years B.P. and the subsequent decrease (*7, 20*). The decrease in $\delta^{13}C$ in N17 has been discussed elsewhere (*21*).

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3. The depletion in ^{18}O of 0.65 ± 0.15 per mil for *Cibicidoides* relative to the equilibrium value is the average of relationships inferred from the following: modern *C. wuellerstorfi* from the East Pacific Rise [F. Woodruff, S. M. Savin, R. G. Douglas, *Mar. Micropaleontol.* **5**, 3 (1980)]; a comparison of Pleistocene *Uvigerina* and *C. wuellerstorfi* [N. J. Shackleton and N. D. Opdyke, *Quat. Res.* **3**, 39 (1973)]; and a comparison of Miocene *Uvigerma* and *C. wuellerstorfi* at site 289 (this study).
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Hibernation and Longevity in the Turkish Hamster *Mesocricetus brandti*

Abstract. *A positive correlation was found between the length of life of 288 Turkish hamsters and the amount of time spent in hibernation, suggesting that the process of aging is slowed during hibernation.*

Although the concept of suspended animation and resulting longer life has formed the basis for innumerable fictional stories, there is little scientific data to indicate that hibernation affects longevity in any mammal. Brace (*1*), using four woodchucks, concluded that either exposure to cold or hibernation prolongs the life-span of red blood cells, and Brock (*2*) demonstrated that elution, random destruction, and aging of red blood cells tagged with chromium-51 are greatly reduced in hibernating Syrian hamsters. The experiments of Hrůza *et al.* (*3*) with the tail tendons of dormice can be criticized because the hibernation periods were extremely short compared to the life-span of the species (more than 4 years) (*4*).

Tagging experiments in the field show that bats live much longer than other mammals of comparable size—21 to 30 years (*5, 6*). Bats living in the temperate zone undergo periods of daily torpor during summer and long periods of uninterrupted hibernation during winter. Griffin (*5*) suggested that this might contribute to their longevity, but the concept has not been tested in the laboratory. Herreid (*7*) concluded from field studies that tropical and semitropical bats, which do not hibernate, live as long as the bats that hibernate.

The study of the relation between hibernation and aging requires a species which can be raised in the laboratory so that its age and history are known, and which hibernates for long periods when exposed to the cold. These requirements are met by the Turkish hamster, *Mesocricetus brandti*, which we first imported into the United States in 1965 (*8*). In contrast, North American ground squirrels breed in the laboratory only rarely and under special conditions, and the Syrian hamster, although easily raised in the laboratory, hibernates in an irregular manner. Our native microchiropteran bats are difficult to breed and maintain, and their long life-span challenges the middle-aged investigator to see the end of the experiment.

A total of 288 laboratory-bred Turkish hamsters was used in this experiment. Each animal was housed separately in a 24 by 17 by 17 cm cage with wood shavings and given unrestricted access to water and Purina Lab Chow. Oats and a slice of apple were provided weekly. Half of the hamsters were designated as controls and kept at 22° ± 3°C throughout their lives. The 144 experimental animals were kept at the same temperature until mid-November each year, then moved to a cold room (5° ± 2°C) until the end of April the following year. Daily illumination for all the animals paralleled the natural cycle at the latitude of Boston, Massachusetts. Each animal was numbered by tattoo. Except for 42 animals, matched pairs of littermates (one experimental and one control) of the same sex were used. The animals were adults—that is, fully grown (4 to 6 months) and capable of reproduction—when they were first moved to the cold room. Periods of hibernation were monitored by sprinkling oats on the exposed backs of the hibernating animals. Spontaneous arousal resulted in displacement of the oats, which were replaced when the animal resumed hibernation.

None of the controls ever hibernated, and hibernation among the animals exposed to cold varied considerably. For comparison, three categories were arbitrarily established among the cold-exposed group after the raw data were collected: poor hibernators, or animals that hibernated 0 to 11 percent of their lives ($N = 47$); moderate hibernators, or animals that hibernated 12 to 18 percent of their lives ($N = 48$); and good hibernators, or animals that hibernated 19 to

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33 percent of their lives (N = 49). To a limited extent, the time of year in which an animal dies affects the percentage of its life that it spent hibernating. Thus, among a hypothetical group of animals hibernating continually throughout their exposure to cold, the percentage of hibernation is least in the animal that dies on the last day of its next sojourn in the warm. This may cause a maximum variation of 3 percent in time spent hibernating—negligible in groups of this size and range.

Of the 144 hamsters exposed to the cold, nine never hibernated. These animals tended to be short-lived, with a mean life-span of 544 days. Nevertheless, the mean life-span of the cold-exposed animals (914 ± 297 days) was significantly greater (P = .001) than that of the controls (812 ± 222 days) (*9*). The mean life-span of the good hibernators (1093 ± 285 days) was significantly greater (P = .002) than that of the moderate hibernators (916 ± 268 days), and the mean life-span of the moderate hibernators was significantly greater ($P \leq .001$) than that of the poor hibernators (727 ± 216 days). While the mean life-span of the moderate hibernators was significantly greater than that of the controls (P = .018), the latter lived longer than the poor hibernators (P = .023). The mean life-span of the good hibernators was greater than that of either the controls or the poor hibernators, and these differences have, respectively, less than one chance in 8×10^7 and one in 1×10^{20} of being wrong.

Figure 1 summarizes the population decrease over time for the various groups, and Fig. 1b shows the enhanced longevity of the better hibernators. Figure 2 correlates the life-span for all cold-exposed hamsters with the percentage of hibernation. The equation of the line is age at death = 653.20 + (18.002 × percentage of hibernation), and both regression coefficients, r and P, are highly significant. The correlation between time spent in hibernation and total life-span is clearly positive.

The standard deviation in the life-span of the cold-exposed animals is greater than that of the warm-room animals, which complements the visual evidence (Fig. 3) that both the long and short extremes of life-span are in the former group. Some of the animals in the cold room lived much longer than any controls. These animals were the moderate and good hibernators, as indicated by the life-span curves in Fig. 1b and the regression line in Fig. 2.

The female control animals averaged a significantly longer life (865 ± 211 days) than the males (762 ± 222 days) (P = .005). This contrasts with a longer life reported for male Syrian hamsters subjected to various stressful conditions (*10*). There was no significant difference between the mean life-span of the experimental males (924 ± 324 days) and females (903 ± 265 days), and the percentage of hibernation was only slightly higher in the males. As might be expected, the mean life-span of the experimental males was significantly longer than that of the control males ($P \leq .001$). The life-span of the females showed the same trend, but the difference was not significant. Autopsies indicated that neither the cold-exposed hamsters nor the controls suffered from a disease peculiar to their group.

It is tempting to conclude that hibernation prolongs life, but this causality has not been firmly established. The experiment requires that the control animals be maintained under conditions that maximize their life-span, but the exact conditions are unknown. Absence of stress, as manifested by a relatively low metabolic rate, should serve as an ideal condition for longevity, and the metabolic rate of the control animals was lower than that of the cold-exposed animals that did not hibernate. The cold-room temperature was well below the zone of thermal neutrality for Turkish hamsters; oxygen consumption doubled upon the first exposure to 5°C (*4*). There is no indication that metabolism increases during the winter months in hibernating species that are held at room temperature during the winter; indeed, Kayser (*11*) and others maintain that the metabolic rate of potential hibernators in a thermally neutral environment decreases as autumn approaches.

The evidence that cold exposure without hibernation is a stress, and that it may shorten life, is persuasive. Animals that did not hibernate, or hibernated for less than 11 percent of their lives, lived a significantly shorter time than the con-

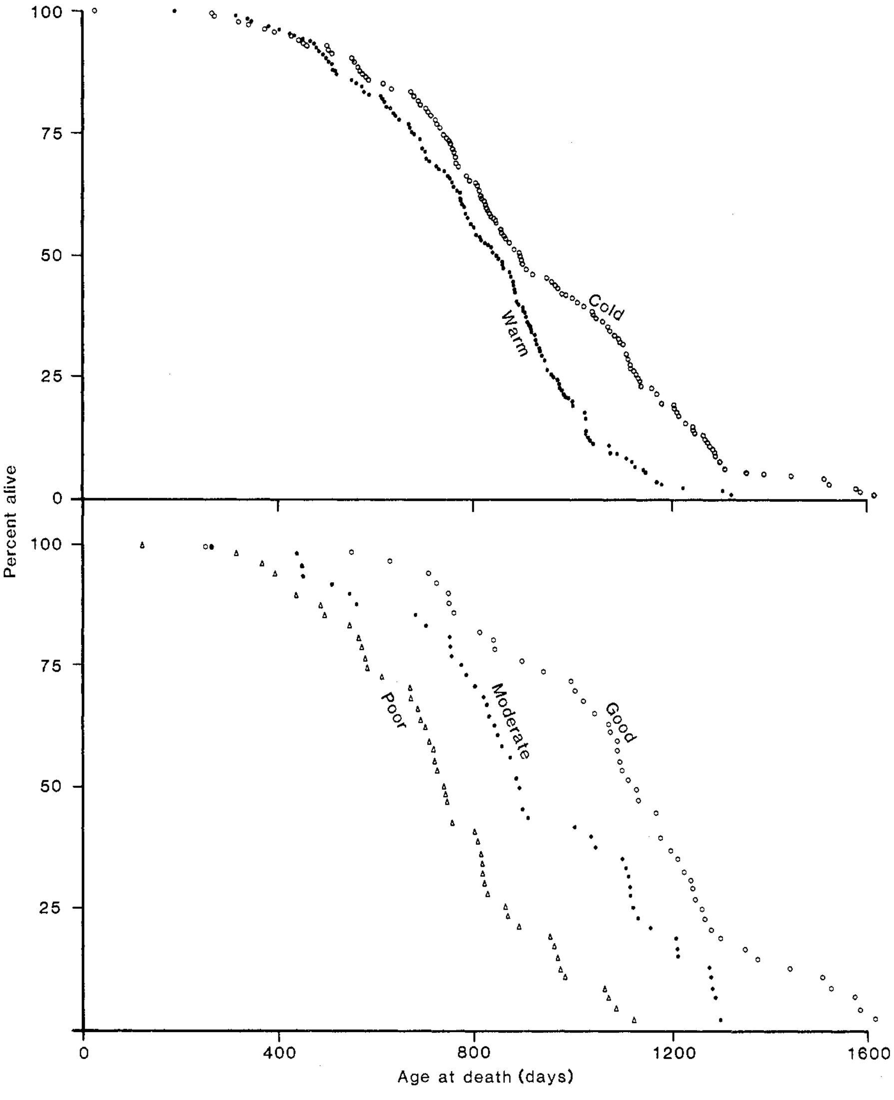
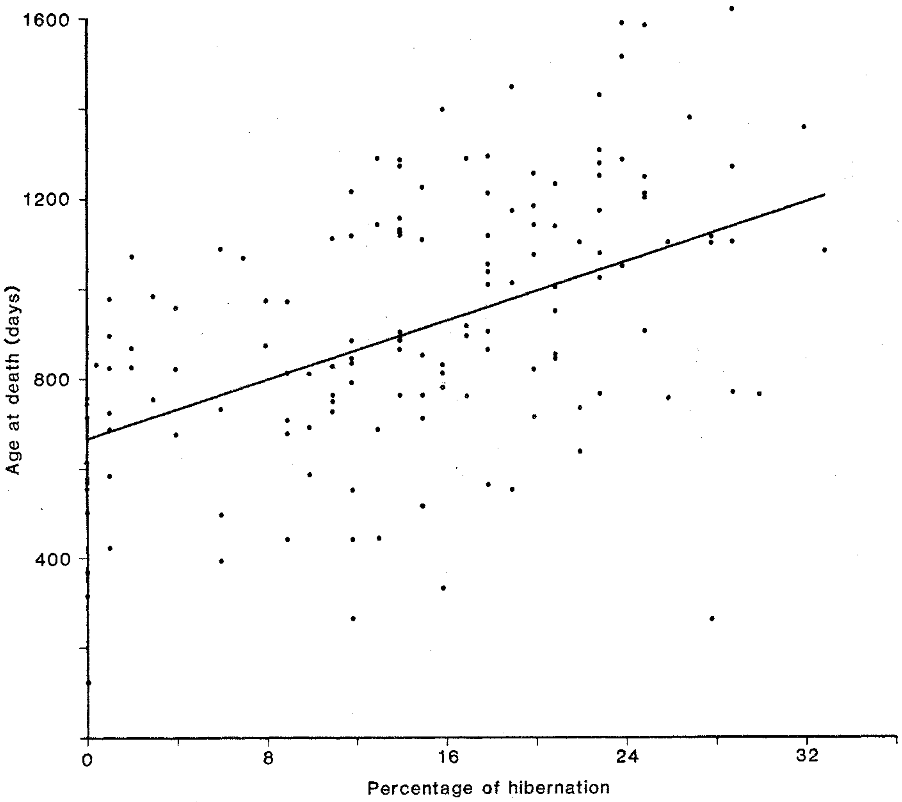


Fig. 1. (a) Longevity of all hamsters in the study. (b) Longevity of the poor, moderate, and good hibernators.

trol animals, and old but apparently healthy individuals that were exposed to cold for a third season tended to die within a very short period.

It is paradoxical that hibernation may prolong life whereas the stress of exposure to cold shortens it. Instead of fighting the cold, the hibernator takes advantage of the extremely low metabolic rate that accompanies a low body temperature. This results in great metabolic savings over a season, notwithstanding the expense of periodic arousals (*12*). Ground squirrels and other hibernators which, unlike hamsters, do not store food for the winter are presumably threatened by starvation when they enter hibernation, and by hibernating they greatly prolong their ability to live without food. Evidently the metabolic frugality of hibernation also prolongs the life of the animal. This is in agreement with theories postulating that every animal is born with finite stores of basic physiological functions and that death occurs when the stores are exhausted (*13*).



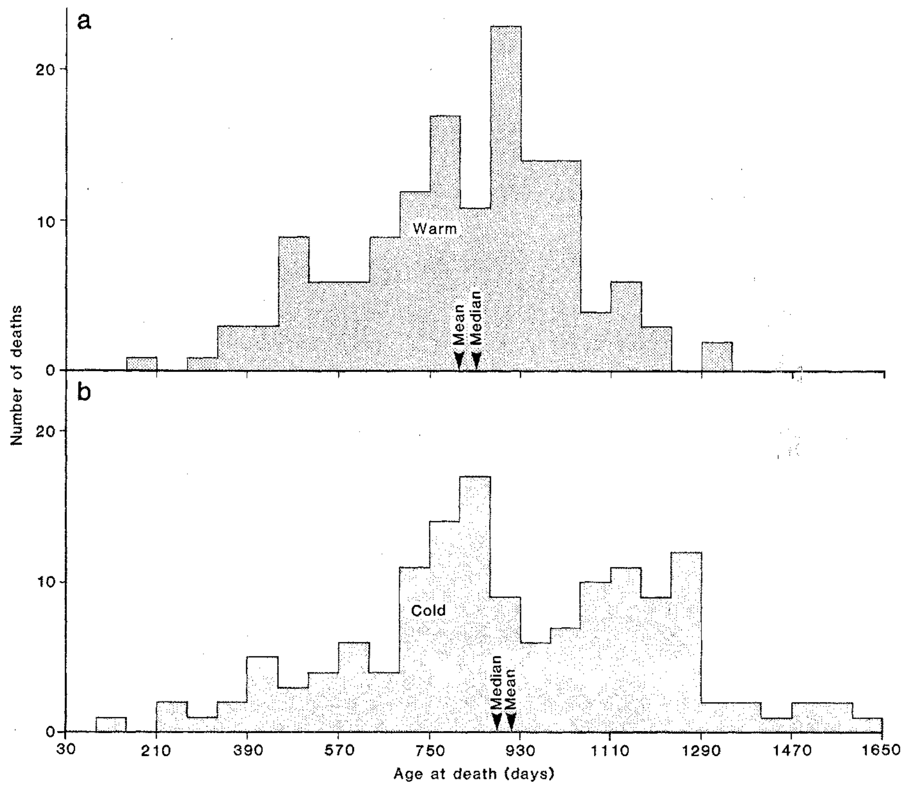


Fig. 2 (top). Regression line correlating age at death with percentage of hibernation for all cold-exposed hamsters ($\bar{y} = 914.41$, $\bar{x} = 14.510$, $r = .522$, $P < .001$). Fig. 3 (bottom). Histograms plotting number of deaths against age at death at intervals of 60 days for (a) control hamsters (mean = 812 days, median = 843 days) and (b) experimental hamsters (mean = 914 days, median = 884 days).

Certain morphological changes, such as accumulation of cross-linkages in collagen fibers or of lipofuscin granules, occur as a mammal grows older and may be involved in the senility and death of the animal (*13*). It is not known whether the progression is a function of metabolic rate or some other basic activity over a period of time, or whether the progression occurs immutably, with its rate dependent on time alone. Whether hibernation is causally related to longevity or not, the data show that hamsters that hibernated for protracted periods lived longer than the animals that hibernated briefly or not at all. Thus, it should be possible to examine further the factors that influence the progression of the morphological changes that occur with aging by using closely related animals with different life expectancies.

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