REACTIONS OF POOR-WILLS TO LIGHT AND TEMPERATURE

By JOSEPH BRAUNER

Proof that the Poor-will (*Phalaenoptilus nuttallii*) hibernates (Jaeger, 1949) recently stimulated interest in this bird. Torpidity in Poor-wills has been known, however, for three-quarters of a century. Belding (1890) noted the report of a torpid Poor-will at the North American Hotel, 30 miles east of Stockton in Calaveras County, California, in January, 1879. Culbertson (1946) reported a Poor-will found in a torpid condition on February 6, 1946, in Fresno County, California. Howard L. Cogswell (personal communication) discovered a Poor-will on February 14, 1935, near a road cut under construction in the San Gabriel Mountains, Los Angeles County, California. At that time, he believed it to be injured but in light of present knowledge, he now feels that the bird was probably torpid. Herbert De Tracy of Bradley, California (personal communication), reported that he found a female Poor-will in a torpid condition in January, 1943, at the base of a tree stump. He stepped on it accidentally and killed it. De Tracy reported another torpid bird in a ploughed furrow of an open area in December or January of an unrecorded year. The bird was held in the hand for a short time after which it recovered and flew off.

The foregoing reports, together with those cited by Jaeger (1949), strongly suggest that hibernation commonly occurs in Poor-wills. If this is correct, the seasonal movements of this species should be reinterpreted. Poor-wills have been thought to migrate down into the valleys from the mountains, or south along the Colorado River, for the winter. It now appears possible that at least some populations may be sedentary throughout the year. Jaeger's hibernating bird returned to the same hole in a rock for four consecutive years.

METHODS AND MATERIALS

All the data which follow, except for the temperatures recorded from birds collected in the field, were taken from a female Poor-will which I raised. Temperature readings were cloacal and were taken with a rapid recording mercury thermometer. Light intensities were measured with a Model 603 Weston Illumination Meter which measures to 0.01 foot-candle. A constant temperature chamber was made available through the courtesy of Dr. George A. Bartholomew, Jr., at the University of California at Los Angeles.

The study area was situated on the south side of the Santa Monica Mountains north of Brentwood, Los Angeles County, California. The area is crossed by a network of fireroads and trails and is covered by chaparral consisting mostly of *Ceanothus megacarpus, Ceanothus spinosa, Rhus laurina, Rhus ovata, Adenostoma fasciculatum,* and *Salvia mellifera.*

Acknowledgements.—I am indebted to the late Dr. A. J. van Rossem for guidance throughout parts of this study and to Dr. George A. Bartholomew, Jr., particularly, for aid in the writing of this report.

REACTIONS TO LIGHT

Repeated field observations have shown clearly that the onset of Poor-will activity is indicated by calling. The time of first calls was noted and the intensity of the overhead light was measured. The photocell was placed on the ground pointed upward to take a reading of the zenith. The resulting reading was approximately the same as an average of a west plus east horizon reading. The duration of the period of the bird's activity was noted as was the phase of the moon and weather conditions.

The observations in the study area were begun on February 15, 1949, when a Poor-will was heard at 6:00 p.m. as twilight was changing to darkness. The term twilight will be used to indicate the period between sunset and darkness. During the next two weeks, the onset of calling was noted daily and was found to occur with great regularity. The time of first call did not vary between two consecutive days by more than three minutes but the mean time became progressively later. During these two weeks, the weather was relatively uniform. On a clear sunny day, I could predict within one to two minutes when the Poor-wills would begin to call.

As the season advanced, greater variations in the onset of calling developed. On overcast days, the calling began earlier, and on brighter days, later. First, one bird would utter one, two, or three notes with short intervals between, followed within 30 seconds

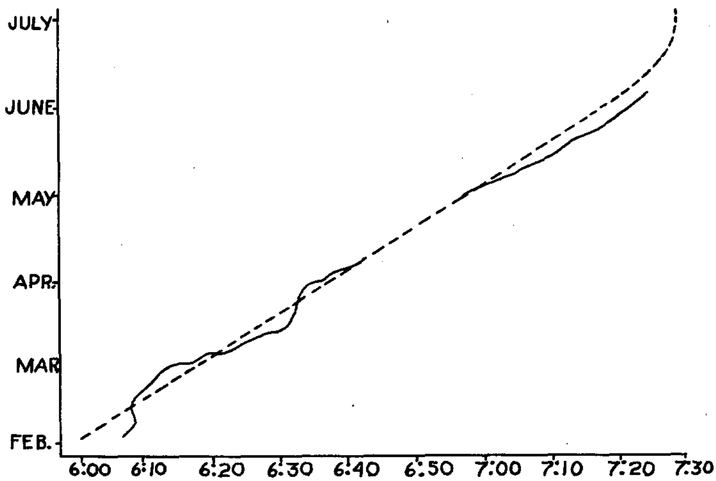

Fig. 1. Onset of activity of Poor-wills in relation to sunset. Broken line represents sunset time plus 20 minutes; solid line, activity. Gap in solid line is period when no observations were made.

by a regular cadence. Thirty seconds to two minutes later, other birds would start to call and the frequency of calls would become maximal almost immediately. Within 30 to 60 seconds of the onset of calling, birds could be seen hawking after moths.

Curves drawn for the time of first activity and sunset to see if there was a relationship showed considerable similarity (fig. 1). To represent the end of the twilight period, 20 minutes were added arbitrarily to the time of sunset. Minor variations caused by daily fluctuations in weather were balanced by taking a running average. Thirty-eight measurements of light intensity at the onset of evening activity were taken. Of these readings, 28 measured less than one foot-candle. Of the 10 readings over one foot-candle, six are probably special cases; four of these measurements were recorded at a nest from which the adult birds had been driven earlier in the day, the adults apparently being eager to return to their young; the other two measurements were recorded on overcast rainy days and appeared to be evoked by the calls of a California Quail.

Although there are no known instances of spontaneous activity by Poor-wills in the daytime, there are a few records of daytime calling. Dr. A. H. Miller (personal communication) reported one calling approximately six times at the Hastings Reservation, Monterey County, California, at 9:00 a.m. in May, 1947. Scott (1886:429) mentions numerous records of daylight singing in Poor-wills and cites an unusual instance of one "singing continuously from 12:00 m. until 12:20 p.m." in bright sunshine in the Catalina Mountains of Arizona at 4000 feet on July 15, 1884. I have never seen an undisturbed Poor-will moving in a light intensity higher than 0.85 foot-candles.

There was relatively less opportunity to make field observations of morning activities. The light meter was available for only ten mornings. The light intensity at the cessation of calling was usually less than one foot-candle, although the range was from 0.3 to 1.9. Little importance can be attached to readings of over 1.5 foot-candles, for in most instances they were associated with disturbances of one sort or another. It appears that Poor-wills are not active through the night when undisturbed. They normally feed at dawn and dusk only when the light intensity is less than approximately one foot-candle.

DURATION OF ACTIVITY

One of the chief reasons for the difficulty in finding Poor-wills is their limited period of activity. From the preceding discussion it is apparent that the birds are active only for brief periods at dawn and dusk. All day long they sit quietly on the ground. As it darkens, they become active and their feeding period lasts half an hour or less. It is during this period of activity that Poor-wills can be called in most easily. Once they have enough food, they retreat to their roosts on hillsides and remain there until the morning activity period. They are quite reluctant to move after they have fed and rarely do so, although an individual bird may call a few times during the night. Observations on a captive Poor-will over a period of ten months showed that it would move about at the end of twilight and again just before dawn but would remain stationary the rest of the time.

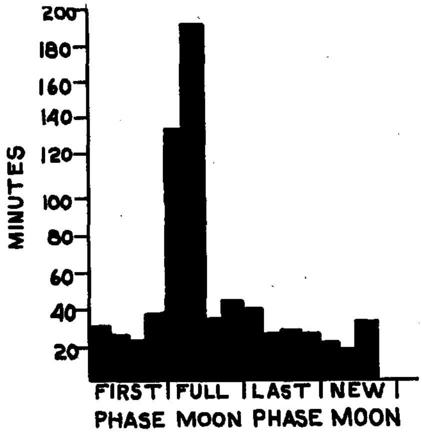

Fig. 2. Duration of activity in relation to phases of moon.

The length of the period of activity is apparently affected by weather conditions and phases of the moon. On days following or during a rainy period, the numbers of moths decreased and the period of Poor-will activity was longer. Under normal weather conditions moths were plentiful and the period of feeding was short. Birds collected from three to seventeen minutes after the beginning of activity had from 20 to 61 large beetles and noctuid moths in their stomachs. The shortest recorded period of activity was three minutes whereas the longest was 192 minutes. The mean duration for 33 observations was 32 minutes; this figure indicates the degree of efficiency of the Poor-will's feeding activities. Duration of activity was plotted in relation to phases of the moon (fig. 2). The longest periods of activity were during the full moon, but even here, there was a well defined period of maximal activity. Even during nesting, the feeding periods were limited to the early evening and predawn hours. Since the light of the full moon at the zenith is only 0.02 foot-candles, I was unable to measure light intensities at night.

REACTION TO TEMPERATURE

The data presented are taken from field records of collected birds, nestlings, and a captive Poor-will. During the past three years, I have had an opportunity to collect a number of Poor-wills. Each one was actively flying prior to the collecting. Cloacal, ground, and air temperatures were taken immediately. The 19 cloacal temperatures range from 40.6° to 43.1°C. (table 1). There is no apparent correlation between air or ground temperature and because of the small number of temperature records, seasonal changes, if any, are not apparent.

Table 1

Temperature Data from Poor-wills Collected in the Field

Date	Time	Cloacal temperature	Ground temperature
Mar. 7, 1947	10:30 p.m.	40.6°C.	10.0°C.
Aug. 7, 1947	7:00 p.m.	41.2	30.3
Aug. 9, 1947	7:15 p.m.	42.0	....
Aug. 17, 1947	evening	42.5	19.8
June 13, 1948	evening	42.6	15.8
June 14, 1948	evening	41.4	26.8
June 14, 1948	evening	42.4	26.8
Aug. 20, 1948	evening	40.5	....
Feb. 20, 1949	6:15 p.m.	42.1	12.7
Mar. 8, 1949	6:18 p.m.	41.0	8.4
Mar. 24, 1949	6:40 p.m.	43.1	8.6
Mar. 24, 1949	6:42 p.m.	42.2	8.6
Aug. 17, 1949	7:10 p.m.	42.8	15.8
Aug. 17, 1949	evening	42.3	15.3
Aug. 19, 1949	7:03 p.m.	42.7	18.0
Aug. 19, 1949	evening	42.8	13.6
Feb. 17, 1950	6:05 p.m.	42.2	16.4
Feb. 21, 1950	6:25 p.m.	41.7	13.0
Mar. 11, 1950	6:22 p.m.	42.2	10.5

Daily rhythm in body temperature.—Baldwin and Kendeigh (1932) experimented on eight species of passeriform birds and corroborated the conclusions of Simpson and Galbraith (1905) that the temperature curve of diurnal birds has the maximum early in the afternoon and the minimum early in the morning. In nocturnal birds, the curve is inverted. In order to determine whether or not the Poor-will's temperature curve fitted either of these patterns, data on its rhythm for a 24-hour day were gathered.

A series of temperatures (cloacal and environmental) and light readings were taken on a captive Poor-will at three-hour intervals for a period of four and one-half days. During this time the captive bird was in an open box on a substrate of loose soil and sand. The box was placed in front of a window. Except at dawn and dusk the bird sat on the dirt or perched on the end of the box without moving except to preen or scratch occasionally. The temperature cycle of the captive Poor-will is markedly different from that of either a completely diurnal or completely nocturnal animal and resembles that of other crepuscular forms (Pearson, 1947). Two maximal and two minimal points are found during a 24-hour period (fig. 3). Maximal temperatures were found at approximately 6:00 a.m. and 6:00 p.m. Minimal readings were found at approximately 2:00 a.m. and 12:00 noon. In the majority of minimal readings, the lowest were found during the daytime. Thus to a certain degree, this fact places the Poor-will closer to the nocturnal group. Changes in body temperature were not associated with any obvious activity by the bird.

The environmental temperature fluctuated from 16.8°C. to 26.3°C., but showed no correlation with the bird's temperature. Light intensity fluctuated from 0 to 260 foot-candles, depending on the time of day.

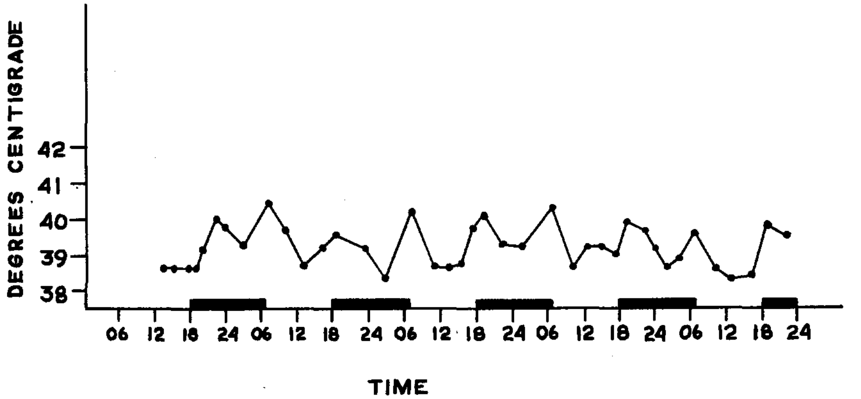

Fig. 3. Daily temperature cycle of Poor-will under room conditions. Time scale shows five 24-hour days. Black areas on abcissa indicate periods of darkness.

Exposure to cold in darkness.—The Poor-will was exposed several times in a refrigerator for from 30 to 90 minutes at temperatures of 0°C., or slightly lower. During the 30-minute exposure, the bird's temperature tended to rise sometimes as much as 0.6°C., but if the exposure were continued for from 60 to 90 minutes, the bird's temperature would fall as much as 0.7°C. from its initial level. To test the Poor-will's capacity for temperature regulation, it was kept for 12 hours (8:00 a.m. to 8:00 p.m.) in total darkness for each of 17 days at a mean temperature of —2°C. The bird's temperature was taken just before it was placed in the refrigerator and as soon as it was taken out.

In every instance the bird's temperature was lower when it was removed from the refrigerator than when it was put in. The decreases in body temperature ranged from 0.7°C. to 2.9°C. with a mean of 1.7°C. It is clearly evident that the Poor-will is capable of regulating its temperature but that its temperature varies slightly with the environment.

Exposure to cold under daylight conditions.—It was shown earlier that cloacal temperatures tended to be slightly lower during the daytime period of quiescence. This is what one might expect in a crepuscular bird. If the Poor-will were to show any tendency toward becoming torpid under cold conditions, it might be expected to best demonstrate this during the daytime when its temperature is normally the lowest.

To test this supposition, the captive Poor-will was kept during the daylight hours of March in a constant temperature chamber and subjected to a temperature of 4°±1°C. and a light intensity of 125 foot-candles. During the night, the bird was kept in the dark at room temperature (18° to 24°C.). The bird's temperature was taken approximately every three hours night and day for four days.

In every instance the bird's temperature was lower when it was removed from the refrigerator than when it was put in. The decrease in body temperature ranged from 1.0°C. to 3.1°C. with a mean of 1.7°C. As before, we see a well developed temperature regulating ability. That the generation of body heat was in part due to muscular activity is suggested by the fact that the bird shivered frequently and strongly.

It is of interest that even when its temperature was at a minimum (36.5°C.), the bird fed with every sign of normality.

REACTION TO DAY LENGTH

Since the captive bird did not become torpid owing to low temperature, the next step was to duplicate reasonably closely the natural conditions of the period of torpidity. The latest date of Poor-will activity in the field noted by me in the Santa Monica Mountains was November 28, 1949, and the earliest resumption of activity was on January 22, 1950. Dr. Joe T. Marshall, Jr. (personal communication) noted as latest and earliest activity dates in Tucson, Arizona, December 1, 1949, and February 4, 1950. These periods coincide fairly well with Jaeger's statement (1950:109) that the period of lethargy for his bird was from November 26, 1947, to February 14, 1948.

Although the shortest time between sunrise and sunset during this period was ten hours, the effective day length for Poor-wills was twelve and one-half hours. The bird was subjected to days of nine and one-half hours duration for sixteen days at room temperature. During the daytime, it was left free in its open box in front of the window. During the period of darkness it was kept in a covered box. It was fed twice under a

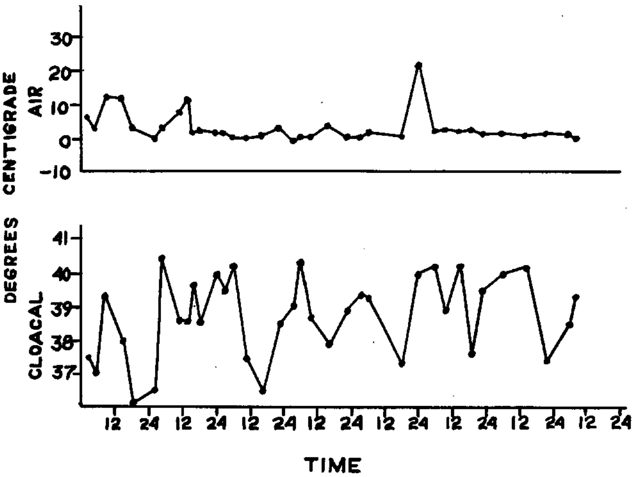

Fig. 4. Fluctuation of cloacal temperature in relation to air temperatures. Horizontal time scale in hours identical for both parts of graph.

dim red light during the dark period. The feeding never exceeded three minutes. At the end of sixteen days, the bird showed no obvious differences, behavioral or otherwise. In this instance, short days alone did not induce torpidity.

Following these artificially shortened days, the bird was confined continuously to the constant temperature chamber and was conditioned to temperatures ranging from 0°C. to 12°C. It was exposed to artificial light of 125 foot-candles for eight hours per day. After 1½ days, the temperature of the chamber was adjusted to 1°±1.5°C. for 6½ days. The lowest ground temperature in the study area taken from thermograph readings was 2.7°C. Approximately every three hours, cloacal temperatures were taken and the bird was fed. During the period that the bird was in the constant temperature chamber, its temperature fluctuated from 36.1° to 40.6°C. on a daily basis (fig. 4).

These fluctuations became progressively smaller on each succeeding day and the mean temperature of the bird actually increased during the experiment. This reaction seemed to indicate an adjustment to the environment. Even after six days, there were no behavioral changes in the bird. It fed well, flew easily and was clear-eyed and alert. The temperature cycle (fig. 4) was not the same as demonstrated earlier under room conditions (fig. 3). More than one maximal point daily is indicated but there was no regularity of occurrence.

REDUCED FOOD SUPPLY

Prior to the period of torpidity the food supply available to Poor-wills under natural conditions is limited. It is at least possible that the onset of torpidity is associated with reduced food supply. Therefore, on the seventh day of the experiment, the food supply was reduced to approximately one-third. On the eighth day, it was reduced still further. On the ninth day the bird was found dead. Dissection showed that the bird was not emaciated. On the skull were a number of blood clots indicating that it had injured itself in flying up against an upper shelf which acted as a roof for its box.

MISCELLANEOUS OBSERVATIONS

I have noted that when a Poor-will is excited or has become heated, it vibrates its white throat patch. It was observed that the bird can relax the pharyngeal muscles so as completely to expose the large and prominent blood vessels of the neck for a considerable distance down the throat. It seems highly probable that this is a mechanism by which the Poor-will may cool itself. This is apparent only in live birds when the glottis is open. I placed a Poor-will in the sun on a hot day in June, 1949, and after 14 minutes the bird's throat began to flutter, followed shortly by the opening of the mouth. The bird was in apparent discomfort and tried to move toward shade. Prior to the exposure to the sun, the bird's cloacal temperature was 40.6°C. After 14 minutes, at the onset of throat flutter, the cloacal temperature was 42.5°C. The bird was then placed in the shade for one hour at which time the cloacal temperature was 40.5°C. This experiment was repeated several times with the same result. Cowles and Dawson (1951) have reported similar reactions in nighthawks.

Table 2

Temperatures of Poor-will Chicks

Approximate age (days)	Cloacal temperature	Environmental temperature	Approximate age (days)	Cloacal temperature	Environmental temperature
3	25.1°C.	15°C.	6	33.4	18.2
3	26.7	15	7	34.5	18.8
3	20.3	12.6	7	35.3	18.8
3	21.0	12.6	11	37.3	17.8
6	33.9	18.2	12	36.2	18.2

Poor-will chicks demonstrated a poikilothermic stage like that of the House Wren as described by Baldwin and Kendeigh (1932). In June, 1949, the cloacal temperatures of young Poor-wills of the same brood were taken (table 2). It can be seen that the body temperature became progressively higher as the chicks aged except for the record of the 12-day old bird. This lower reading may have been due to the fact that the parent bird was away from the young for four and one-half hours at night prior to the reading. The environmental temperatures remained relatively constant. These measurements would seem to indicate that the temperature-controlling mechanism was still developing.

On April 9, 1950 (the earliest nesting record known), a Poor-will was found brooding two young which were approximately three days old. One hour and twenty minutes after the parent bird left, the cloacal temperatures of the nestlings were 25.1° and 26.7°C., while the environmental temperature was 15°C. Two hours and ten minutes later when the environmental temperature was 12.6°C., the cloacal temperatures were 20.3° and 21.0°C. The correlation between body temperature and environmental temperature suggests poorly developed temperature regulation. At the time of the last reading, the chicks were shivering. Therefore, it can be said with reasonable assurance that there was some temperature-controlling mechanism in these semi-poikilothermic young.

DISCUSSION

The induction of torpidity in the Poor-will seems to involve a combination of several factors: light, temperature, food, and possible psychological influences. Further experiments with more individuals under controlled conditions will be necessary before a satisfactory explanation can be found. It seems possible that light may be a major factor in bringing about torpidity; certainly the activity of Poor-wills is closely correlated with light conditions during any twenty-four hour period.

I have not found a torpid bird despite many hours of searching areas where they have been active. During their nesting period, I have found them highly sedentary. To find an active Poor-will by flushing it when a few feet away is a major problem but to find one while it is hibernating by deliberate search has yet to be accomplished. Therefore, the possibility remains that they often stay in the same area throughout the year.

SUMMARY

The onset and cessation of Poor-will activity at dusk and dawn coincides with a light intensity usually lower than one foot-candle.

The duration of activity is limited and is apparently related in length to phases of the moon and to weather.

Cloacal temperatures of active Poor-wills range from 40.6°C. to 43.1°C.

Poor-wills can control their body temperature at low environmental temperatures.

The daily temperature curve of a Poor-will has two high and two low points differing from nocturnal and diurnal birds which show only one of each during any twenty-four hour period.

Neither exposure to cold during daylight, shortened days with and without reduced temperatures, nor reduced diet caused torpidity in a captive Poor-will.

Apparently, Poor-wills cool themselves by vibrating their throats and moving air across the large exposed blood vessels of this area.

Poor-will chicks demonstrate semi-poikilothermy.

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