Dormancy, Hibernation, And Estivation In Warm-Blooded VertebratesThe term hibernation is often loosely used to denote any state of sustained torpor, inactivity, or dormancy that an organism might exhibit. Properly speaking, however, use of the term should be conﬁned solely to warm-blooded homoiotherms—i.e., birds and mammals whose feathers or fur serve as insulation to reduce heat radiating from the body and aid in the maintenance of constant body temperatures, which normally are independent of those of the environment. Because warm-bloodedness gives animals an internal physiological stability, they are less dependent on many environmental restrictions, particularly those limitations imposed on organisms by ambient temperatures. For example, only two species of reptiles are found north of the Arctic Circle, but great numbers of birds live and breed there. Warm- bloodedness also signiﬁes a high metabolic rate, a factor that undoubtedly inﬂuences normal learning, which depends heavily on the frequency and recency of experiences. Because periods of lowered metabolism interrupt continuous learning experiences, they may explain in part why birds and mammals are so much easier to train than any other animal. The beneﬁts of warm-bloodedness require the expenditure of large amounts of energy through the year and make a heavy demand on available food supplies. The term hibernation is also used to delineate the dormant state only during winter. In arid regions a reverse phenomenon is seen in which the animal becomes torpid during the hot, dry, barren summer; such hibernation is called estivation. As a means of avoiding environmental stresses, hibernation and estivation are not common devices among warm-blooded animals and they are far less common among birds than among mammals.Some warm-blooded organisms exhibit thermic instability, a heterothermous condition that allows their metabolic rate to be reduced, with a commensurate reduction in body temperature. Heterothermy is a transitional state between cold-bloodedness and warm-bloodedness; the animal is awake and moving during its temperature ﬂuctuations. The body temperature, although not as constant as in humans, is not so low as to force the organism into deep hibernation. Among mammals, two monotremes, the spiny anteater and the duckbill platypus, are thermally unstable; many of the marsupials, including the opossum, the pouched mouse, and the native cat (a weasel-like spotted marsupial of the family Dasyuridae), are also unable to maintain a ﬁxed body temperature.The true hibernator not only possesses adaptations that enable it to respond as a homoiothermous animal during certain periods of the year but can also adapt to stressful environmental situations and become essentially a poikilothermous animal during other periods. An animal exposed to food shortages, low temperatures, or lack of water, for example, may “turn off its thermostat” and hibernate until the environment becomes more favourable. Unlike poikilotherms, however, hibernators still retain a measure of temperature control and can change their metabolic levels as required. They can arouse themselves to full activity, whatever the environmental temperature, whereas the arousal of a poikilotherm is dependent upon increased environmental temperatures.During the period prior to hibernation an animal must make a considerable number of gradual physiological and metabolic adjustments that appear to be correlated with temperature, light, and the availability of food. No one set of conditions applies equally to all hibernators: some store food, others do not;some become excessively fat, others gain a more moderate amount of weight. Generally, as the season advances and as the hibernator becomes progressively more prepared for hibernation, there is an increase of fat deposition and a general readjustment of body temperature, metabolism, and heart rate to lowered levels of activity.Although no single factor or condition can be said to determine when an animal will go into hibernation, speciﬁc changes include an increase in the quantity of magnesium in the blood and a reduction in the activity of endocrine glands, such as the pituitary, thyroid, and adrenals. A reduction in gonadal activity has also been observed; hibernation does not occur when the gonads are in an actively functional state. Perpetuation of the species requires that the animal be warm and active during the mating and pregnancy periods.There appears to be a relationship between sleep and hibernation; available evidence suggests that hibernation is entered into from a state of sleep. If hibernation is to be considered a form of sleep, then it must be considered a remarkably complex one. Hibernation and sleep are somewhat similar in that essential body processes continue during both periods at a lowered level. Insleep, the heart beats less rapidly, and breathing is slower; the body produces less heat, necessitating that a sleeping person be protected from the cold.Hibernation in birdsTemperature variationsBirds normally have higher and more variable temperatures than do mammals. Whereas mammalian temperatures normally range between 36 and 39 °C (97 and 102 °F), avian temperatures range between 37.7 and 43.5 °C (99.9 and 110.3 °F), with the majority between 40 and 42 °C (104 and 108 °F). Although the nesting temperature of most passerine species (perching songbirds) is about 40.5 °C (104.9 °F), primitive bird species—like primitive mammals—have lower temperatures than do the more advanced species. The kiwi, for example, has an average coenothermic body temperature of 37.8 °C (100 °F). In general, the temperatures of small birds ﬂuctuate more than do those of large birds. The temperature of a house wren (Troglodytes) may ﬂuctuate 8 °C (14 °F) in 24 hours, that of a robin (Turdus) ﬂuctuates about 6 °C (11 °F), and that of the domestic duck only about 1 °C (2 °F).The circadian period of activity and rest in birds is accompanied by a temperature cycle. Birds active in the daytime have their highest temperatures late in the afternoon and their lowest in the early morning. Nocturnal species, however, such as owls and the kiwi, have their maximum body temperatures at night, when they are most active. Seasonal temperature variations are also found in birds, and, like mammals, certain birds exhibit thermic instability. Although some are capable of maintaining a highly stable body temperature, others have a ﬂuctuating body temperature. A torpid poorwill (Phalaenoptilus nuttallii) is an example of a bird that demonstrates both thermic instability and true hibernation. Its coenothermic body temperature is relatively constant; it can, however, through the inﬂuence of a thermoregulatory centre (the hypothalamus) in the ﬂoor of the brain, become essentially poikilothermous. Under such inﬂuence, its body temperatures approximate those of the environment.Energy conservationConsidering that hibernation and estivation are devices to avoid such factors as stressful extremes of temperature, lack of water, unavailability of food, or lessened photoperiod, they also must be energy-conservation devices for the animals concerned. Even short periods of torpor can conserve energy. The eﬃciency of this energy-conservation system can be demonstrated by comparing the smallest bird, the hummingbird, which exhibits circadian torpor, with the shrew, the smallest mammal, which remains active throughout a 24-hour period. Oxygen consumption is an indicator of metabolic rate, and at an environmental temperature of 24 °C (75 °F) during the day, an awake but resting hummingbird consumes about 14 millilitres of oxygen per gram per hour. At dusk, the rate drops ﬁrst to a sleeping level and then plunges to a torpid level of about 0.8 millilitre of oxygen per gram per hour. Just before daybreak, the bird awakens for another activity period. The hummingbird has the highest metabolic rate and the greatest metabolic range of any vertebrate. The shrew, in contrast, consumes about the same amount of oxygen as the hummingbird does during the day and even increases the amount slightly at night.The hummingbird uses about 10.3 calories (units of heat energy) during each 24-hour period if it sleeps at night without becoming torpid but only 7.6 calories if it becomes torpid. As it wakes from the torpid state, its temperature increases about 1 °C (2 °F) per minute to a maximum; the entire process takes less than 30 minutes and sometimes as little as 10 minutes. The energy required to warm the tissues of the hummingbird is relatively small; a hummingbird that weighs four grams expends only 0.114 calorie to warm its body from 10 to 40 °C (50 to 104 °F). This is only / of the total 24-hour expenditure of energy of a hummingbird in nature.The behaviour of the hummingbird can be contrasted to that of a larger bird, such as the poorwill, which is a nocturnal, insect-catching bird. During an average 24-hour day, the poorwill has brief periods of activity at dusk and just before dawn, the total of which is scarcely more than an hour. The temperature of the poorwill during these periods of activity, which are correlated with the bird’s feeding habits, is between 40.5 and 43.1 °C (104.9 and 109.6 °F). Between periods of activity, the bird rests quietly, and its body temperature drops 1 to 3 °C (2 to 5 °F).During periods when a supply of ﬂying insects is not available, the bird hibernates in depressions in rocks or other suitably protected places to whichhibernates in depressions in rocks or other suitably protected places, to which it returns each year. When hibernating, the bird’s temperature is frequently within 1 °C (2 °F) of that of the environment; as a result, the energy saved is great. A poorwill whose body temperature is 5 °C (41 °F) has a metabolic rate only 3 percent of its metabolic rate at normal body temperature. Because the poorwill is a larger bird than a hummingbird, it may take more than an hour for it to emerge from hibernation.Types of hibernation in mammalsIt takes longer for larger animals than for smaller ones to go into hibernation because heat must radiate from the body before the temperature can be lowered. Thus, it would require a considerable amount of time for large birds or mammals to go into and emerge from hibernation each day, as do bats and hummingbirds. A 200-kilogram (440-pound) bear, for example, would need 5,100 calories to warm from 10 to 37 °C (50 to 99 °F). Unlike the hummingbird, which uses only / of its total daily energy expenditure to emerge from hibernation, the amount expended by a bear would be equivalent to its full 24- hour energy budget. Even if there were enough time in 24 hours for a large animal to enter into and emerge from dormancy, therefore, it would be metabolically extravagant, thus defeating a purpose of hibernation.Actually, the most common misapplication of the term hibernation is in relation to the bear, which is not a true hibernator. Its body temperature, which normally averages 38 °C (100 °F), drops during its winter lethargy to about 34 °C (93 °F), seldom getting below 31.2 °C (88.2 °F). Hence, a bear’s temperature during the winter does not approximate that of the environment.This is indicative of winter rest rather than true hibernation. During this inactive period, the bear sleeps but is, nonetheless, warm and capable of activity when stimulated, unlike a true hibernator. Moreover, it is also during this period when females give birth to cubs that suckle and are maintained bymaternal warmth until they emerge from the den in the spring. This behaviour is in contrast with that of the Arctic ground squirrel, whose normal temperature is the same as that of the bear but whose temperature during hibernation drops to near freezing and, in some cases, to a degree or two below 0 °C (32 °F).Although certain mammals are said to hibernate, they do not necessarily enter a state of deep hibernation during winter. Instead, for weeks at a time they may be inactive and lethargic in behaviour, with a slightly depressed body temperature. The chipmunk (Eutamias) is an example of what has been termed a shallow hibernator, as are bears and raccoons. Superﬁcial hibernation, apparently a compromise between the minimum energy requirements of a deep hibernator and the high energy expended by an animal that remains active during the winter, saves energy without the stress of hibernation. The animal can thus conserve food, while still being able to escape from predators and such dangers as ﬂooding of its burrow. The main energy source during the winter in this shallow hibernation state is food stored in the winter nest. There are instances, however, of shallow hibernators, such as the chipmunk, that enter a state of deep hibernation, particularly if without food.True mammalian hibernationOmitting the thermally unstable mammals, the true mammalian hibernators are those whose lowered body temperatures approximate that of the environment and those who require extensive and complex physiological changes to turn from a warm-blooded animal into an essentially cold-blooded one for an appreciable length of time. Only three orders of placental mammals display such behaviour: the Erinaceomorpha, as exempliﬁed by the hedgehog; the Chiroptera, the bats; and the Rodentia, including the marmot, hamster, dormouse, hazel mouse, and ground squirrel.A typical mammalian hibernator, such as the Arctic ground squirrel, ﬁnds a protected environmental niche—in this case, a burrow beneath the surface— and builds a nest of grass, hair, and other materials to provide still further insulation. The usual hibernating position is one of being curled up in a ball with the extremities tucked tightly against the body so there is a minimal surface-to-volume ratio. After the temperature of the animal has dropped near that of the ambient temperature, it appears to be dead: its respiration is imperceptible, about three irregular breaths per minute; it does not react to outside stimuli in an observable fashion; nor does it react to being handled and uncurled, although such handling will trigger wakening mechanisms.The internal organs, such as the digestive tract and the endocrine glands, are almost totally inactive. Because the process of hibernation necessitates the mobilization of all body resources, it places great demands on the tissues, all of which are directed toward the problem of maintaining the animal’s metabolism at the minimal level necessary for life during the hibernating period. This means that all activity not immediately germane to the process of living at the lowest possible metabolic level ceases. Even bones and teeth deteriorate during hibernation. The hibernator apparently is balanced on a very narrow line between the maintenance of life at a level that makes recovery from hibernation possible and a reduction of metabolism to a level that will lead to death. Evidence obtained from tissues indicates that the process of hibernation is a precarious method of survival at best and one from which many animals do not awaken. As a mechanism of species survival, hibernation seems effective; for the survival of the individual, however, it is an uncertain and dangerous process.The hibernator does not remain in a continuous state of hibernation from the time it enters in the fall until it emerges in the spring. Hibernating Arctic ground squirrels, for example, awaken at intervals of every three weeks or less. During this time the animals may move about and sometimes emerge from the burrow. These periods of arousal are more frequent at the beginning and end of a hibernation period than in mid-hibernation; and the lower the temperature at which an animal hibernates, the fewer the awakenings.During the period of hibernation about 40 percent of the total body weight is lost, an average of about 0.2–0.3 percent per day. One period of arousal and wakefulness consumes more heat and energy than many days in hibernation. About 90 percent of the total heat production and weight loss during hibernation takes place during the arousal periods; only 10 percent is required to maintain the animal in hibernation. Thus, in the case of an unusually long or hard winter, the animal may be called upon to use all of its available energy sources in periodic arousals; it then enters one ﬁnal hibernation period from which it does not awaken. Animals that store food in the nest have a chance to renew their energy requirements by eating when they awaken periodically.Entrance into hibernationHibernating mammals can be divided into four major groups according to the way they enter hibernation. One group is exempliﬁed by the golden hamster; it waits a variable time of from one to three months in the cold and then enters hibernation in one major temperature reduction. This is accomplished when the biochemical and physiological preparations have been suﬃcient to lower the animal to a level at which it is receptive to the hibernating stimulus, which causes the abandonment of the temperature differential between ambient and body temperatures.A second group, of which the pocket mouse (Perognathus) is an example, prepares for hibernation relatively rapidly, waiting only a few days before becoming torpid in one major temperature decline. The third group, which constitutes most of the mammalian hibernators, includes ground squirrels and marmots. These animals wait only a few days before entering hibernation and then go through a series of steps of torpor and arousal, each one at successively lower body temperatures, until the level dictated by the stage of preparation for hibernation is reached.The fourth group, which includes most of the bats, becomes inactive in the poikilothermous manner; that is, the body temperature follows the ambient temperature. Even though the bat seems ready to hibernate at any season, survival during hibernation depends upon more adequate preparation than is necessary for the transitory periods of torpor. Bats not only exhibit true hibernation during the winter but also have natural periods of hypothermia (subnormal temperature), which are unrelated to hibernation, during the remainder of the year.The woodchuck, the dormouse, and the California ground squirrel enter hibernation in successive stages, with a complete or nearly complete awakening between each one. In the woodchuck, an initial decline in temperature is followed by an arousal. During the second decline there is a lower and more pronounced fall in body temperature, followed by a less pronounced rise. This process continues until the body temperature is essentially the same as that of the environment.Physiological changes during mammalian hibernationHeart rate and circulationThe body temperature of a hibernating mammal is affected by changes in respiration, heart rate, and oxygen consumption; all are apparently mediated by a part of the nervous system. The heart rate decreases prior to a decline in body temperature. In the woodchuck, the rate may drop from 153 to 68heartbeats per minute within 30 minutes. In the California ground squirrel, the heart may beat as slowly as once a minute at 5 °C (41 °F). In contrast, the hearts of non-hibernators generally will not beat at all at temperatures below 10–20 °C (50–70 °F).As an Arctic ground squirrel prepares for hibernation, its heart rate and its blood pressure decrease. Both may be detected before a decrease in body temperature can be noted. When the animal enters hibernation, temperatures of both the heart and abdominal regions are identical, indicating an even blood ﬂow between the anterior (front) and posterior (rear) parts of the body. As the body temperature drops, the resistance to blood ﬂow in the peripheral parts of the circulatory system increases because of the increased viscosity (resistance to ﬂow) of the chilled blood and the constriction of the distal arterioles (small arteries) of the body. This peripheral resistance maintains blood pressure at relatively high levels in the deeply hibernating squirrel, even when the heart beats only three or four times a minute.Neural changesThe nervous system of hibernators also is acclimated; certain speciﬁc structures and pathways are seemingly maintained to regulate and coordinate metabolism as temperatures drop. This adaptation of the nervous system enables changes in the environment to be perceived, even when the animal is torpid. In the Arctic ground squirrel, measurements of the general electrical activity of the brain indicate a 90 percent reduction when the animal is in hibernation, at which time brain temperatures approximate 6 °C (43 °F). During hibernation, both the peripheral nervous system (all the nerves outsidethe brain and spinal cord, which constitute the central nervous system) and the spinal cord have an increased sensitivity to certain stimuli; in addition, the areas of the brain that regulate temperature as well as cardiac (heart) and respiratory function remain active at ambient temperatures, below which the mammalian nervous system normally ceases to function.Changes in the circulatory system involving constriction (narrowing) of posterior vessels and the favouring of anterior circulation allow the brain temperature of hibernators to remain a few degrees warmer than the environmental level. This enables the temperature of the brain to remain constant despite ﬂuctuations in the temperature of the skin.Endocrine activityThe male sex hormone testosterone stimulates reproductive activity. The golden hamster will not hibernate if injected with more than ﬁve milligrams of a hormonal preparation. Hibernation is also prevented if the animal is fed or injected with thyroid hormones or thyroid-stimulating extracts. The latter would seem to implicate the thyroid as another endocrine gland that plays an important role in hibernation. There is, in fact, a seasonal progression and regression of thyroid activity in hibernators; maximal activity occurs in the spring and minimal activity in the fall. And because hibernation does not take place in the absence of the adrenal glands, it appears that a minimal adrenal activity is also necessary for hiberation and survival.The importance of timing in the annual rhythm of activity and dormancy can be demonstrated: when hibernators are exposed to cold temperatures in spring and summer, they react as do all homoiotherms by increasing their thyroid activity and metabolic rate to maintain normal body temperature. But if they are exposed to cold temperatures in the fall, the thyroid activity and metabolic rate of hibernators are lowered. In some species, a combination of decreased food and lower ambient temperature is required to reduce activity of the thyroid gland and to produce hibernation, although cold alone is suﬃcient in ground squirrels and the dormouse.Although hibernation does not take place during periods of gonadal activity or Although hibernation does not take place during periods of gonadal activity or stimulated thyroid activity, it can occur during increased activity of the pituitary gland. This would suggest that there is a dissociation of cellular growth and hormone synthesis that is normally controlled by hormone secretion of the pituitary and its target organs. Thus, the triggering mechanism for the resumption of normal endocrine activity apparently resides elsewhere than in the pituitary. The function of the hypothalamic region of the brain in regulating appetite, fat deposition, water intake, and diuresis (increased excretion of urine), as well as in the control of temperature and sleep, would appear to make it a key area in directing life processes of the hibernator. Furthermore, the fact that the hypothalamus regulates the pituitary and other endocrine glands not only supports this thesis but also indicates that this area of the brain is the prime, or master, regulator of the entire hibernation process.Reproductive cyclesThe Arctic ground squirrel may spend more than half its life in hibernation. It thus must be able to breed, rear young, maintain its home burrow, and prepare for the period of hibernation during an activity period of less than six months. This requires considerable adaptation of both metabolic and behavioral patterns. Prior to entering hibernation in late September or early October, there is a renewal of sexual activity in the testes of males, and, throughout the period of hibernation, they continue to grow. On the Arctic slope in early May, the male ground squirrel emerges from its burrow. As it utilizes the remaining fat and eats the stores of seeds and other food still in the nest, the male reaches a period of reproductive readiness. Mating takes place in the middle of May, and the young are born in the middle of June, after a gestation period of about 25 days. By the middle of July the young are above ground and eating the green Arctic vegetation, which they continue to eat until the onset of hibernation. By October, both the young of the year and the adults from the previous year weigh nearly 1,000 grams (2.2 pounds).In the bat, the reproductive cycle is interrupted by hibernation. Gonadal activity in the male reaches its maximum in the fall, when copulation with the female occurs. The animals then hibernate, and the production of sperm in the male ceases. The sperm deposited in the female are stored in her reproductive tract throughout the period of hibernation; fertilization occurs the next spring, when the eggs are ovulated (released from the ovaries) within a few days after awakening from hibernation.The only exception to the general hibernation–reproduction pattern of bats is the vespertilionid bat (Miniopterus), in which there is no delayed ovulation and fertilization. In this species the eggs are ovulated soon after copulation, in the fall, and fertilized immediately. During the ensuing period of hibernation embryonic development is initiated and slowed, but it does not actually cease. The young are born in the early summer, soon after hibernation ends. The introduction of hibernation during pregnancy makes the gestation period several months longer than in non-hibernating tropical members of the same genus.Cyclical reproductive activity has thus become adapted to the shortened activity season available to the hibernator. But although the annual sequence of reproductive events is known, the external stimuli that regulate the reproductive cycles of bats and other hibernators are not known. More knowledge is needed concerning the endocrine and nervous mechanisms that presumably regulate reproductive processes internally. It has been suggested that the pituitary–gonadal relationship inﬂuences the hibernating cycles aswell as the reproductive cycle, hence both the latter and homoiothermism are controlled by a common mechanism. Such a suggestion is attractive in that the mechanism solves the regulation problems, but more needs to be known of the way in which hibernation directly or indirectly modiﬁes the action of endocrine and neural mechanisms that direct the reproductive cycle.Protection from disease and radiationHibernating organisms have a certain degree of resistance to infectious diseases that appears to be attributable to at least three factors, all of which are related to temperature. One is the fact that the lowered temperature of the host and the commensurate slowing of its metabolic processes prevent the multiplication of parasites to a greater extent than they affect the host’s defensive mechanisms. Second, lower temperatures are more harmful to the development of a disease organism than to the host, as has been shown with the parasite Trichinella spiralis. In bats hibernating at 5 °C (41 °F), only larvae have been recovered from the intestines; but mature adult worms have been recovered from the intestines of bats kept at 35 °C (95 °F). The third factor is that the inﬂuence of low temperature on the chemical composition of the host tissues may also affect infectious organisms.Hibernation also seems to protect animals from radiation. When ground squirrels are irradiated with radioactive cobalt while hibernating, they are found to be more resistant to the effects of the radiation than are squirrels irradiated while warm and active. This resistance, which is apparent over a wide range of doses, suggests that protective mechanisms function in the hibernating animal. In both hibernating and non-hibernating animals, repair processes within cells occur the ﬁrst day after irradiation; however, when the metabolic requirements of cells are small, as in hibernation, the injured cells seem to be more capable of repair, and survival is greater. The large metabolic requirements imposed on injured cells of warm and active animals appear to render them incapable of an adequate repair response.Awakening from hibernationThe process of awakening in the Arctic ground squirrel takes about three hours. There is a rapid rise in heartbeat and a decrease in peripheral circulatory resistance; the area around the head and heart warms more rapidly than the posterior part of the animal. This differential vasodilatation (widening of the blood vessels) in the anterior part of the body is a unique and vital part of the awakening process. The concentration of active circulation in this region results in a high blood pressure and an eﬃcient and rapid warming. If a drug is administered during awakening that causes vasodilatation throughout the body, there is a marked drop in blood pressure even though the heart may almost double its rate; thus, the heart cannot maintain a high blood pressure at this time if all blood vessels are dilated. Later during the arousal process, after the anterior part of the body has been warmed, the posterior part of the animal warms rapidly.Despite the deterioration of glands and tissues and the drastic reduction of all metabolic activity during hibernation, within 24 hours after arousal, all the squirrel’s physiological processes are essentially normal. This rapid repair and recovery mechanism is one that requires further study.