THE CONDOR

VOLUME 59 | MAY-JUNE, 1957 | NUMBER 3

TORPIDITY IN THE WHITE-THROATED SWIFT, ANNA HUMMINGBIRD, AND POOR-WILL

By GEORGE A. BARTHOLOMEW, THOMAS R. HOWELL, and TOM J. CADE

In recent years there has been considerable interest in torpidity and reduced body temperature or hypothermia among birds. The hibernation (Jaeger, 1948, 1949, 1952; Thorburg, 1953; Marshall, 1955) of the Poor-will (*Phalaenoptilus nuttallii*), the nocturnal torpidity (Huxley, Webb, and Best, 1939; Pearson, 1950, 1953) of hummingbirds, and the labile temperatures (Koskimies, 1948) of the European Swift (*Apus* (*Micropus*) *apus*) have shown that constant high temperature is not an invariable rule even among adult birds. The present study provides quantitative data on hypothermia for two species previously investigated, the Poor-will and the Anna Hummingbird (*Calypte anna*), and information on a hitherto unstudied member of the Apodiformes, the White-throated Swift (*Aëronautes saxatalis*).

MATERIALS AND METHODS

We attempted to obtain simultaneous records of body temperatures and metabolic rates under controlled environmental conditions. Temperatures were measured with silver-soldered thermocouples made of 30-gauge copper-constantan duplex wire and were recorded to the nearest tenth of a degree C. on a recording potentiometer. Environmental or ambient temperatures were controlled within one degree C. by an insulated chamber equipped with heating and cooling units, a fan, lights, and an insulated glass port for observation.

Oxygen consumption was used as a measure of metabolic rate. During the experiments, air was metered through a chamber containing the bird and was delivered to a Beckman paramagnetic oxygen analyzer which, in conjunction with a recording potentiometer, provided a continuous record of oxygen consumption. All volumes of oxygen have been corrected to 0°C. and a pressure of 760 mm. Hg.

WHITE-THROATED SWIFT

The White-throated Swift is abundant over western North America and ranges south through México into Guatemala and El Salvador. It is migratory in the northern part of its range and winters from west-central California south at least into México. The usual roosting and nesting sites are crevices in rocky cliffs.

For the present study, 19 swifts were captured at a roosting site in a cliff about two miles southeast of Lompoc, Santa Barbara County, California, on February 26, 1956. The birds were banded and divided into three groups. Eight were placed in the dark at 4 to 5°C. without food, four were placed in the dark at 20 to 22°C. without food, and seven were kept under 12 hours of light and 12 hours of darkness at 20 to 22°C. The latter birds were fed beef heart, *Tenebrio* larvae, water, and powdered multivitamin capsules. The swifts were fed by hand about four times per day during the light period. They soon learned to seize food morsels presented to them and seemed to eat well, but their body weights declined steadily in the week that they were kept. Water administered by pipette, usually alternated with food morsels, was taken readily. The swifts were docile and easy to handle. They rarely attempted to fly but crawled and climbed easily and rapidly. At rest they tended to huddle together at the top of the cage, often crowding in so closely that they overlapped one another like shingles.

Body temperatures before experimentation.—The swifts were captured at sundown and immediately put into a large sack. About five hours later, they were removed and placed in cages in the laboratory at the University of California at Los Angeles. The birds huddled closely together in the sack, and a quick-registering mercury thermometer inserted into the mass of swifts recorded a temperature of 37.3°C. (room temperature about 20°C.). Individual cloacal temperatures at this time ranged from 35.6 (one bird away from the huddled mass) to 41.0°C. (average 38.6°C.).

Weight.—Individual weights taken five hours after capture ranged from 29.0 to 33.5 gm. (average 30.5 gm.). No segregation by sex was possible as there are no external sexual differences in this species.

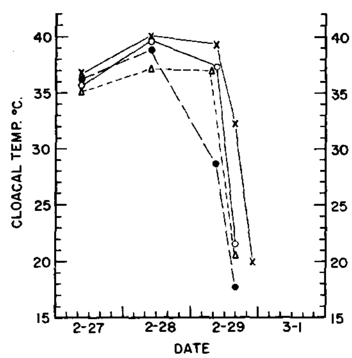

Fig. 1. Cloacal temperatures in unfed White-throated Swifts maintained in the dark at 4–5°C. Experiment was terminated at last readings shown. All four birds subsequently aroused completely.

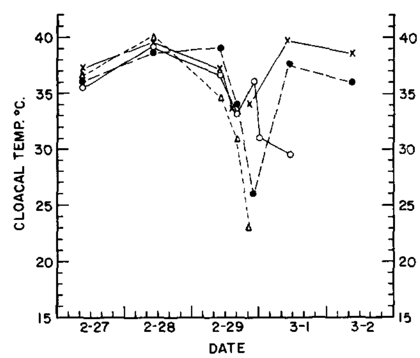

Fig. 2. Cloacal temperatures in unfed White-throated Swifts maintained in the dark at 20–22°C.

In darkness, unfed, at 4 to 5°C.—Eight birds were subjected to these conditions starting at 12 noon on February 27, 18 hours after capture. Three birds died within 45 hours, and a fourth died about 25 hours later. These four birds maintained high body temperatures for at least the first 22 hours, and the one that survived longest had a high temperature at the 45-hour reading. We do not know whether or not the birds experienced prolonged hypothermia before death. The four remaining birds became hypothermic on the third day of the experiment (fig. 1), and all subsequently returned to the active range of body temperature (see section on arousal).

In darkness, unfed, at 20 to 22°C.—The four birds subjected to this treatment maintained high body temperatures for about 48 hours (fig. 2). Six hours later there was a marked drop in body temperature. Subsequently one bird failed to recover, one made a partial recovery, and two returned to normally high body temperatures (fig. 2).

Twelve hour photoperiod, fed, at 20 to 22°C.—Birds kept under these conditions maintained high body temperatures for at least 72 hours (fig. 3), during which time some of them were subjected briefly to ambient temperatures down to 12°C. All seven of the birds in this group showed a steady loss in weight despite our efforts to feed them adequately, and two of them died. By the fifth day after capture, the five surviving birds showed markedly depressed body temperatures (fig. 3), and four readily roused from this hypothermic state. The four that survived were those that had best maintained their body weight. One of these had damaged wing feathers and could not fly, but the others were released a few hours after arousal from hypothermia. All three birds flew off at once, and two that remained in view began catching insects in a normal manner. It therefore seems reasonable to assume that these swifts had recovered fully.

Arousal from hypothermia.—Body temperatures of fed and unfed birds were measured during arousal from hypothermia at both 4 to 5°C. and 20 to 22°C. (fig. 4). No differences were evident in rate of arousal in fed and unfed birds; arousal was as rapid at 4 to 5°C. as at 20 to 22°C. A rise in body temperature of about 0.4°C. per minute was typical. Some birds underwent as many as four cycles of hypothermia and arousal in the course of the experiments.

During hypothermia the birds kept their body plumage fluffed out, and they clung strongly to anything with which their feet were in contact—usually a vertical side of the cage.

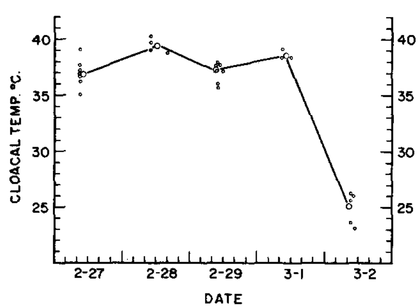

Fig. 3. Cloacal temperatures in fed White-throated Swifts maintained on a 12-hour photoperiod at 20–22°C. The large circles indicate mean temperatures.

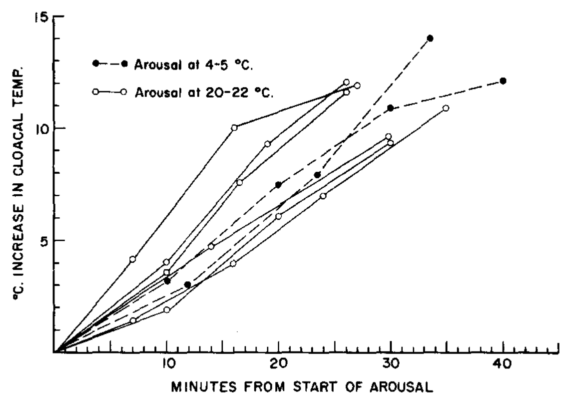

Fig. 4. Increase in cloacal temperature in White-throated Swifts during arousal from torpor. All starting temperatures were between 20 and 26°C.

Behavior of nine different birds during arousal is summarized in table 1. The lowest body temperature from which swifts subsequently returned to normal was 20.0°C., but some birds survived for at least four hours at body temperatures between 15.8 and 20°C. As shown in table 1, swifts were capable of effective, coordinated movement at body temperatures as low as 25.8°C., and at body temperatures of 35°C. their activity appeared to be normal. The lowest body temperature at which spontaneous flight was observed was 36.2°C.

Table 1

Summary of Behavior of Nine Swifts During Arousal at 20–22°C.

Cloacal temperature, °C.	Behavior
15.8	Alive, but completely motionless and unresponsive.
17.7–20.5	Moves wings and feet slightly; no corneal reflex; cannot right, but clings with feet; eyes closed.
22.0–24.0	Elevates wings vertically when touched; crawls slowly; eyes open.
24.0	First visible shivering; still crawls slowly.
25.8–35	Strong shivering, vigorous crawling and climbing; wings fluttered at 31.0°C.
35–41	Alert and normal, able to fly.

It was difficult to obtain satisfactory oxygen consumption readings from the swifts as the birds rarely remained quiet while in the respirometer. However, one bird with a body temperature of 37.9°C. at an environmental temperature of 20°C. remained inactive for several hours and consumed oxygen at an average rate of 5.2 cc./gm./hr.

ANNA HUMMINGBIRD

This species, which is a common resident in most of California, has previously been shown to undergo torpidity (Pearson, 1950). On December 13, 1955, an adult male Anna Hummingbird that had flown into the University Library was captured at 10:30 a.m., not more than two hours after its entry. Its weight was 4.6 gm., its deep esophageal temperature was 41.9°C., and it appeared to be in perfect condition. At 11:30 a.m. the bird was placed in the respirometer and its oxygen consumption was measured for 22

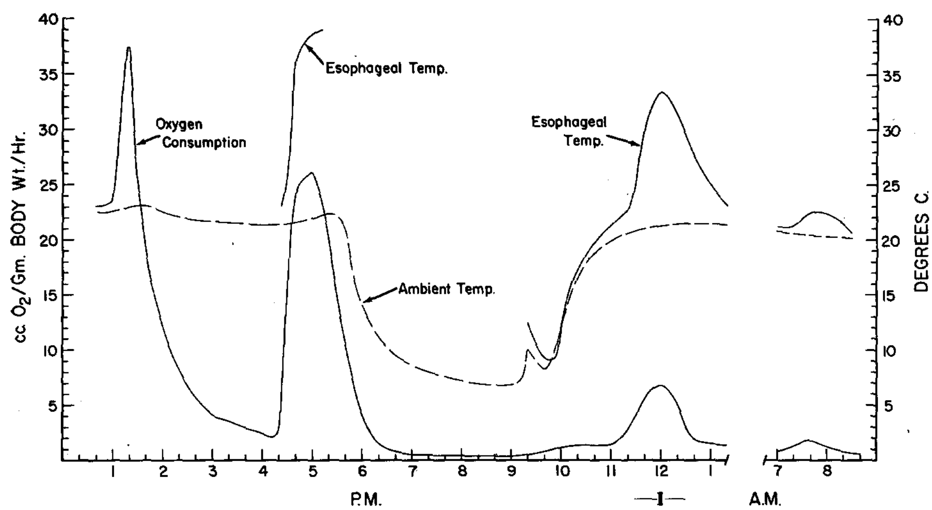

Fig. 5. Oxygen consumption and body temperature in an adult male Anna Hummingbird exposed to varying ambient temperatures.

consecutive hours. For about 13 of these hours, a continuous record of body temperature was obtained from a thermocouple placed 5 to 10 mm. down the bird's esophagus and secured to its culmen. In the course of the experiment, the ambient temperature was varied through a range of 16°C. The bird was not given food or water at any time.

On August 10, 1956, an immature Anna Hummingbird of unknown sex was obtained. It had a broken leg and an injured wing; how long it had been without food is not known, but it weighed only 2.65 gm. at the time of capture. This bird was maintained by feeding it a mixture of water, honey, cane sugar, and gelatin, and its responses to various low ambient temperatures were measured.

The measurements obtained from the adult male hummingbird are summarized in figure 5; those obtained from the immature bird are given in figure 6. The adult male became torpid at an ambient temperature of 21 to 23°C. and also as ambient temperature declined from 23 to 7°C. (fig. 5). The immature bird became torpid at an ambient temperature of 2°C. and also at 23°C. during the night in its cage (body temperature 26°C.).

Entry into torpor was marked by a steady decline in oxygen consumption and body temperature (figs. 5 and 6). As the birds became torpid, they sat quietly with eyes closed, feathers fluffed out, and bill pointed upward at an angle of about 45°. We recorded a body temperature as low as 8.8°C. (ambient temperature 8.2°C.) in the adult bird, and at that time it was completely motionless. When the bird was handled at a body temperature of 12°C., it uttered a few faint "peeps" and spread the rectrices widely, but it slumped to one side and lay motionless when set down. When the immature bird was handled at a body temperature of 15.5°C., it spread its wings and waved them slowly. At a body temperature of 17.4°C. the immature bird was able to right itself, and at 21.9°C. it cheeped and struggled rather feebly when held in the hand. At body temperatures of 35.5°C. both birds appeared normally active—struggling, squeaking, and "buzzing" their wings.

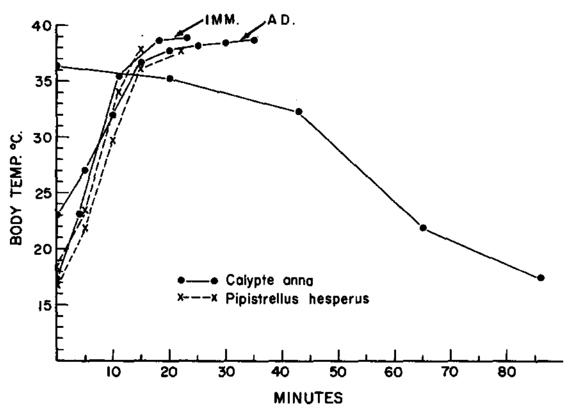

Fig. 6. Rates of arousal from torpor of two Anna Hummingbirds weighing 4.6 and 2.65 gm. and two bats weighing 4.5 and 3.7 gm. The descending curve shows entry into torpor of an immature Anna Hummingbird at an ambient temperature of 2°C.

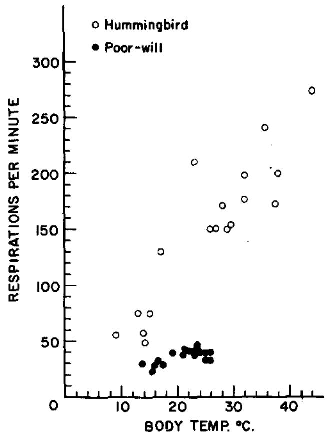

Fig. 7. The relation of body temperature and respiratory rate (excluding periods of apnea) in Anna Hummingbird and Poor-will.

Respiratory rate increased directly with body temperature (fig. 7). At body temperatures below 20°C. respiration tended to be irregular, and at lower body temperatures (9 to 12°C.) periods of cessation of breathing up to five minutes in duration occurred. The maximum respiratory rate of 273 per minute was recorded from an excited bird with a body temperature of 41.9°C. (ambient temperature 22°C.).

Increase in oxygen consumption and body temperature during arousal is strikingly rapid (figs. 5 and 6). The rate of increase in body temperature for the first arousal in each bird was about 1 to 1.5°C. per minute at ambient temperatures of 21 to 23°C. In the adult male, which went through three cycles of torpidity and arousal without food in a 22-hour period, the rate and extent of arousal decreased progressively (fig. 5). Presumably this was due to a progressive decline in the bird's energy reserves. It may be mentioned here that the immature hummingbird consumed one gram of saturated cane sugar solution—almost 38 per cent of its body weight—immediately after arousal from torpor.

We were unable to detect obvious shivering during arousal. Shivering probably occurs but may be obscured by the rapid, deep respiratory movements and the variable quiverings noted in both arousing and fully active hummingbirds.

POOR-WILL

This species, which ranges from central and western North America to central México and which is migratory in the northern part of its range, is the only bird yet known to hibernate under natural conditions (see for example, Jaeger, 1948, 1949, 1954; Brauner, 1952). On November 12, 1955, an adult male Poor-will (*P. n. californicus*) was captured in the Library of the University of California, Los Angeles. According to members of the Library staff, the bird had inhabited the rotunda of the Library at least since November 1, and it had attracted attention by fluttering about in the late afternoons. At the time of capture its weight was 32.0 gm.; as this is less than the weight of any adults recorded by Marshall (1955), it is clear that the bird had not obtained much food. The Poor-will was netted on a high ledge while asleep, and its cloacal temperature within one minute of capture was 39.1°C. These data indicate that the bird, although underweight, was not hiberating.

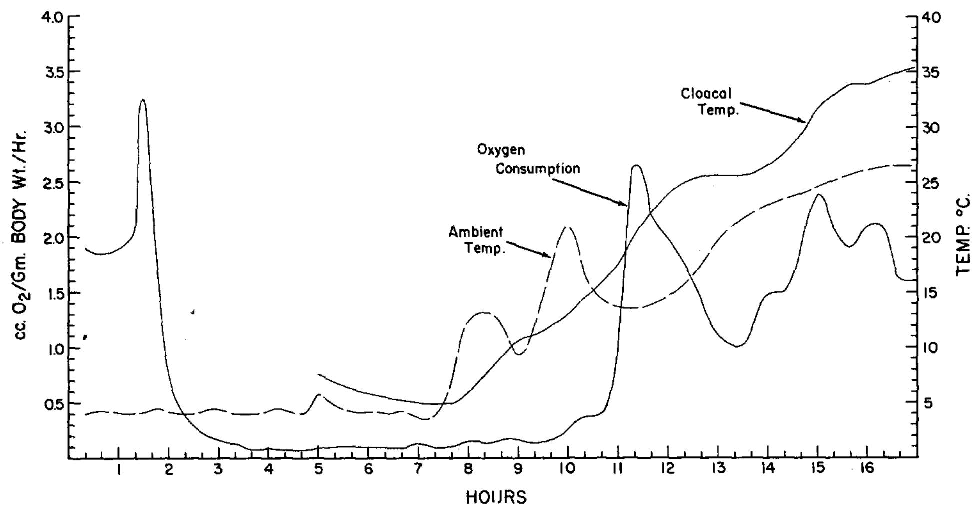

Fig. 8. Body temperature and metabolic rate in a Poor-will exposed to varying ambient temperatures.

The bird was fed *Tenebrio* larvae, beef heart, and lettuce, but was otherwise left undisturbed for two days. On the afternoon of November 14, it was placed in the respirometer at an ambient temperature of about 4°C. At this time the bird weighed 36.5 gm. Except for the disturbance incidental to the attachment of a cloacal thermocouple at 11:00 a.m. on November 15, the bird was left in the respirometer until 9:45 a.m. on November 16.

A record of oxygen consumption during entry into torpor, during torpor, and during arousal, and a record of body temperature during the latter two phases are given in figure 8. Although we have no data on body temperature during entry into torpor, the rapid fall in oxygen consumption (fig. 8) indicates that there was an uninterrupted decline. Body temperature reached a minimum of 4.8°C. and then passively paralleled increasing ambient temperature to 15°C. Body temperature then rose more rapidly than ambient temperature until the bird completed its arousal (fig. 8). Oxygen consumption was extremely low during torpor, but it increased sharply when active arousal began at a body temperature of 15°C.

Respiratory rates in this species are difficult to determine by observation, and for long periods we were unable to detect any respiratory movement although the bird's temperature was increasing. Our limited data (fig. 7) indicate only that the rate varies from 24 to 46 respirations per minute at body temperatures of 13.5 to 26°C.

The posture of the bird during torpidity was exactly as figured by Jaeger (1949:109). No spontaneous movement or changes in position were noted at body temperatures below 15°C. When the bird was handled at a body temperature of 7.5°C., it moved its legs feebly and attempted to elevate its wings but resumed its motionless state when put down. At body temperatures of 15 to 25°C., spontaneous wing-quivering was noted; possibly this was a manifestation of shivering. At body temperatures above 21°C. the side-to-side rocking movement characteristic of Poor-wills was observed. The eyes were kept closed at body temperatures below 22°C. but were usually partly to fully open at higher temperatures. At body temperatures above 32°C. there were quick spontaneous movements as though the bird were alert, and at temperatures of 34 and 35°C. it was able to fly.

During torpidity at the lowest body temperatures, oxygen consumption approximated 0.06 cc./gm./hr. Before torpor the oxygen consumption varied from 1.5 to 3.3 cc./gm./hr., with an average rate of about 2 cc./gm./hr.

PHYSIOLOGY

Torpidity has been reported in a wide variety of birds, but reliable first-hand accounts of this condition are quite rare. There are credible records of torpidity for caprimulgids, swifts, hummingbirds, colies (*Colius*), swallows, and mistletoe birds, *Dicaeum* (McAtee, 1947). However, instances that are documented with data on body temperature or oxygen consumption are known only for the following species: Poor-will (Jaeger, 1949; Thorburg, 1953); Trilling Nighthawk, *Chordeiles acutipennis* (Marshall, 1955); Anna Hummingbird and Allen Hummingbird, *Selasphorus sasin* (Pearson, 1950); Estella Hummingbird, *Oreotrochilus estella* (Pearson, 1953); European Swift (Koskimies, 1948); White-throated Swift, and the Speckled Coly (*Colius striatus*). The last species has been observed in South Africa by Dr. Raymond B. Cowles of the Department of Zoology, University of California at Los Angeles, and he has kindly allowed us to use some of his notes. Cowles found that an individual of this species, when confined in the dark at an ambient temperature of 22°C. for two and one-half hours, experienced a drop in body temperature to 24°C. After one-half hour in the sun, the bird appeared to be fully recovered and had a body temperature of 39.2°C.

In addition to the above instances, a condition of semi-torpor in the Leach Petrel (*Oceanodroma leucorhoa*) has been reported by Folk (1949, 1951).

Temperatures of birds in general are more labile than was formerly realized, but for nearly all species so far studied this lability involves only an increase in body temperature above the usual resting level (38–40°C.). Most adult birds show a negligible decrease in body temperature when subjected to very low environmental temperature (Irving, 1955; Udvardy, 1955). The three species investigated in the present study show a markedly different condition. Normal activity occurs at body temperatures as low as 35°C., and under certain conditions there is a rapid reversible decline in body temperature to 20°C. or more below the usual level.

Entry into torpor.—The physiological factors controlling hypothermia in birds and mammals remain unknown, but there is now sufficient descriptive data to indicate that in birds, as in mammals, this phenomenon is not the same in all species. In contrast to many hibernating mammals (Lyman and Chatfield, 1955:408), birds appear to enter torpor rapidly and uninterruptedly. In swifts and hummingbirds, low environmental temperatures are not essential for entry into or maintenance of torpidity. Although neurological data are lacking, the abruptness of the decline in body temperature and/or metabolic rate in these species and in the Poor-will suggests central nervous control of the initiation of hypothermia.

In both *Apus* and *Aëronautes*, hypothermia occurred only after considerable loss in weight. There is no evidence at present that hummingbirds must undergo weight loss before becoming torpid. The role of weight loss in the onset of torpidity in caprimulgids is not clear. The three cases in which captive Poor-wills had become torpid all involved birds which had lost considerable weight, but such was not the case with the Trilling Nighthawks reported by Marshall (1955) or the wild Poor-will reported by Jaeger (1949)—the latter bird weighed over 52 grams.

The onset of torpidity in the Anna Hummingbird and Allen Hummingbird, and doubtless other trochilids, is rapid and presumably nightly except in advanced nestlings and incubating females (Pearson, 1950:147; Pearson, 1953:18; Howell and Dawson, 1954).

Neither the experimental procedures of Koskimies (1948) nor our own allowed determination of whether or not a daily period of torpor can occur in adult swifts that have not experienced prior weight loss.

Torpor.—Both the Poor-will and the Anna Hummingbird experienced body temperatures within a few degrees of 0°C. without ill effects, but the White-throated Swifts did not tolerate depression of body temperature below about 20°C. In the three species mentioned above, the capacity for effective behavior improved as body temperature increased. Movements were weak and poorly coordinated at body temperatures below 20°C., well enough coordinated to have survival value between 25 and 30°C., and essentially normal at 35°C.

As active hummingbirds have exceptionally high metabolic rates, it is of interest to compare their oxygen consumption while in torpor with that of a small torpid mammal and that of a small reptile with similar low body temperatures (table 2). The metabolic rates of hummingbirds at body temperatures of 20 to 24°C. are more than twice as high as those of a bat, *Myotis lucifugus* (Hock, 1951), and a lizard, *Sceloporus occidentalis* (Dawson and Bartholomew, 1956) of similar weight at similar body temperatures.

Table 2

Comparison of Metabolic Rates of Small Vertebrates at Low Body Temperatures

Animal	Source	Body temp. Degrees C.	Weight in grams	cc. O_2/gm./hr.
Calypte anna	Present paper	20°	4.3	1.7
	Pearson, 1950	24°	4.3	.8
Selasphorus sasin	Pearson, 1950	22°	3.2	1.24
Sceloporus occidentalis	Dawson and Bartholomew, 1956	20°	4.0	.28
Myotis lucifugus	Hock, 1951	20°	6.2	.39

Arousal.—The rate of arousal from hypothermia is most rapid in the Anna Hummingbird, somewhat less rapid in the White-throated Swift, and much slower in the Poor-will. The first two arouse in a matter of minutes; our observations and those of Marshall (1955) indicate that the Poor-will requires several hours to arouse.

In *Aëronautes*, arousal to normally high body temperatures can occur at environmental temperatures at least down to 4°C.

Since bats and hummingbirds are the only endotherms known to undergo daily cycles of torpor, a comparison of their rates of increase in body temperature during arousal is of interest. In figure 6, arousal curves of two *Pipistrellus hesperus* of weights approximating those of *Calypte anna* are plotted with comparable data for two Anna Hummingbirds. The curves are strikingly similar. The two species shown are among the smallest of birds and mammals, and we therefore assume that their rates of increase of body temperature are close to the maximum possible.

Oxygen consumption in non-torpid Anna Hummingbird and Poor-will.—Our calculation of the average metabolic rate of a resting non-torpid Poor-will at an ambient temperature of 20°C. is 2.0 cc. 0_2/gm./hr., which is lower than usual for a bird of its size. Unfortunately, there are no other data on metabolism in this species. However, Scholander, Hock, Walters and Irving (1950:264–267) have determined metabolic rates in terms of Calories per day in three individuals of the tropical caprimulgid *Nyctidromus albicollis*. Assuming that one liter of 0_2 consumed by the bird is equivalent to the production of 4.8 Calories, the Poor-will's metabolic rate was 8.06 Calories per day. This is well within the range (7.6 to 13.0 Calories per day) given by Scholander *et al.* for *Nyctidromus*. These authors suggest that the relatively low metabolic rates of their examples of *Nyctidromus* are "probably due to their faculty of hibernation." However, no evidence of hibernation in *Nyctidromus* was obtained, and the authors were merely extrapolating from the case of the Poor-will (Hock, personal communication). As low metabolic rates have been demonstrated in these two species, it may be that other caprimulgids are similar in this respect whether or not they undergo hibernation.

The only published data on the oxygen consumption of hummingbirds are those of Pearson (1950), and our data are consistent with his in those respects which are comparable.

ECOLOGY

Some of the advantages offered to each of the species discussed by its particular pattern of hypothermia have been suggested by the various authors who have published on avian torpidity. Similar suggestions have been made by those who have studied torpor in bats and hibernation in other mammals. We will not attempt to summarize these interpretations but only to add to them where our data permit.

Hummingbirds.—Pearson (1950, 1953, 1954) has pointed out the value of energy conservation through torpidity to these small, rapidly metabolizing birds. A similar interpretation applies to bats, which of course represent an analogous situation in mammals. We would add that the extremely rapid arousal rates (about 1 to 1.5°C./min.) could be advantageous to hummingbirds by reducing the time they are exposed to diurnal predators at sunrise.

Swifts.—The advantages of torpidity to swifts, which are subjected to periods of fasting during unfavorable weather, have been discussed by Koskimies (1948) and Udvardy (1954). Our data show that White-throated Swifts can crawl about at body temperatures as low as 22°C. and can arouse repeatedly even at environmental temperatures as low as 4°C. This means that swifts could move about in their roosts even while hypothermic and that they could arouse and leave in search of food even if the ambient temperature in the roost were near freezing. White-throated Swifts roost in inaccessible locations that are relatively safe from predators, and a more rapid arousal than they showed in the laboratory would not seem to provide any special advantage.

Poor-will.—This species is also an aerial feeder and subject to food shortage during unfavorable weather and cold winters. The advantages to the bird of energy conservation through hibernation are obvious and need not be labored here. It is of interest, however, to use our data on metabolic rates to see how long a torpid Poor-will might survive on its energy reserves. As previously mentioned, our calculation of the metabolic rate in the resting, non-hibernating Poor-will is about 8 Calories per day. A torpid bird at a body temperature of 10°C. consumed almost exactly one-tenth as much oxygen as the resting bird, giving a value of 0.8 Calories per day while in torpor. One gram of fat when oxidized yields 9.2 Calories; for convenience and conservatism, we will assume that a Poor-will derives only 8 Calories from the oxidation of one gram of its fat. One gram of fat could, therefore, meet the energy needs of a resting bird for one day or of a torpid bird for 10 days. Ten grams of fat could sustain a torpid bird for 100 days, or for even longer if the bird's temperature remained below 10°C. It should be recalled that the weight (52 gm.) of the naturally hibernating Poor-will studied by Jaeger (1949) indicates that an assumed fat deposit of 10 gm. is entirely reasonable.

Arousal rates in the Poor-will seem to be slow and several hours may be required to reach an active body temperature from deep torpor. The Poor-will, however, is protectively colored to an exceptional degree and there is little chance of detection by predators even while the bird is in a torpid or semi-torpid condition. The slow arousal rate, therefore, should offer no particular disadvantage.

SUMMARY

Body temperature and oxygen consumption were measured in captive examples of the White-throated Swift, Anna Hummingbird, and Poor-will subjected to varying conditions of food intake and environmental temperature.

Swifts underwent reduced body temperature and arousal at environmental temperatures of 4°C. and 22°C. but did not recover from body temperatures lower than 20°C. Birds that had lost much weight became torpid more readily than others. The rate of increase in body temperature during arousal was 0.4°C. per minute at external temperatures of both 4°C. and 22°C. Swifts appeared fully active at body temperatures as low as 35°C.

Anna Hummingbirds became torpid at environmental or ambient temperatures from 2°C. to 23°C. A body temperature as low as 8.8°C. was recorded, and metabolic rate during torpor went as low as 0.3 cc. 0_2/gm./hr. Arousal was rapid, with body temperature increasing at the rate of 1 to 1.5°C. per minute at an ambient temperature of 23°C.

A Poor-will became torpid at an ambient temperature of 3.5°C., and body temperature went as low as 4.8°C. Oxygen consumption of the resting, non-torpid Poor-will averaged 2.0 cc./gm./hr., which is relatively low for a bird of this size, and during torpor declined to 0.06 cc./gm./hr. Arousal occurred while the ambient temperature was raised gradually to 22°C. Several hours were required for body temperature to reach 35°C., and the bird appeared fully active at that level.

Arousal rates of hummingbirds and small bats are almost identical, but the metabolic rates of torpid hummingbirds are over twice as high as those of torpid bats or lizards of similar size at similar low body temperatures.

Reduced body temperature and torpor provide a means of energy conservation and are associated with high metabolic rates during activity (hummingbirds) or survival during long periods of fasting (swifts and Poor-will). Calculations show that a torpid Poor-will could survive for at least 100 days on the energy derived from only 10 gm. of fat.

LITERATURE CITED

Brauner, J.
1952. Reactions of poor-wills to light and temperature. Condor, 54:152–159.

Dawson, W. R., and Bartholomew, G. A.
1956. Relation of oxygen consumption to body weight, temperature, and temperature acclimation in lizards *Uta stansburiana* and *Sceloporus occidentalis*. Physiol. Zool., 29:40–51.

Folk, G. E., Jr.
1949. Body temperature of Leach's petrel. Anat. Rec., 105:590.
1951. Observations on the body temperature of Leach's petrel. Anat. Rec., 111:541–542.
Hock, R. J.
1951. The metabolic rates and body temperatures of bats. Biol. Bull., 101:289–299.
Howell, T. R., and Dawson, W. R.
1954. Nest temperatures and attentiveness in the Anna hummingbird. Condor, 56:93–97.
Huxley, J., Webb, C. S., and Best, A. T.
1939. Temporary poikilothermy in birds. Nature, 143:683–684.
Irving, L.
1955. Nocturnal decline in the temperature of birds in cold weather. Condor, 57:362–365.
Jaeger, E. C.
1948. Does the poor-will "hibernate"? Condor, 50:45–46.
1949. Further observations on the hibernation of the poor-will. Condor, 51:105–109.
1954. Bird that "sleeps" all winter. Desert Mag., 17:21–22.
Koskimies, J.
1948. On temperature regulation and metabolism in the swift, *Micropus a. apus* L., during fasting. Experientia, 4:274–276.
Lyman, C. P., and Chatfield, P. O.
1955. Physiology of hibernation in mammals. Physiol. Rev., 35:403–425.
Marshall, J. T., Jr.
1955. Hibernation in captive goatsuckers. Condor, 57:129–134.
McAtee, W. L.
1947. Torpidity in birds. Amer. Midl. Nat., 38:191–206.
Pearson, O. P.
1950. The metabolism of hummingbirds. Condor, 52:145–152.
1953. Use of caves by hummingbirds and other species at high altitudes in Peru. Condor, 55:17–20.
1954. The daily energy requirements of a wild Anna hummingbird. Condor, 56:317–322.
Scholander, P. F., Hock, R., Walters, V., and Irving, L.
1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull., 99:259–271.
Thorburg, F.
1953. Another hibernating poor-will. Condor, 55:274.
Udvardy, M. D. F.
1954. Summer movements of black swifts in relation to weather conditions. Condor, 56:261–267.
1955. Body temperature of parids in the arctic winter. Ornis Fennica, 32:101–107.

Department of Zoology, University of California, Los Angeles, California, November 12, 1956.