die Winterschläfer. Verhandl. d. Phys.-Med., N. F., 15: 187–219.

HOWELL, A. H. 1915. Revision of the American marmots. N. Am. Fauna, No. 37.

HOY, P. R. 1875. On hibernation as exhibited in the striped gopher. Proc. Amer. Assoc. Adv. Sci., 24: 148–150.

HULK, A. H. 1885. Human hibernation. Nature, 31: 361.

HUNTER, J. 1837. Experiments and observations on animals with respect to the power of producing heat. The Works of John Hunter (London), 4: 131–155.

JOHNSON, G. E. 1917. The habits of the thirteen-lined ground squirrel. Quart. Jour. Univ. N. Dakota, 7: 261–271.

———. 1925. Some conditions affecting the hibernation of the thirteen-lined ground squirrel. Anat. Rec., 31: 337.

———. 1927. The influence of precooling, castration, and body weight on the production of hibernation of Citellus tridecemlineatus (Mitchill). Anat. Rec., 37: 125.

———. 1928. Hibernation of the thirteen-lined ground squirrel, Citellus tridecemlineatus (Mitchill). I. A comparison of the normal and hibernating states. Jour. Exp. Zool., 50: 15–30.

———. 1929a. Hibernation, etc., II. The general process of waking from hibernation. Am. Nat., 63: 171–180.

———. 1929b. Hibernation, etc., III. The rise in respiration, heart beat and temperature in waking from hibernation. Biol. Bull., 57: 107–129.

———. 1929c. The fall in temperature in ground squirrels going into a state of hibernation. Anat. Rec., 44: 199.

———. 1930. Hibernation, etc., V. Food, light, confined air, pre-cooling, castration and fatness in relation to production of hibernation. Biol. Bull., 59: 114–127.

JOHNSON, G. E., and HANAWALT, V. B. 1926. The influence of thyroxin and of pituitrin on the hibernation of Citellus tridecemlineatus pallidus Allen. Anat. Rec., 34: 137.

———. 1930. Hibernation, etc., IV. Influence of thyroxin, pituitrin and desiccated thymus and thyroid on hibernation. Am. Nat., 64: 272–284.

KALABOUKHOV, N. I. 1929. Aestivation of the ground squirrel. Trans. Lab. Exp. Biol. Zoopark of Moscow, 5: 163–176.

KASHKAROV, D., and LEIN, L. 1927. The yellow ground squirrel of Turkestan, Cynomys fulvus oxianus Thomas. Ecology, 8: 63–72.

KOELSCH, A. 1925. Der Mechanismus des Winterschlafs. Kosmos, Heft 1, (Jan.): 14–17.

MANGILI, M. 1807. Ueber den Winterschlaf der Thiere. Arch. f. d. Physiol. (Reil), 8: 427–448. A similar article in Ann. d. Mus. hist. nat., 9: 106–117; 10: 434–465, (1807).

MANN, F. C. 1916. The ductless glands and hibernation. Amer. Jour. Physiol., 41: 173–188.

MANN, F. C., and DRIPS, D. 1917. The spleen during hibernation. Jour. Exp. Zool., 23: 277–285.

MARES, M. F. 1892. Expériences sur l'hibernation des Mammifères. Comp. rend. Soc. biol., 44: 313–320.

MARTIN, C. J. 1901. Thermal adjustments and respiratory exchange in Monotremes and Marsupials. Proc. Roy. Soc. London, 68: 352–353.

MERRIAM, C. H. 1901. The prairie dog of the great plains. U. S. Dept. Agr. Yearbook, pp. 255–270.

MERZBACHER, L. 1903a. Untersuchungen über die Function des Centralnerven-systems der Fledermaus. Arch. f. d. ges. Physiol., 96: 572–600.

———. 1903b. Untersuchungen an winterschlafenden Fledermäusen. I. Mittheilung. Das Verhalten des Centralnervensystems in Winterschlafe und während des Erwachens an demselben. Arch. f. d. ges. Physiol., 97: 569–577.

———. 1904. Allgemeine Physiologie des Winterschlafes. Ergebn. d. Physiol., 3 (Abt. 2): 214–258.

MILLS, W. 1892. Hibernation and allied states in animals. Trans. Roy. Soc. Canada, Sec. IV: 49–51. A part also in Trans. Pan-Amer. Med. Congr. Wash., 1893, Pt. II: 1274.

MILNE-EDWARDS, H. 1857–63. Leçons sur la Physiologie (Paris), 2: 490–491; 2: 519–525; 4: 76; 8: 58–68.

MONTI, R., and MONTI, A. 1900. Osservazioni su le marmotte ibernanti. Reale Inst. Lombardo di sci. e let. Rend. Ser. II, 33: 372–381.

MURRAY, J. 1826. On the torpidity of the tortoise and dormouse. Edinburgh Jour. Sci., 4: 317–322.

PAYNE, N. M. 1927. Freezing and survival of insects at low temperatures. Jour. Morph., 43: 521–546.

PEMBREY, M. S. 1895. The effect of variations in external temperature upon the output of carbonic acid and the temperature of young animals. Jour. Physiol., 18: 363–379.

———. 1898. Animal heat. Textbook of Physiology (Edited by Schafer), 1: 785–867.

PEMBREY, M. S. 1901. Observations upon the respiration and temperature of the marmot. Jour. Physiol., 27: 66–84.

———. 1903. Further observations upon the respiratory exchange and temperature of hibernating mammals. Jour. Physiol., 29: 195–212.

PEMBREY, M. S., and WHITE, W. H. 1896. The regulation of temperature in hibernating animals. Jour. Physiol., 19: 477–495.

PEMBREY, M. S., and PITTS, A. G. 1899. The relation between the internal temperature and the respiratory movements of hibernating animals. Jour. Physiol., 24: 305–316.

POLIMANTI, O. 1912. Il Letargo. Roma.

PRATT, H. S. 1923. Vertebrate Animals of the United States. Blakistons, Philadelphia.

QUINCKE, H. 1881. Ueber die Wärme-regulation beim Murmelthier. Arch. f. exp. Path., 15: 1–21.

RASMUSSEN, A. T. 1915. The oxygen and carbon dioxide content of the blood during hibernation in the woodchuck (*Marmota monax*). Amer. Jour. Physiol., 39: 20–30.

———. 1916a. Theories of hibernation. Am. Nat., 50: 609–625.

———. 1916b. A further study of the blood gases during hibernation in the woodchuck (*Marmota monax*). The respiratory capacity of the blood. Amer. Jour. Physiol., 41: 162–172.

———. 1916c. The corpuscles, hemaglobin content and specific gravity of the blood during hibernation in the woodchuck (*Marmota monax*). Amer. Jour. Physiol., 41: 464–482.

———. 1917. Seasonal changes in the interstitial cells of the testis in the woodchuck (*Marmota monax*). Amer. Jour. Anat., 22: 475–509.

———. 1918. Cyclic changes in the interstitial cells of the ovary and testis in the woodchuck (*Marmota monax*). Endocrin., 2: 353–404.

———. 1921. The hypophysis cerebri of the woodchuck (*Marmota monax*) with special reference to hibernation and inanition. Endocrin., 5: 33–66.

———. 1923. The so-called hibernating gland. Jour. Morph., 38: 147–205.

REEVE, H. 1809. An Essay on the Torpidity of Animals. London.

SAISSY, J. A. 1811. Observations sur quelques mammifères hybernans. Mém. Acad. d. Sci. d. Turin, pt. 2: 1–21.

———. 1815. Untersuchungen über die Natur der winterschlafenden Säugethiere. Arch. f. d. Physiol., 12: 293–369.

SCHENK, P. 1922. Ueber den Winterschlaf und seine Beeinflussung durch die Extrakte innersekretorischer Drüsen. Arch. ges. Physiol., 197: 66–69.

SEMPER, K. 1881. Animal Life as Affected by the Natural Conditions of Existence. Appleton, New York.

SETON, E. T. 1928. Lives of Game Animals, Vol. 2. Doubleday, Page and Co., Garden City, N. Y.

SHAW, W. T. 1921. Moisture and altitude as factors in determining the seasonal activities of the Townsend ground squirrel in Washington. Ecology, 2: 189–192.

———. 1925a. The hibernation of the Columbian ground squirrel. Canad. Field Nat., 39: 56–61 and 79–82.

———. 1925b. Observations on the hibernation of ground squirrels. Jour. Agr. Res., 31: 761–769.

———. 1925c. Duration of the aestivation and hibernation of the Columbian ground squirrel (Citellus columbianus) and sex relation to the same. Ecology, 6: 75–81.

SHELDON, E. F. 1924. The so-called hibernating gland in mammals: A form of adipose tissue. Anat. Rec., 28: 331–347.

SIMPSON, S. 1911–12. The relation of external temperature to hibernation. Amer. Jour. Physiol., 29: xii. Also in Proc. Soc. Exp. Biol. and Med., 10: 180–181 (1913).

———. 1912. The food factor in hibernation. Proc. Soc. Exp. Biol. and Med., 9: 92.

SPALLANZANI, L. 1803. Mémoires sur la respiration, traduits en Français, par Jean Senebier, Genève. pp. 106–117.

SUMNER, F. B. 1913. The effects of atmospheric temperature upon the body temperature of mice. Jour. Exp. Zool., 15: 315–377.

STOCKARD, A. H. 1930. Observations on the seasonal activities of the white-tailed prairie dog, *Cynomys leucurus*. Papers, Mich. Acad. Sci., Arts and Let., 11: 471–479.

SWENK, M. H. 1915. The prairie dog and its control. Bul. 154, Neb. Agr. Exp. Sta.

TAIT, J., and BRITTON, S. W. 1923. Quart. Jour. Exp. Physiol., Sup. Vol. 226.

TOWER, W. L. 1906. An investigation of evolution in Chrysomelid beetles of the genus Leptinotarsa. Carnegie Inst. Wash. Pub. No. 48: 1–320.

VALENTIN, G. 1857. Beiträge zur Kenntnis des Winterschlafes der Murmelthiere. Unters. zur Naturl. des Menschen und der Thiere, von Jac. Moleschott, 1: 206–258 and 2: 1–55. (A series of 27 articles, 1857–1888).

WADE, O. 1930. The behavior of certain spermophiles with special reference to aestivation and hibernation. Jour. Mammal., 11: 160–188.

WILLIAMS, S. R. 1909. On hibernation in the raccoon. Ohio Naturalist, 9: 495–496.

ZONDEK, B. 1924. Untersuchungen über den Winterschlaf. Klin. Wchnschr., Heft 34, 3: 1529–1530.