BODY TEMPERATURE, OXYGEN CONSUMPTION, EVAPORATIVE WATER LOSS, AND HEART RATE IN THE POOR-WILL

By George A. Bartholomew, Jack W. Hudson, and Thomas R. Howell

The physiology of the Poor-will (*Phalaenoptilus nuttallii*) is of unusual interest. Not only is it one of the very few birds which can undergo long periods of dormancy comparable in most respects to mammalian hibernation, but over much of its summer range it is exposed to severe conditions of heat because of its habit of spending the daylight hours, even in the desert, sitting quietly in the open.

During the past year we have had the opportunity to make a series of observations on two captive, adult Poor-wills, one (*P. n. hueyi*) captured by Mr. Donald Schroeder in the Coachella Valley, Riverside County, California, and the other (*P. n. californicus*) found in a torpid condition in Eagle Rock, Los Angeles County, California, by Mrs. Gerald Massey. Both birds were maintained for many months in captivity and were fed on a diet of meal worms (*Tenebrio* larvae) and canned cat food.

The limited information on the physiology of Poor-wills has previously been summarized (Bartholomew, Howell, and Cade, 1957; Howell and Bartholomew, 1959) and need not be reviewed here.

METHODS

Oxygen consumption and evaporative water loss were measured simultaneously. The post-absorptive bird was placed in a wire mesh cylinder in which it could move about freely. The cylinder was put inside a 500 cc. respirometer chamber. Excreta produced during the period of measurement fell through the floor of the cylinder and sank beneath a 2 cm. layer of mineral oil in the bottom of the chamber. This arrangement minimized urinary and fecal contributions to measurements of evaporative water loss. The respirometer chamber was equipped with a thermocouple and ports for the introduction and removal of the air. Air was dried by passage through small mesh anhydrous calcium chloride and was metered through the chamber at a rate of 400 cc. per minute. The air leaving the respirometer was passed through two drying tubes of calcium chloride of known weight and delivered to a Beckman recording paramagnetic oxygen analyzer which gave a continuous record of oxygen consumption. Evaporative water loss was measured by weighing the drying tubes at one hour intervals. Ambient temperature was controlled to within 1°C. by placing the respirometer chamber in a constant temperature box with externally adjustable controls. Body temperature and ambient temperatures were measured with copper-constantan thermocouples connected to a recording potentiometer. Continuous records of body temperature were obtained by inserting a vinyl-sheathed thermocouple into the cloaca to a depth of about 2 cm. and securing it in place by attaching its leads to the bird's rectrices with surgical clips. This arrangement did not seem to disturb the birds and during periods of measurement they remained quiet and apparently were undisturbed by the thermocouple leads. Esophageal temperatures were taken manually. Heart rates were measured on a Grass Polygraph from electrocardiographic leads clipped to gold-plated safety pins attached through the skin on the right shoulder and right and left thighs. The occurrence of shivering was determined from the electrocardiograms.

RESULTS

Body temperature.—Captive, normally alert Poor-wills in good nutritional state (approximately 40 grams in weight) may have body temperatures as low as 35°C. and as high as 43.5°C. The body temperature of an active bird may increase when the ambient temperature increases above 35°C., whereas the body temperature of a non-torpid bird remains essentially constant when the ambient temperature is anywhere between 35° and 0°C. (fig. 1). When the body temperature reaches about 41.5°C. in conjunction

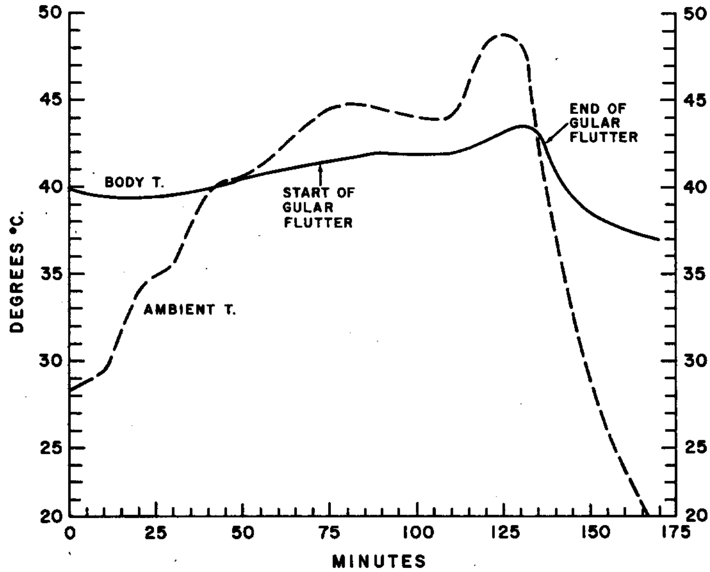

Fig. 1. The effects of changes in ambient temperature on body temperature in the Poor-will (*Phalaenoptilus nuttallii*).

with increasing ambient temperature, the bird intensifies its evaporative cooling by the initiation of vigorous gular flutter. In this way, the Poor-will can maintain a stable body temperature of about 42°C. in an ambient temperature of 44° to 45°C., at a relative humidity of 10 to 20 per cent. Even with the ambient temperature above 48°C., the Poor-will can hold its body temperature well within the range which most birds can tolerate.

Oxygen consumption.—The relation between oxygen consumption and ambient temperature is quite regular (fig. 2). When the ambient temperature falls below 35°C. (the lower critical temperature), the oxygen consumption increases linearly with decreasing ambient temperature and thus a constant body temperature is maintained. The metabolic rate at 5°C. is approximately three and a half times that at 35°C. The zone of minimum metabolism (thermal neutrality) extends from air temperatures of 35°C. to at least 44°C., and we did not find a point (upper critical temperature) at which the metabolism increases in the process of dissipating heat. The mean metabolic rate of the Poor-will in thermal neutrality is 0.8 cc. 0_2/gm./hr., which is only about one-third the value predicted on the basis of body size (see Discussion). When extrapolated, a line relating values for oxygen consumption to ambient temperatures below thermal neutrality intercepts the abcissa at about 42°C. (fig. 2). This is several degrees above the usual level of body temperature for Poor-wills in the absence of heat stress. Thus, in this species, the relation of metabolic heat production to ambient temperature does not conform as closely with the biological applications of Newton's law of cooling as it does in the instances presented by Scholander *et al.* (1950).

Evaporative water loss.—When the ratio of evaporative water loss to oxygen consumption is compared (table 1), it can be seen that at 25°C. 1.5 mg. of water is lost

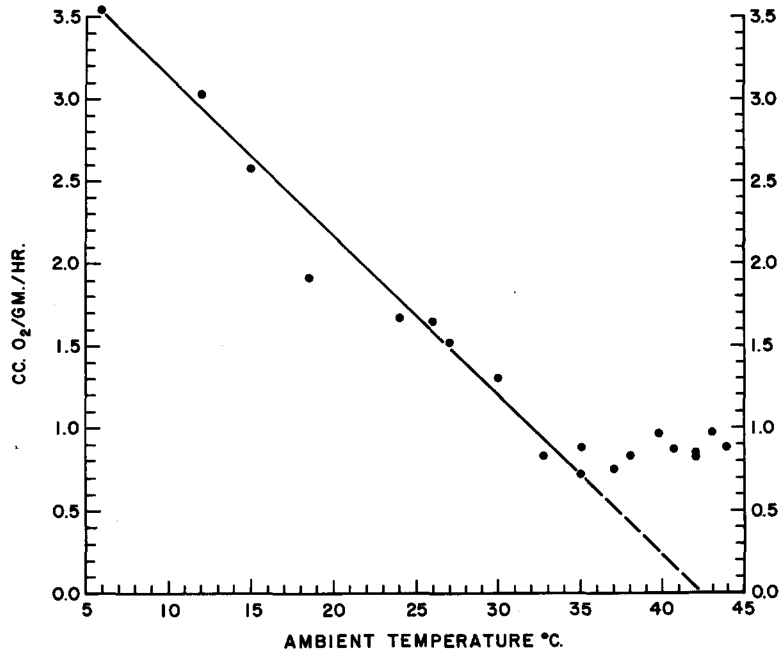

Fig. 2. The relation of oxygen consumption to ambient temperature. Each point represents the minimum metabolic rate maintained for at least 30 minutes at a given temperature. All values have been corrected to 0°C. and 760 mg. Hg.

per cc. of oxygen consumed. Above 39°C. the ratio increases rapidly and reaches 14.4 mg. H_2O/cc. O_2 at 44°C. As might be expected, the increase is most rapid in the range of ambient temperatures in which the birds ordinarily employ gular flutter.

TABLE 1

EVAPORATIVE WATER LOSS

Temperature		$\frac{\text{mg. } H_2O \text{ evaporated}}{\text{cc. } O_2 \text{ consumed}}$
Ambient	Body	
25.4	......	1.55
33.4	......	2.82
35.0	40.2	2.17
35.0	39.2	3.70
38.0	......	3.60
39.7	40.6	2.97
42.0	40.6	6.84
42.0	40.4	10.88
43.0	......	11.89
44.0	41.6	14.40

Heart rate during normal activity.—The extremely placid behavior of Poor-wills in captivity made it possible to record electrocardiograms (EKG's) easily. At ambient temperatures below the lower critical temperature, the electrical activity associated with invisible shivering obscured the electrical manifestations of heart beat. However, we were able to obtain clear EKG's even at low ambient temperatures by the following procedure. The ambient temperature was held at a given level for at least half an hour so that the bird could reach a condition of equilibrium. The ambient temperature was then raised about 1°C. This increase was almost invariably followed by a marked diminution in shivering which permitted easy recording of the EKG's. Like metabolic rate, heart rate is clearly influenced by ambient temperature and shows a minimum level which coincides with the thermal neutral zone (fig. 3). At ambient temperatures below 15°C. heart rate approximates 500 beats per minute, whereas at 35°C. the rate is be-

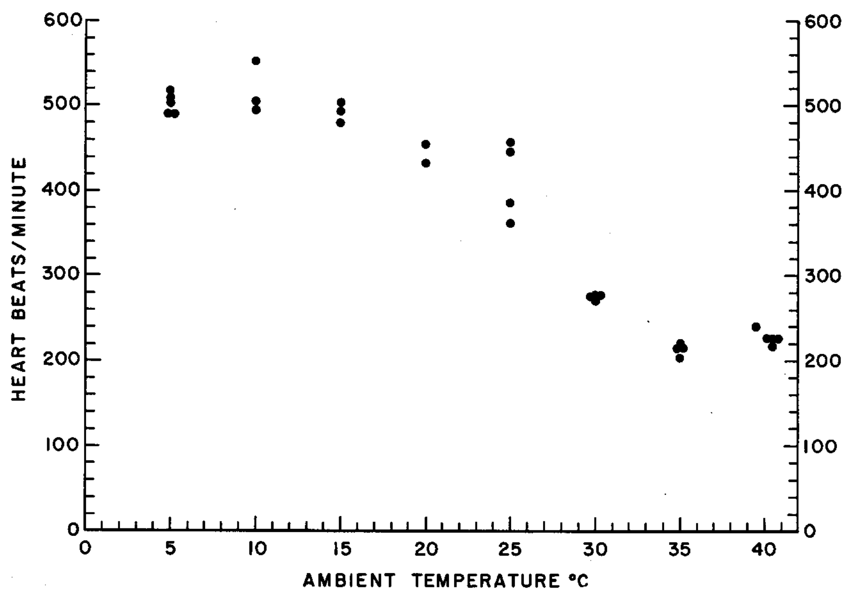

Fig. 3. The relation of heart rate to ambient temperature. Each point represents the minimal rate observed at a given temperature after at least one-half hour of exposure to that temperature.

tween 200 and 220. The decrease in heart rate between ambient temperatures of 15° and 35°C. is linear and has approximately the same slope as the decrease in oxygen consumption over this range of temperatures. Heart rate increases slightly between 35° and 40°C.

Heart rate and torpidity.—During entry into torpor, heart rate declines steadily and somewhat more rapidly than does the body temperature (figs. 4, 5). The rate of heart beat during torpor depends on body temperature and this in turn depends on ambient temperature. As shown in figure 5, when body temperature during torpor rises passively in response to an increase in ambient temperature, the heart rate shows a parallel increase. When active arousal is initiated, as indicated by the onset of shivering, both body temperature and heart rate increase with about the same slope. Unfortunately we were unable to obtain a complete record of the increase in heart rate during arousal because the intense shivering obscured the EKG's completely.

Shivering during torpor.—Shivering is one of the principal methods of heat production of homeotherms exposed to low ambient temperature. Incidental to the recording of EKG's we obtained considerable information on the occurrence of shivering during episodes of torpidity. Some electrical manifestations of shivering were perceptible at all ambient temperatures below thermal neutrality, and the lower the ambient temperature the more intense the shivering. During entry into torpor, shivering is much weaker than

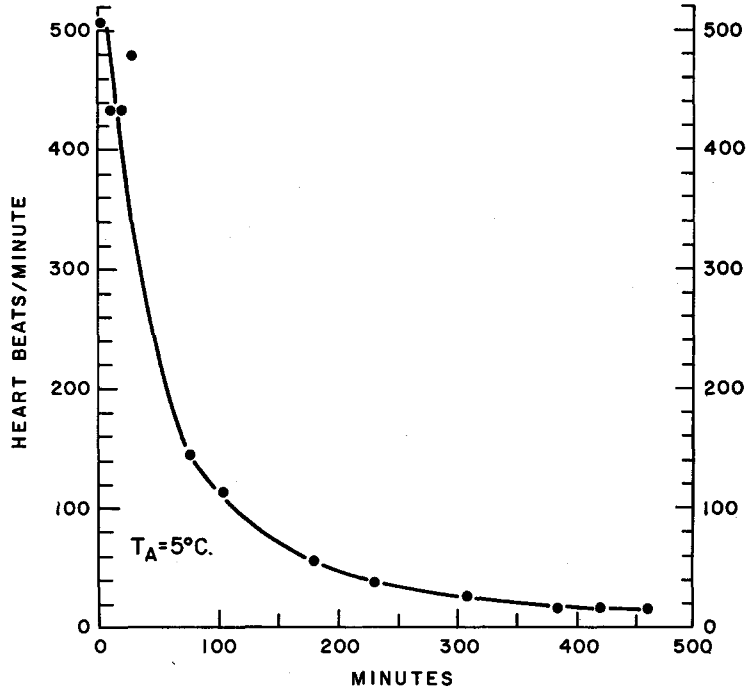

Fig. 4. The decline in heart rate during entry into torpor. Ambient temperature (T_A) = 5°C.

when a normally high body temperature is being maintained at the same ambient temperature. Nevertheless, slight shivering is apparent during the entire entry into torpor. Once the body temperature is stabilized at or near the prevailing ambient temperature, almost no indications of shivering were apparent on the EKG record, although an

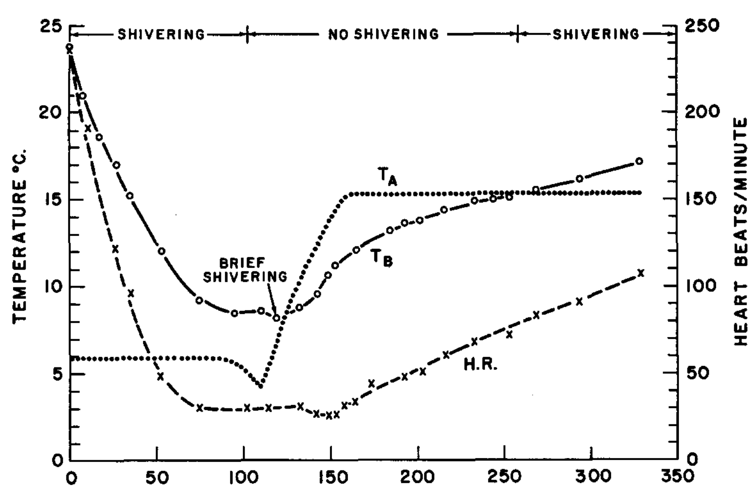

Fig. 5. The relations of body temperature (T_B), heart rate, and shivering to ambient temperature (T_A) during an episode of torpor.

abrupt decrease in ambient temperature evoked shivering. When the body temperature was increased passively by an elevation of the ambient temperature, we observed no electrical indications of shivering until the body temperature reached 15°C., at which point slight shivering was apparent. Once active arousal was initiated, shivering was very powerful (fig. 5) and clearly visible externally.

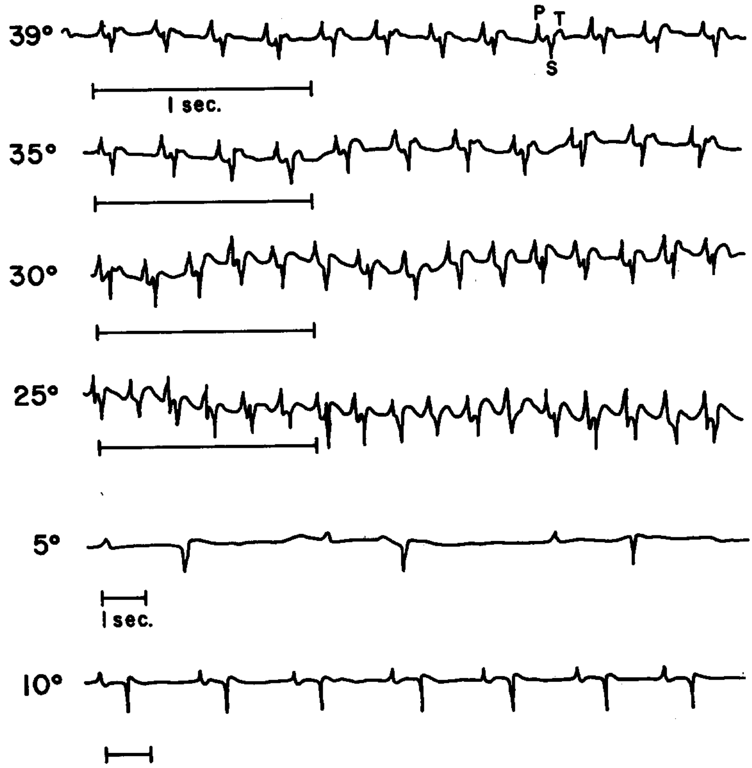

Fig. 6. Representative electrocardiograms at various ambient temperatures. The records at 5° and 10°C. are from torpid birds with body temperatures within 1°C. of ambient temperature. The other records are from alert birds with normal body temperatures.

Pattern of electrocardiograms.—There are no published records of electrocardiograms from birds of the order Caprimulgiformes. However, by analogy with the normal EKG of the domestic chicken (Sturkie, 1954), we interpret our data (fig. 6) as follows: There is a marked P wave. The S–T interval is absent and the S wave is negative. Aside from time relationships, notably a prolongation of the P–S interval during hibernation, there are no major qualitative differences between the EKG's of an alert Poor-will with normally high body temperature and of a torpid bird with a body temperature of 5° or 10°C.

DISCUSSION

The ability of the Poor-will to tolerate exposure to intense heat for many hours is dependent on a complex of physiological, morphological, and behavioral attributes. These include a remarkably low basal metabolism, a mechanism for evaporative cooling which minimizes metabolic heat production, and lack of movement during exposure to heat.

Metabolic rate.—Scholander (1955:24) has pointed out that the basal metabolic rate is not adapted to climatic conditions and that "heat dissipation is the main avenue for climatic thermal adaptation." There seems little doubt that this generalization applies cogently to arctic species, for their primary thermoregulatory problem is heat retention and this can be facilitated by effective insulation. However, the principal thermoregulatory problem of birds and mammals living in hot climates is the facilitation of loss of heat from the body to the environment. Part of this heat that must be lost from the body comes from metabolism. Thus, a low metabolic rate should be of adaptive advantage to homeotherms exposed to high environmental temperatures or intense solar radiation because it would reduce the metabolic contribution to the total heat load and thus minimize the problem of thermoregulation.

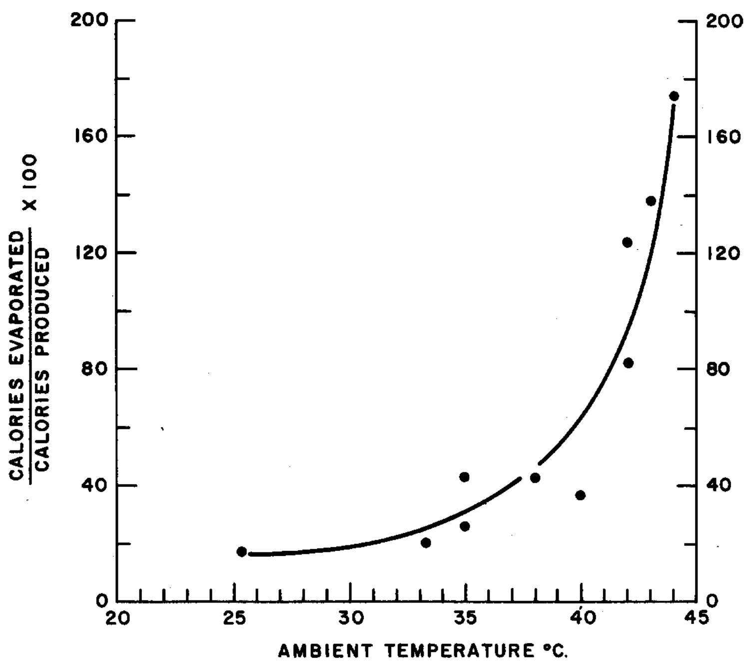

Fig. 7. The relation of evaporative cooling to metabolic heat production at various ambient temperatures. The calculations assume that the consumption of one cc. of O_2 yields 4.8 calories and that the evaporation of one mg. of water requires 0.58 calories.

We have rearranged Brody's (1945) equation relating avian metabolism to body weight, Cal./day $= 89 \times$ kg.$^{0.64}$, to more convenient units. Assuming that 4.8 calories are produced for each cc. of oxygen consumed, Brody's equation may be written thus: cc. O_2/gm./hr. $= 9.3$ gm. $^{-0.36}$. Using this equation, the predicted metabolism of a 40 gram bird would be 2.5 cc. O_2/gm./hr. The metabolic rate of the Poor-will at thermal neutrality (0.8 cc. O_2/gm./hr.) is only one-third of the predicted value. Consequently, the Poor-will's physiological adaptation to high environmental temperature is at least two-fold. First, it has a much reduced basal metabolic rate, and second, its zone of thermal neutrality extends to an unusually high temperature. This combination allows the Poor-will to sit quietly for many hours in a hot environment with a minimum of dependence on evaporative cooling.

In the Poor-will, the rate of increase of metabolism with decreasing ambient temperature is similar to that of the Cardinal (*Richmondena cardinalis*) and the Evening Grosbeak (*Hesperiphona vespertina*) both of which are adapted to cold climates (Dawson, 1958; Dawson and Tordoff, 1959). Thus the Poor-will's metabolic response to temperatures below its lower critical temperature is as effective as that of species adapted to much colder climates. However, at any given ambient temperature below the lower critical temperature, the extent of increase in metabolic rate above the basal level is much greater in the Poor-will than in the other two species. Thus, the relative energy cost to the Poor-will of high body temperature maintenance at low ambient temperatures is higher than that in more cold-adapted forms.

Evaporative cooling.—In other adult birds for which data are available, panting dissipates less than half of the metabolic heat (Dawson, 1958). The Poor-will, like other caprimulgids, has a remarkably large mouth with extensive and highly vascular inner surfaces from which evaporation can occur. When the gular area is fluttered vigorously, an activity requiring very little energy expenditure, evaporation is increased at a remarkably low metabolic cost. Gular flutter appears to be much more efficient than the typical pattern of panting shown by most small birds. For example, at high ambient temperatures the Poor-will can dissipate by evaporation a quantity of heat equal to that which it produces by metabolism, and in addition it can unload much of the heat which it gains from the environment (fig. 7). In the Poor-will the ratio of heat dissipated by evaporation to heat produced by metabolism at an ambient temperature of 40°C. is 1.8 times as great as that which Dawson (1958) found in the Cardinal. However, the absolute amount of water evaporated at this temperature is slightly less in the Poor-will than in the Cardinal.

Heart rate.—The dependence of the heart rate on ambient temperature in the Poor-will emphasizes the point made by Odum (1945) that valid comparisons of heart rates in birds cannot be made without reference to the thermal neutral zones of the species being compared. The heart rate of the Poor-will in the thermal neutral zone is about 200 beats per minute, which is only half that of passerine birds of comparable weight (Odum, *op. cit.*). This situation is consonant with the low metabolic rate of the Poor-will in thermal neutrality.

The heart rate and the shivering during episodes of torpor have patterns similar to those which have been reported for various species of mammalian hibernators. It is of interest that the rate of decline in body temperature of the Poor-will during entry into torpor is partly controlled by shivering and that decreases in body temperature during deep torpor evoke shivering. This suggests that in the Poor-will, as in mammalian hibernators, some thermoregulatory activity continues during hibernation.

SUMMARY

Body temperature in captive, normally alert Poor-wills may vary from 35° to 43.5°C. At ambient temperatures above 35°C., body temperature rises conspicuously. The lower critical temperature is at 35°C. and thermal neutrality extends at least to 44°C. The basal metabolic rate is 0.8 cc. 0_2/gm./hr., which is one-third the value predicted for a bird weighing about 40 grams. Evaporative water loss increases with increasing ambient temperature above 25°C., and by vigorous gular flutter the bird can dissipate a quantity of heat equal to more than 160 per cent of its metabolic heat production —the greatest efficiency of evaporative cooling so far reported in a bird. Heart rate is minimal (200 beats/min.) in the thermal neutral zone and is about half the rate of that

of a passerine of comparable size. Heart rate increases to approximately 500 beats per minute in a non-torpid bird when the ambient temperature drops to 15°C. Heart rate decreases during entry into torpor and varies directly with body temperature during torpor. Decline in body temperature during entry into torpor and during torpor is partly controlled by shivering.

The very low basal metabolic rate of the Poor-will makes possible the tolerance of sustained high environmental temperatures and contributes to the remarkable efficiency of its evaporative cooling. The apparent adaptive nature of its much reduced basal metabolic rate represents a major departure from the situation in most birds and mammals.

LITERATURE CITED

Bartholomew, G. A., Howell, T. R., and Cade, T. J.
1957. Torpidity in the white-throated swift, Anna hummingbird and poor-will. Condor, 59:145–155.

Brody, S.
1945. Bioenergetics and growth (Reinhold Publ. Corp., N.Y.).

Dawson, W. R.
1958. Relation of oxygen consumption and evaporative water loss to temperature in the cardinal. Physiol. Zool., 31:37–48.

Dawson, W. R., and Tordoff, H. B.
1959. Relation of oxygen consumption to temperature in the evening grosbeak. Condor, 61:388–396.

Howell, T. R., and Bartholomew, G. A.
1959. Further experiments on torpidity in the poor-will. Condor, 61:180–185.

Odum, E. P.
1945. The heart rate of small birds. Science, 101:153–154.

Scholander, P. F.
1955. Evolution of climatic adaptation in homeotherms. Evolution, 9:15–26.

Scholander, P. F., Hock, R., Walters, V., Johnson, F., and Irving, L.
1950. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull., 99:237–258.

Sturkie, P. D.
1954. Avian physiology (Comstock Publ. Assocs., Ithaca, N.Y.).

Department of Zoology, University of California, Los Angeles, California, May 29, 1961.