FURTHER EXPERIMENTS ON TORPIDITY IN THE POOR-WILL

By THOMAS R. HOWELL and GEORGE A. BARTHOLOMEW

In a previous paper (Bartholomew, Howell, and Cade, 1957) we reported the results of experiments on torpidity in the Poor-will (*Phalaenoptilus nuttallii*) and reviewed the information on torpidity in birds published since the extensive compilation of McAtee (1947). In November, 1957, we acquired another live Poor-will and were able to corroborate and extend the results obtained from the captive bird previously studied by us.

MATERIALS AND METHODS

On the morning of November 2, 1957, a male Poor-will was discovered by a student on a lawn in the central section of Los Angeles. When the bird was approached, it flew against the side of a house. The student captured the bird and kept it for three days, attempting unsuccessfully to feed it seeds and fruit. It was then taken to Gerhard Bakker of the Department of Life Sciences at Los Angeles City College, and he kindly presented the Poor-will to us on the morning of November 6. When we received the bird it was in vigorous condition, weighed 43.5 grams, and had a cloacal temperature of 38.6°C. It had taken no food or water since its capture.

The apparatus and procedure used in the present experiments were the same as those described in our earlier paper. Oxygen consumption was measured with a Beckman paramagnetic oxygen analyzer and temperatures were measured with silver-soldered thermocouples made of 30-gauge copper-constantan duplex wire. Recording potentiometers provided continuous records of oxygen consumption and temperature. Body temperatures were obtained by inserting a vinyl-sheathed thermocouple into the cloaca to a depth of about 15 mm. and securing it in place by attaching its leads to the bird's rectrices with surgical clips. This arrangement did not seem to affect the bird in any adverse way.

RESULTS

At 4:15 p.m. on November 6 we placed the Poor-will in a cold chamber at an ambient temperature varying between 4° and 6°C. At 9:50 a.m. on November 7 the bird was fully awake, normally active, and had a cloacal temperature of 36°C. At 2:00 p.m. the same day the bird was still alert and awake but was shivering slightly. At 9:30 a.m. on November 8 the bird was torpid—wings hunched forward, eyes closed, head bent down at a 45° angle. For the next 11 days the bird was subjected to various experimental procedures, and from November 20 to December 1 it was kept under observation in captivity. It was released in good condition on the evening of December 1. The Poor-will thrived on a diet of *Tenebrio* larvae, horse meat, occasional pieces of lettuce, and water.

Entry into torpor.—Continuous records of cloacal temperature during entry into torpor were obtained at environmental temperatures of 2° to 6°C., and 17° to 19°C. (fig. 1). Oxygen consumption was measured during entry into torpor while environmental temperature diminished from 21° to 3.5°C. (fig. 2).

Body temperature declines very slowly at first and may fluctuate erratically around 34°C. for several hours before descent into torpor actually commences. However, once the period of rapid fall in body temperature begins, the trend is usually not reversed. The rate of decrease in body temperature is apparently dependent on environmental temperature; the lower the ambient temperature, the more rapid the fall in body temperature. In the two instances of entry into torpor for which we have continuous records of body temperature, the rate of decline was 0.14°C./min. at an air temperature of 2° to 6°C. and 0.05°C./min. at 17° to 19°C. (fig. 1).

Oxygen consumption during entry into torpor shows a pattern generally compatible with the course of body temperature just described. In the early stages of entry into torpor, as body temperature declined from 38° to 27°C., oxygen consumption fluctuated between 0.5 and 1.5 cc./gm./hr. This is well below the basal rate in Poor-wills, which appears to be approximately 2.0 cc./gm./hr. (Bartholomew *et al.*, 1957). Oxygen consumption then fell precipitously but smoothly to 0.1 cc./gm./hr. and declined even further when the bird was in deep torpor at body temperatures near 5°C.

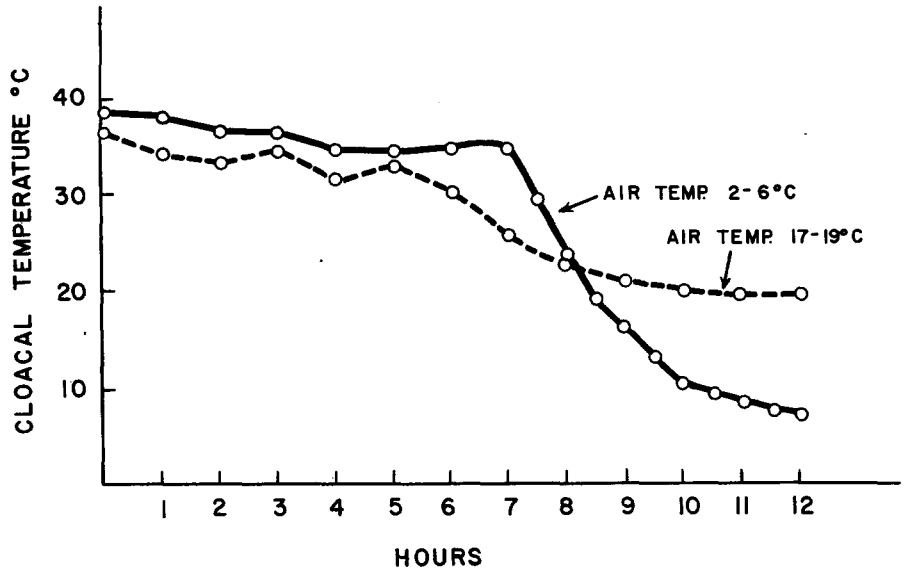

Fig. 1. Body temperatures during entry into torpor.

Torpor.—Apparently the metabolism of an undisturbed torpid Poor-will produces insufficient heat to maintain body temperature more than a fraction of a degree above ambient temperature if this is not high enough to initiate arousal. During one period of 20 hours of torpor at temperatures between 5.8° and 8.6°C., continuously recorded cloacal and ambient temperatures remained within 0.1°C. of each other. In fact, there was considerable doubt in our minds while viewing this temperature record that the bird was still alive.

Arousal.—Behavior during arousal is summarized in table 1. Although these observations were made during one specific arousal, they are typical of those made during several other arousals of this bird and the previously studied Poor-will. The rate of arousal depends initially on the temperature of the bird and the ambient temperature at which arousal occurs. If a torpid bird at low body temperature is exposed to a warm environment, the rise in body temperature appears to be passive until a temperature of about 15° to 19°C. is reached. The higher the air temperature is above that point, the faster the passive rise in body temperature will be.

Under the conditions of our experiments, when body temperature reached the range of 15° to 19°C., there was a distinct increase in the rate of rise of body temperature. This marked the beginning of the active stage in arousal and was accompanied by noticeable tremors, increased respiration, and a steep rise in oxygen consumption (fig. 2). The rate of increase in body temperature continued more or less uniformly until a body tem-

perature of 34°C. or slightly higher was reached. Even with a body temperature of only 34°C., the Poor-will appears capable of its customary activities although its temperature is still 4° or 5°C. below that of the normally active bird.

The rates of increase of body temperature during the active phase in the four arousals (fig. 3) for which we have adequate data were quite similar, varying only from 0.30° to 0.37°C. per minute.

We were unable to obtain continuous simultaneous measurements of oxygen consumption and body temperature during entry into torpor, but concurrent records were obtained during torpor and during arousal. The handling incidental to the attachment

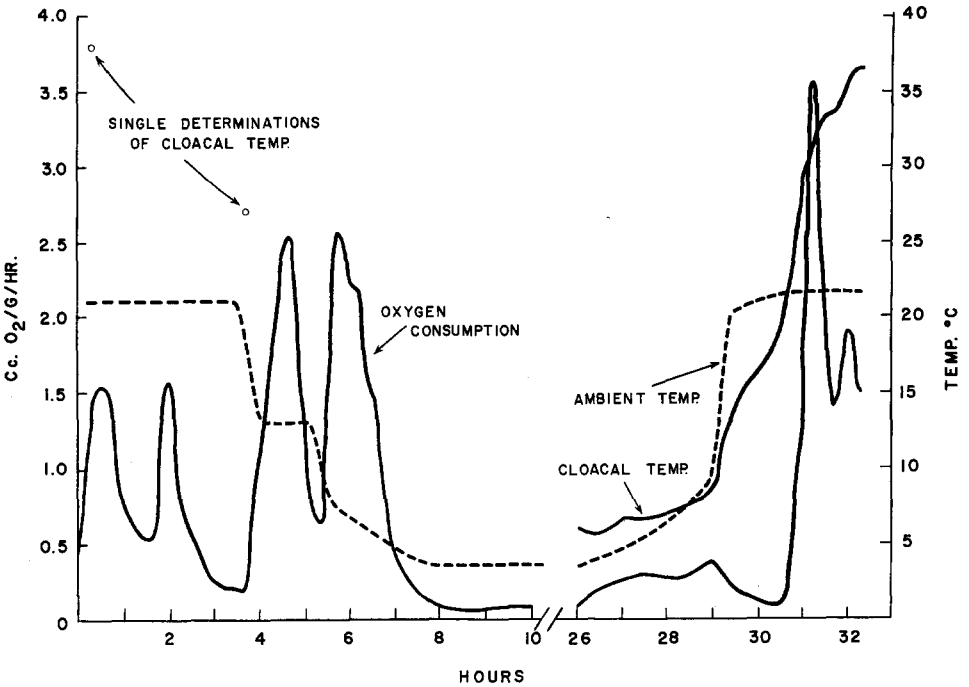

Fig. 2. Body temperature and oxygen consumption during entry into torpor, torpor, and arousal.

of a thermocouple to the torpid Poor-will caused some increase in body temperature, but the disturbance alone was insufficient to arouse the bird. During the three hours following the attachment of the thermocouple in the experiment summarized in figure 2, the bird's temperature and oxygen consumption rose only slightly. When the temperature of the experimental chamber was increased from 4° to 21°C. in 20 minutes, the bird's temperature also rose. The fact that the oxygen consumption declined during this interval indicates that the rise in body temperature was passive. When the bird's temperature reached 17.5°C., however, oxygen consumption increased strikingly and body temperature also showed an upswing in the rate of increase. When body temperature reached about 34°C., oxygen consumption dropped rapidly to about the normal resting level although body temperature continued to increase slowly.

DISCUSSION

Our previous paper (Bartholomew, Howell, and Cade, 1957) discussed the published information on torpidity in the Poor-will up to the close of 1956. One additional record

of a torpid Poor-will in nature has since appeared (Stebbins, 1957), but no body temperatures were reported. Fog and Petersen (1957) reported that a captive Nightjar (*Caprimulgus europaeus*) which was subjected for 12 hours to ambient temperatures between 4° and —2.5°C. did not become torpid or show evidence of lowered temperature. We know of no other recently published data on torpidity in caprimulgiform birds, but two references (Ruschi, 1949; Wagner, 1955) with original data on avian torpidity not cited in our earlier paper may be mentioned here for the sake of completeness.

The present study reports for the first time continuous records of body temperature during entry into torpor, both at low and at moderate ambient temperatures (fig. 1). The latter record is of special interest as it shows that low environmental temperatures are not essential for the onset of torpor in the Poor-will.

The data on body temperature and oxygen consumption during torpor corroborate our previous results. If air temperature remains uniform enough for the body temperature to stabilize, the two are essentially the same, at least to within a few degrees of zero C. Whether or not the torpid bird increases its heat production when its body temperature approaches dangerously close to freezing has not been determined.

Despite its general inertness, a torpid Poor-will moves with surprising vigor when disturbed by handling. It may move stiffly extended wings up and down slowly, giving

Table 1

Behavior During Torpor and Arousal of Poor-will Removed from 5° to 21°C., November 8 (fig. 3)

Cloacal temperature in degrees C.	Behavior
7.5	When undisturbed: eyes closed; head drooped at 45° angle, posterior crown feathers raised; wings hunched forward but not spread; tail not spread or elevated. When disturbed by handling and insertion of thermocouple: wings spread fully and directed forward, each at 45° angle to long axis of body, then "flapped" very slowly; head spasmodically raised and lowered during "flapping"; eyes remained closed.
10.5	Wings half spread, tips touching substrate; occasional slow trembling, not always bilaterally symmetrical; bird "rocked" several times, settling into original hunched position with wings not spread.
15.0	Still in hunched position, leading edge of primaries resting on substrate; head about 15–20° below horizontal, neither bill nor rictal bristles touching substrate; crown feathers down, but malar, subocular, and auricular feathers fully fluffed out; very slight rhythmic movement of wings, possibly indicating breathing; no noticeable shivering.
16–17.0	Slight (5 mm.) but quick lateral head movements; after several spasmodic shudders of body, head raised to horizontal position.
19.0	Extremely slight head tremors; slight respiratory movements in throat region at rate of about 20–30 per minute.
20.0	Marked shivering; head raised repeatedly; "rocked" rapidly; wings off substrate but still hunched; eyes still closed.
21.8	Stronger shivering; respiratory movements pronounced, about 30 per minute; breast feathers fully fluffed out.
24.0	Continued strong shivering; respiration about 40 per minute; scapular feathers fluffed out.
29.0	Strong shivering stopped; respiratory rate increased to about 60 per minute but shallower; eyes opened to about 1 mm.
34.6	Eyes open a little wider; short periods of stronger shivering and deeper and faster respiration alternating with longer periods of mild shivering, slower and shallower respiration.
36.0	Apparently awake and alert; slight, quick movements of head; some "rocking."
38.0	Shivering and respiratory movements no longer visible.

an appearance of flapping as seen in slow-motion cinematography. We observed this behavior on three occasions, and similar wing extension has also been reported by Jaeger (1948). Other examples of activity during torpor and arousal are given in table 1.

In the present study we obtained four continuous records of body temperature during arousal at three different but relatively constant environmental temperatures. We observed no indications of active arousal until body temperatures reached at least 15°C.

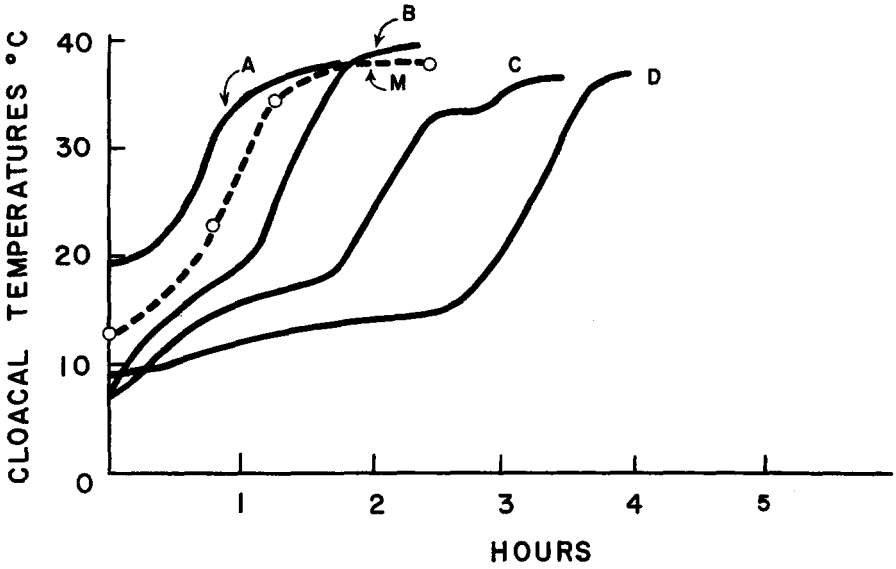

Fig. 3. Rates of arousal at various ambient temperatures. A, 19°C.; B, 21°C.; C, 20° to 23°C.; D, 14° to 17°C.; M, 14.5° to 19.5°C. (data from Marshall, 1955:131).

Thereafter, the increase in body temperature approximated 0.3°C./min. The active period of temperature increase lasted between 60 and 90 minutes, which corresponds well with the single Poor-will arousal for which Marshall (1955) obtained temperature data (fig. 3). It thus appears that Poor-wills are relatively slow rousers compared to swifts and hummingbirds. As the Poor-will is a larger bird than these, a slower rate of arousal is not surprising. However, the oxygen consumption of the Poor-will studied was no more than 3.6 cc./gm./hr. even during the most rapid part of arousal, and this is a modest rate of active metabolism for a bird weighing only about 40 grams. For example, Dawson (1954) found the resting metabolism of the Brown Towhee, *Pipilo fuscus*, (mean weight, 43.7 gm.) to be 2.8 cc. O_2/gm./hr. at an air temperature of 20° to 25°C.

The fact that a Poor-will may enter torpor at temperatures from 2° to 19°C. makes any physiological distinction between aestivation and hibernation impossible. Furthermore, it appears that both prolonged hibernation and daily torpor may occur in this species. Air temperatures below 19°C. (66°F.) can be expected at any season in much of the geographic range of this species, and it seems probable that daily periods of torpor may be interspersed between longer periods of hibernation. Marshall (1955:131) reported daily cycles of torpor in captive Poor-wills, and our bird showed four consecutive daily periods of torpor while housed and fed outdoors from November 28 through December 1, 1957. It became torpid each night and roused sometime during the following morning. Air temperatures at night ranged from 10° to 11°C., and morning temperatures reached high points of 18° to 24°C. in this interval.

Our laboratory data and the various field observations which have been published are all consistent with the following general conclusions. The Poor-will under sustained low environmental temperatures may hibernate for days at a time, but if environmental heat warms the bird to 15° to 20°C. it may start to arouse and can reach normal operating body temperature (34° to 40°C.) in an hour or a little more. If the daily environmental temperature is appropriate, the bird may become torpid every night and rouse every day. Torpidity can be induced in capitive Poor-wills by withholding food during exposure to moderately low temperatures, but torpor is by no means obligatory even at low ambient temperatures, and its precise cause under natural conditions is unknown.

SUMMARY

A captive Poor-will was made to undergo repeated cycles of torpor and arousal, and continuous records of body temperature and oxygen consumption were obtained. Torpor was induced at low (2° to 4°C.) to moderate (19°C.) air temperatures. Entry into torpor was preceded by several hours of slightly depressed body temperature, and then a steady and rapid decline in body temperature and oxygen consumption occurred. During torpor environmental and body temperature were virtually identical for long intervals, and the bird was capable of some movement if disturbed. Arousal was induced by increasing the ambient temperature, and body temperature increased passively until a temperature of about 15°C. was reached. Then an active phase of arousal commenced that was marked by strong shivering, increased respiration, and a steep rise in body temperature and oxygen consumption. This continued until normal body temperature was attained. This information is consistent with other data on captive Poor-wills, but the precise factors that induce torpor under natural conditions remain unknown.

DEDICATION

We take pleasure in dedicating this paper to Erwin Stresemann on the occasion of his 70th birthday in recognition of his contributions to ornithology.

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