ADDITIONAL RESPONSES OF THE POOR-WILL TO LOW TEMPERATURES

George T. Austin and W. Glen Bradley

The physiology of caprimulgiform birds, especially the Poor-will (*Phalaenoptilus nuttalli*), has engendered considerable interest since Jaeger (1948) discovered one in a torpid state. Brauner (1952), Marshall (1955), Bartholomew et al. (1957), Howell and Bartholomew (1959) and Bartholomew et al. (1962) have reported on the Poor-will's low temperature physiology. Other studies on torpidity in caprimulgids have been conducted by Peiponen and Bosley (1964) and Peiponen (1965) on the European Nightjar (*Caprimulgus europaeus*); by Lasiewski and Dawson (1964) on the Common Nighthawk (*Chordeiles minor*); and by Marshall (1955) on the Lesser Nighthawk (*C. acutipennis*). Reported here are several additional findings on the Poor-will's low temperature physiology.

Materials and Methods

An active female Poor-will caught at Pakoon Springs Ranch, Mohave County, Arizona on 5 April 1968 weighed about 33 g when brought to us on 7 April. The bird was fed a mixture of ground beef heart, liver, kidney, and canned dogfood supplemented with moths and *Tenebrio* larvae, on which it maintained a weight between 32 and 36 g. It was kept in a laboratory where the ambient temperature (T_a) ranged from 22.4–29.2°C.

A controlled temperature chamber was constructed out of a refrigerator equipped with a small electric heater and a window sealed in the door to facilitate observation. By alternate use of refrigerator and heater, temperature was regulated within 2°C of that desired. The bird was placed on a cardboard platform covered with a 2-cm layer of soil, 25 cm above the heat source. This insulated the bird from direct radiation as soil temperature closely approximated that of the air above it at all times. Temperatures were monitored with thermister probes connected with a YSI Tele-Thermometer. Except for flight trials, body temperatures (T_b) were taken with a thermister inserted 15 mm into the cloaca and attached to the rectrices with tape or a small hair clip. During flight trials, T_b was taken with a Schultheis quick-registering thermometer inserted 15 mm into the cloaca. Cloacal temperatures were found to be within 0.4°C of deep esophageal temperatures. Respiration rates were counted visually and timed with a stopwatch. Food was withheld at least 12 hours before any experiments were conducted.

The procedure for flight trials is similar to that Bradley and O'Farrell (1969) used with bats. It consists of lowering the bird's T_b, removing it from the cooling chamber, recording its T_b, and, usually at 1°C intervals, tossing the bird gently into the air and noting its activity. Time was recorded to the nearest half minute, also comments on the bird's condition, and T_a and T_b before and after each flight attempt. This procedure was repeated until the bird attained good flight. As many as five trials were conducted in succession. Terms used to describe flight activity are:

"Spread wings"—wings spread out from body, no flapping motion.

"Flutter"—some up and down movement of wings, no forward progress.

"Weak flight"—movement of wings, some forward progress.
"Good weak flight"—altitude maintained for several feet.
"Good flight"—some gain of altitude for at least 10 feet.

A definite difference is observable between what we term "good" flight and "normal" flight when the bird's T_b is above 34°C.

Cooling rates were determined by recording T_b before and after a measured time interval in the chamber. On two occasions T_b was monitored continuously. Warming rates of the undisturbed bird were taken at room temperature after the T_b had been lowered. Also, warming rates during disturbance were calculated from the flight trial data.

For one 32.5-hour period the bird was subjected to thermal conditions that it would likely encounter in southern Nevada in November. The temperature regimen used for the first 27.5 hours approximated the mean air temperatures at White Spot Spring, Desert National Wildlife Range in November (from thermograph data). Poor-wills have been seen there in November. After 27.5 hours of simulated field temperatures, the T_a of the chamber was gradually increased at the rate of about 4°C/hour. T_a, T_b, and substrate temperature were monitored at 5-minute intervals. A fluorescent light was turned on and off in the chamber to approximate sunrise and sunset for that time of year. Behavior of the bird was noted throughout the experiment.

All temperatures are given in degrees Centigrade.

RESULTS

Flight trials.—Marshall (1955) reported that a captive Poor-will could not fly with a T_b of 34.4° (cloacal) but could fly with a T_b of 37.5°. Miller (1950) reported a Poor-will flying in the field with a T_b of 34.0° (proventricular). Bartholomew et al. (1957) and Howell and Bartholomew (1959) reported this species capable of normal activity and able to fly at a T_b of 34–35°. Bartholomew et al. (1957) also reported a White-throated Swift (*Aeronautes saxatilis*) capable of flight at a T_b of 35°. Recent studies indicate that bats are able to fly at T_b's as low as 22° in the field and 20° in the laboratory (Bradley and O'Farrell, 1969; Bradley, MS).

We conducted six series of flight trials consisting of 23 individual trials (Table 1). The T_a of the cooling chamber ranged between −9° and +2°. The T_b when removed ranged from 14.6° to 28.0° ($\overline{X}$ = 21.3°).

Good flight was attained at minimum T_bs between 27.4° and 30.8° ($\overline{X}$ = 28.5°). These T_b's at which flight was attained are considerably lower than those reported for the Poor-will and are the lowest reported for birds.

Cooling-warming rates.—Cooling and warming rates for the Poor-will are inadequately known. Bartholomew et al. (1957) indicated that it took almost 9 hours for a Poor-will to raise its T_b from approximately 5° to 35° with a gradual increase in T_a. Active arousal (T_b = 15–35°) proceeded at about 2.9°/hour. Marshall (1955) stated that the species could become fully active in a few hours, if disturbed, at any T_a. Lasiewski and

TABLE 1

RESULTS OF FLIGHT TRIALS

		Body Temperature (°C)					
Date	Trial no.	Good flight	Good weak flight	Weak flight	Flutter	Spread wings	Weight (g)
9 April	1	30.8	29.5	–	–	–	36.6
	2	29.5	29.0	28.0	25.6	–	–
	3	29.5	29.2	28.0	24.0	–	–
	4	28.8	28.0	27.5	–	–	–
	5	28.8	28.0	–	–	–	35.5
11 April	1	28.4	28.2	27.0	–	–	35.7
	2	28.6	26.5	–	24.0	–	35.5
	3	28.8	28.0	26.0	24.0	18.0	35.4
	4	28.8	28.0	26.0	23.4	18.0	35.4
16 April	1	28.4	–	–	–	–	33.8
	2	28.0	–	27.5	24.0	–	33.8
	3	27.6	–	27.0	24.0	–	33.8
	4	27.6	27.2	26.0	21.0	–	33.7
18 April	1	28.2	26.0	24.0	19.8	–	33.8
	2	27.8	27.0	24.0	20.4	–	33.4
	3	27.8	27.0	25.0	22.0	18.0	33.2
	4	27.6	27.4	25.0	20.0	17.8	33.2
20 April	1	27.4	27.0	25.0	20.0	17.8	33.4
	2	27.8	27.0	25.0	20.0	17.8	33.0
	3	27.6	27.0	24.0	19.0	17.2	32.8
	4	27.8	27.0	25.0	–	–	32.8
30 April	1	30.2	29.0	27.5	26.5	–	30.8
	2	30.2	28.0	26.0	22.5	–	30.7
Mean $\pm s_{\bar{x}}$		28.5 $\pm$ 0.20	27.7 $\pm$ 0.21	26.0 $\pm$ 0.31	22.4 $\pm$ 0.55	17.8	–

Lasiewski (1967) and Lasiewski et al. (1967) indicated that arousal from a T_b of about 22° to 35° took 30 minutes (26°/hour). Howell and Bartholomew (1959) reported arousal at a rate of 18–22°/hour.

In our bird undisturbed arousal was intermediate to the extremes previously reported. In three trials the Poor-will was removed from the cooling chamber with T_b's of 15.1°, 15.0°, and 16.0° and left undisturbed at room T_a (27.7°, 25.1°, and 27.6° respectively). Warming rates of 9.8°, 8.6°, and 4.7°/hour, respectively, were found. The T_b rose to 36.0°, 35.9°, and 30.0° in these three trials. Prior to the third trial, the bird had been subjected to flight trials and had not been fed for over 24 hours. As a result, it was in a weakened condition and arousal was considerably slower.

Bartholomew et al. (1962) reported shivering as the principal means of heat production in the Poor-will at low T_a. They also noted that, once T_b was stabilized near T_a, no shivering was evident. Shivering started at a T_b of 15° and became stronger with increasing T_b. Bartholomew et al. (1957) reported a rapid rise in T_b above 15° with wing quivering (possibly shivering) evident at T_b's between 15° and 25°.

We noticed infrequent shivering during arousal. No shivering was evident in any of the trials until T_b equaled or exceeded T_a. Shivering occurred for short periods of a few minutes and then ceased although T_b continued to rise. No shivering was evident during the third warming trial, during which warming was considerably slower above a T_b of 24° than in the other trials. Visible shivering thus appears to be a mechanism of increasing the rate of arousal from torpor in the Poor-will, although isometric muscle contractions must also operate to raise T_b above T_a as nonshivering thermogenesis has not been demonstrated in birds (West, 1965).

During arousal, feathers were generally fluffed, even up to a T_b of 36°. Rocking movements, typical of this species, were noted at T_b's as low as 17°, eyes were opened as low as 20°, and the wings were moved spontaneously as low as 17.5°. During warming the bird spread its wings at least 1.5 cm from the body and perhaps gained some heat from the substrate through convection.

Warming during the 23 flight trials was considerably faster because of disturbance and increased muscular activity. These warming rates averaged 18.8°/hour (11.8°–24.0°/hour).

On cooling rates Howell and Bartholomew (1959) reported a decrease in T_b of 0.14°/minute (8.4°/hour) at a T_a of 2–6° and of 0.05°/minute (3.0°/hour) at a T_a of 17–19°. Lasiewski and Lasiewski (1967) and Lasiewski et al. (1967) indicated that descent into torpor took almost 4 hours at a T_a of 20° (about 5°/hour). Our data for cooling rates were derived from cooling the bird for flight trials and two cooling trials when the bird was monitored continuously. T_b's were found to decrease at an average rate of 10.1°/hour (1.8°–17.1°/hour) in 30 instances ($T_a = -3°$ to $-9°$). Only once did the T_b decrease slowly and fluctuate above 30° as reported by Howell and Bartholomew (1959). The T_b decreased linearly in the first monitored trial (Figure 1). In the second trial, T_b decreased linearly until it reached 28.3°. Then the bird flew to the top of the chamber and T_b rose to 33.2° after which T_b declined steadily again.

Thermal response.—Data from the 32.5-hour simulated field temperature experiment provided results not entirely expected. Figure 2 presents hourly averages for T_a and T_b during the experiment. The bird was placed in the chamber ($T_a = 15°$) with a T_b of 37.8°. The T_b decreased rather rapidly (5.0°/hour) for 3 hours when it reached 21.8° ($T_a = 20.1°$). Subsequently T_b followed T_a to 8° with a lag of no more than 3°. Thereafter T_a was raised to 40.8° and T_b followed, lagging up to 5.2°, through the end of the experiment.

The scapular, head, and breast feathers were fluffed to some extent throughout the 32.5 hours, but were fully fluffed only at a T_b above 23.1°

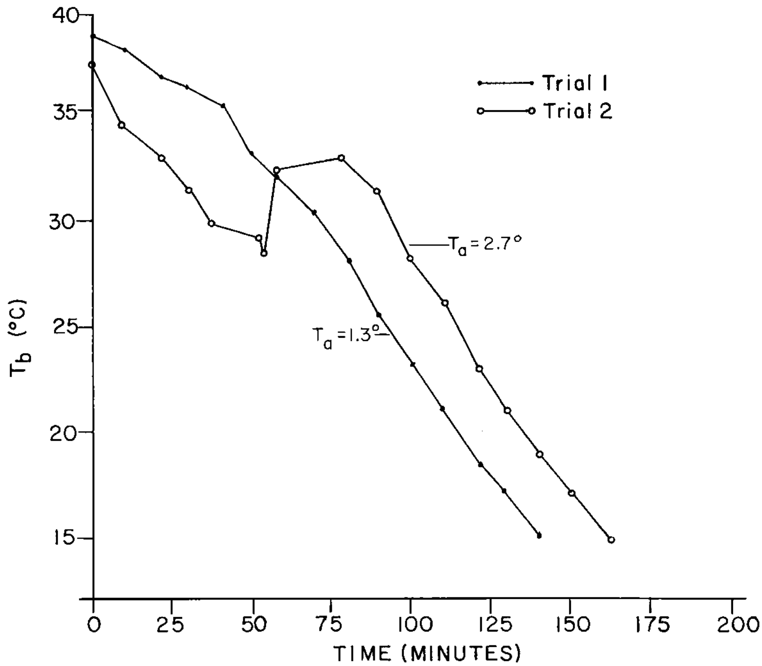

Figure 1. Rates of entry into torpor in the Poor-will.

during descent into torpor. During arousal, feathers were raised until a T_b of 8.5° (T_a = 10.5°) was reached. Afterwards the head feathers were lowered until a T_b of 31.4° was reached when they were raised again for 15 minutes.

The bird remained motionless throughout cooling. When the light was turned on in the chamber the bird lifted its wings over its back (T_b = 8.1°). The first rocking movements were noted at a T_b of 9.1°. This movement was noted intermittently throughout arousal. During arousal the wings were gradually spread from a position close to the body to about 2.5 cm away. Also they were moved forward until at a T_b of 14° the bend of the wing was about 1 cm ahead of the slightly fluffed breast feathers. No shivering was detected throughout the experiment.

When the bird was removed from the chamber, its T_b was 37.3° (T_a = 40.8°) and it flew strongly. It lost 0.1 g (33.6–33.5 g) during the experiment. No excreta were found in the chamber. The weight loss corresponds well with that Bartholomew et al. (1957) reported for a torpid bird.

Respiration rate.—Bartholomew et al. (1957) reported respiration rates from 24 to 46 respirations/minute at T_b's from 13.5° to 26.0°C. Lasiewski

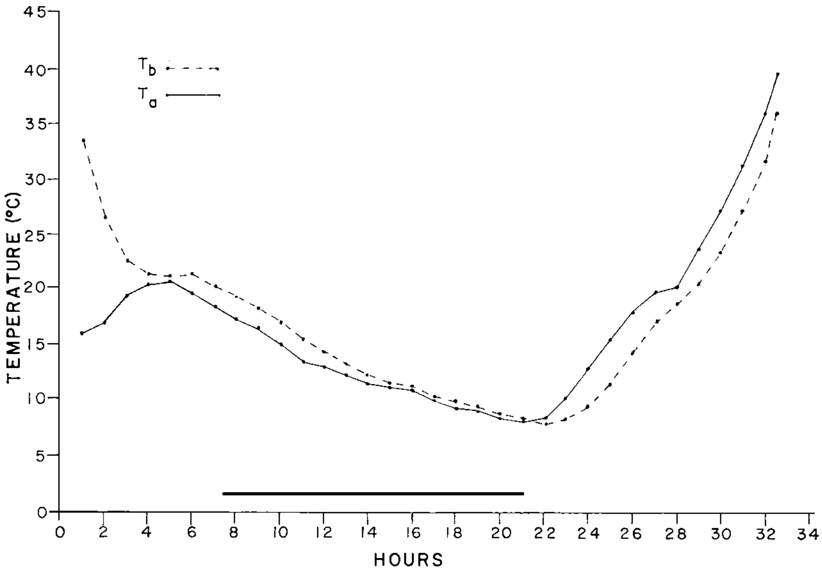

Figure 2. Hourly averages of ambient and body temperatures of the Poor-will during thermal response experiment (bird in dark for period indicated by bar).

and Bartholomew (1966) gave a rate of 15–18 respirations/minute for the Poor-will in the thermoneutral zone (35°–44°).

We have counts of respiration rates from 18.0° to 36.0° during arousal and from 36.5°to 27.5° during descent into torpor (Figure 3). These show a direct relationship with T_b. Highest rates were observed just prior to descent when the bird was evidently thermoregulating and during active arousal when shivering was visible. Below a T_b of 18° no breathing movements were evident externally. During arousal considerable variation in the rate indicated variable degrees of thermoregulation. Observed rates ranged from 1.4 (7 respirations/5 minutes) to 49 respirations/minute during arousal and from 50 to 7 respirations/minute during entry into torpor.

Respiration while the bird was at rest in its cage with a T_b between 39.8° and 40.0° (T_a = 26.4°–26.7°) ranged from 33 to 48 respirations/minute ($\overline{X}$ = 38.6 respirations/minute). This is considerably higher than reported by Lasiewski and Bartholomew (1966) although our bird was at a T_a about 10° below the thermoneutral zone.

DISCUSSION

Recent studies indicate that Poor-wills can become dormant. A combination of low T_a and reduced food appear to be the primary prerequisites for torpidity, although the bird reported by Jaeger (1949) weighed over

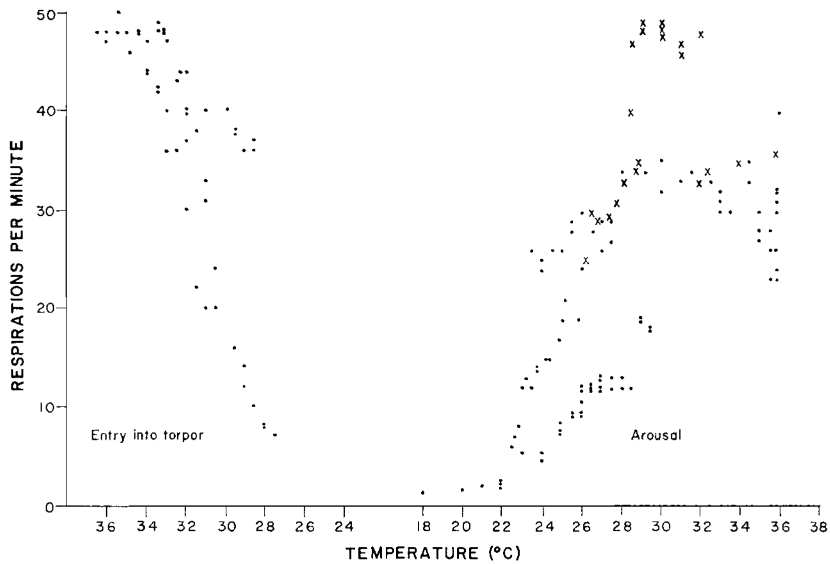

Figure 3. Relation of body temperature and respiration rate in the Poor-will (× signifies shivering).

52 g. Our bird entered torpidity several times within 8 hours after feeding although it appeared healthy. This bird could become semitorpid at T_a's as high as 29.2°. On three mornings the T_b was 24.6°, 29.7°, and 27.6° when the T_a was 24.4°, 29.2°, and 24.4° respectively. These are the highest reported T_a's at which Poor-wills reduce T_b.

The ability to become ectothermic, especially under stress conditions of cold or food shortage, is an efficient mechanism as shown by a weight loss of 0.1 g over a 32-hour period. Over a similar period of time while maintaining T_b above 36° ($T_a = 27°$) our bird lost 4.2 g. With T_b closely approximating T_a a Poor-will does not have to expend energy to maintain T_b and can survive periods of stress on a minimum of energy reserve.

The ability to be active at T_b below the normal (above 36°) allows this species to take advantage of periods of warm weather during the winter. As indicated by the flight trials above, this species can initiate flight at lower T_b's than previously thought. By using a daytime roost situated so that it is exposed at least to the afternoon sun, a torpid bird could be sufficiently warmed passively by sunset to be able to forage actively with a minimum of thermogenic expenditure. An exposed roost has been reported for torpid birds by Jaeger (1948, 1949) and Stebbins (1957) for the Poor-will, Marshall (1955) for captive Lesser Nighthawks, Lasiewski and Thompson (1966) for Violet-green Swallows (*Tachycineta thalassina*), and Stager (1965) for Vaux's Swifts (*Chaetura vauxi*).

The Poor-will is capable of launching itself from the ground at a T_b as low as 28.3°, at which our bird tried to fly out of its chamber during a cooling experiment. Being able to fly with a lowered T_b would also enable it to return to its roost after foraging on a cool evening with a lower thermal gradient between air and body. Thus by being a facultative ectotherm in times of stress, this species could remain in some of the colder portions of its range during the winter and survive unusual cold spells.

ACKNOWLEDGMENTS

We wish to thank those people who assisted in the laboratory, especially Ralph Clark, Michael O'Farrell, and David Turner. We also thank Fenton Kay for assisting in the capture of the bird and Claude Whitmyer for feeding it in our absence. This study was financed in part by N.S.F. Grant No. 5217 issued to D. B. Dill.

SUMMARY

The thermoregulatory responses of a Poor-will, especially to low temperature, were investigated. A Poor-will was found to fly at a body temperature as low as 27.4°, the lowest reported for a bird. Descent into torpor was found to be more rapid and arousal rate was intermediate to data previously reported. The bird was capable of becoming essentially ectothermic under stress. Additional data on respiration rates at a wide range of body temperatures are given. A wider variability in relation to low temperatures is indicated than previously reported.

LITERATURE CITED

BARTHOLOMEW, G. A., T. R. HOWELL, AND T. J. CADE. 1957. Torpidity in the White-throated Swift, Anna Hummingbird, and Poor-will. Condor, 59: 145–155.

BARTHOLOMEW, G. A., J. W. HUDSON, AND T. R. HOWELL. 1962. Body temperature, oxygen consumption, evaporative water loss and heart rate in the Poor-will. Condor, 64: 117–125.

BRADLEY, W. G., AND M. J. O'FARRELL. 1969. Temperature relationships of the Western Pipistrelle, *Pipistrellus hesperus*. Pp. 85–96 *in* Physiological systems in semiarid environments (C. C. Hoff and M. L. Riedesel, Eds.). Albuquerque, Univ. New Mexico Press.

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

HOWELL, T. R., AND G. A. BARTHOLOMEW. 1959. Further experiments on torpidity in the Poor-will. Condor, 61: 180–185.

JAEGER, E. C. 1948. Does the Poor-will "hibernate"? Condor, 50: 45–46.

JAEGER, E. C. 1949. Further observations on the hibernation of the Poor-will. Condor, 51: 105–109.

LASIEWSKI, R. C., AND G. A. BARTHOLOMEW. 1966. Evaporative cooling in the Poor-will and Tawny Frogmouth. Condor, 68: 253–262.

LASIEWSKI, R. C., AND W. R. DAWSON. 1964. Physiological responses to temperature in the Common Nighthawk. Condor, 66: 477–490.

LASIEWSKI, R. C., AND R. J. LASIEWSKI. 1967. Physiological responses of the Blue-throated and Rivoli's Hummingbirds. Auk, 84: 34–48.

LASIEWSKI, R. C., AND H. J. THOMPSON. 1966. Field observations of torpidity in the Violet-green Swallow. Condor, 68: 102–103.

LASIEWSKI, R. C., W. W. WEATHERS, AND H. M. BERNSTEIN. 1967. Physiological responses of the Giant Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol., 23: 797–813.

MARSHALL, J. T., JR. 1955. Hibernation in captive goatsuckers. Condor, 57: 129–134.

MILLER, A. H. 1950. Temperatures of Poor-wills in the summer season. Condor, 52: 41–42.

PEIPONEN, V. A. 1965. On hypothermia and torpidity in the European Nightjar. Ann. Acad. Sci. Fenn., 87: 4–15.

PEIPONEN, V. A., AND A. BOSLEY. 1964. Torpidity in a captive European Nightjar (*Caprimulgus europaeus,* L.) Ornis Fennica, 41: 40–42.

STAGER, K. E. 1965. An exposed nocturnal roost of migrant Vaux Swifts. Condor, 67: 81–82.

STEBBINS, R. C. 1957. A further observation on torpidity in the Poor-will. Condor, 59: 212.

WEST, G. C. 1965. Shivering and heat production in wild birds. Physiol. Zool., 38: 111–120.

Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, Nevada 89109.