PHYSIOLOGICAL RESPONSES TO TEMPERATURE IN THE COMMON NIGHTHAWK

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The family Caprimulgidae contains species which appear to deviate from general avian patterns in certain aspects of their physiology. Lesser Nighthawks (*Chordeiles acutipennis*) and Poorwills (*Phalaenoptilus nuttallii*) can remain torpid for relatively long periods in a manner reminiscent of hibernating mammals (Marshall, 1955; Jaeger, 1949; Thorburg, 1953). Pauraques (*Nyctidromus albicollis*) and Poorwills have lower basal metabolic rates than most birds of comparable size (Scholander, Hock, Walters, and Irving, 1950; Bartholomew, Hudson, and Howell, 1962). Most or all members of this family employ gular fluttering in their evaporative cooling, and this contributes to an unusually effective capacity for temperature regulation in hot environments (see Cowles and Dawson, 1951; Howell, 1959; Bartholomew, Hudson, and Howell, *op. cit.*). Although these features make caprimulgids of special interest from a physiological standpoint, only the Poorwill has been subjected to extensive experimental investigation (Bartholomew, Howell, and Cade, 1957; Bartholomew, Hudson, and Howell, *op. cit.*; Howell and Bartholomew, 1959). Since studies dealing with the physiology of additional species in this group appeared desirable, this investigation of the effects of ambient temperature on oxygen consumption, heart rate, evaporative cooling, and body temperature of the Common Nighthawk (*Chordeiles minor minor*) was undertaken. This species, which is abundant in southeastern Michigan in summer, might be expected to differ from the Poorwill in certain features of its physiology owing to its larger size and more extensive distribution.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

The six Common Nighthawks used in this investigation were obtained on the campus of the University of Michigan at Ann Arbor, Michigan. One bird was captured as an adult, the remainder being procured at hatching (two birds), 10 days after hatching (two birds), or just before fledging (one bird). Nestlings were fed baby foods consisting of beef heart, liver, and egg yolk, supplemented with $CaCO_3$, K_2HPO_4, and cod liver oil. Post-fledging individuals were given moths as long as these insects could be procured in the Ann Arbor area. With the onset of autumn, this diet was gradually replaced by one consisting of dogfood, meal worms (*Tenebrio* larvae), and newborn mice. Only the latter two items were taken readily, and it was necessary to force feed the dogfood. Both nestling and post-fledging individuals received a vitamin mixture (Vipenta) daily. The birds were maintained on a 12-hour photoperiod in a $20 \times 40 \times 40$-inch cage which was covered with nylon curtain material. The immature individuals appeared to develop normally and they reached weights within the range for adults (60 to 85 gm.) within three months after hatching. All six birds remained in good condition for the entire eight months they were maintained in captivity.

Unless otherwise specified, all nighthawks were post-fledging and at mature weight

when studied. Oxygen consumption and evaporative water loss were measured during the day while the birds rested in the dark following a fast of at least 12 hours. An open circuit system was used in which air from a low-pressure line passed successively via tygon tubing connections through an absorbent train for water and carbon dioxide, a flow meter, and, finally, through a Beckman paramagnetic oxygen analyzer (Model G–2). The metabolism chamber was fashioned from a one-gallon can by two simple modifications: a horizontal platform of $\frac{1}{2}$-inch wire mesh was fastened inside the can $2\frac{1}{2}$ inches from the bottom; the airtight lid of this chamber was equipped with fittings for the tygon tubing connections. The bottom of the chamber was covered with a $\frac{1}{2}$-inch layer of mineral oil which trapped feces voided by the birds during the experiments.

The rate of air flow through the open circuit system ranged from 260 to 320 cc. air/min., which was generally adequate to maintain the oxygen and carbon dioxide levels in the chamber above 20 and below one per cent, respectively. It also maintained the relative humidity between 70 and 25 per cent in the temperature interval studied (computed from information on the humidity mixing ratios for various temperatures and on the corresponding ratios for saturated air). Temperature within the metabolism chamber was maintained within $0.2°$ C. of the desired level by placing this container in a 17 cubic foot constant temperature cabinet.

Rates of oxygen consumption by nighthawks were computed from data on the fractional concentrations of oxygen in dry, CO_2-free air before reaching and after leaving the metabolism chamber, and on the rate of air flow out of the system. The concentrations of oxygen were determined from the oxygen analyzer record in the manner described by Dawson and Tordoff (1964), and the flow rate was determined with the flow meter. The method employed for computation provided true rates of oxygen consumption unaffected by variations in respiratory quotients, as discussed by Depocas and Hart (1957). All gas volumes specified in relation to oxygen consumption have been corrected to $0°$ C. and 760 mm. Hg. Rates of evaporative water loss by nighthawks were determined when the oxygen consumption had reached a minimal stable level for the particular temperature. Two drying tubes containing Drierite were placed in the open circuit system between the metabolism chamber and the second absorbent train and kept there for a precisely timed interval of 30 minutes. The gain in weight of these tubes with hydration of the desiccant, measured with a balance sensitive to less than a mg., was taken as evaporative water loss. Blank runs were made periodically, to ensure that dry air was flowing through the system.

Measurements of electrocardiograms, from which heart rates were determined, were performed separately from those on oxygen consumption and evaporative water loss. The nighthawk was fitted with two intramuscular electrodes, one in either side of the pectoral musculature, and with a third electrode placed beneath the dorsal feather tract. The animal with electrodes in position was placed in a shielded cage within the temperature cabinet referred to previously. The leads from these electrodes were connected to a high gain, a.c. preamplifier that comprised part of a channel of a recording oscillograph (Sanborn Model 1154). The heart rates presented represent minimal values for the various animals resting in the dark under the conditions specified.

Rates of gular fluttering and breathing were determined visually through a glass port in the temperature cabinet. The birds were confined in the illuminated cabinet in a small ($4 \times 4 \times 12$ inches) cage of $\frac{1}{2}$-inch wire mesh. When the nighthawks were subjected to high ambient temperatures, they commenced fluttering the gular area. The flutter frequency was determined stroboscopically in the following manner. A notched disc 15 inches in diameter was placed between the bird and the observer at the port in

the cabinet in such a manner that the gular area was only visible when the notch was at a particular point. The disk was rotated by an electric motor, the speed of which could be adjusted with a variable transformer. The speed of rotation was signaled by an arm on the disk, which tripped a microswitch with each complete revolution. This actuated a circuit which produced a deflection of the writing arm in a channel of the recording oscillograph referred to previously. A marker on this same channel was actuated by the observer when the rotation of the disk reached a speed sufficient to "stop" the gular flutter.

Body temperatures for birds resting in the dark at moderate temperatures and those in torpor were obtained by inserting the bulb of a Schultheis thermometer through the cloacal opening to a depth of one inch. A fine thermocouple fashioned from 30-gauge copper and constantan wires was similarly inserted for measurements at high ambient temperatures. This thermocouple was placed in the bird prior to the experiment and was held in place by attaching its lead wires to the rectrices with surgical clamps. The lead wires were then connected to a suitably calibrated Brown recording potentiometer so that the body temperature of the bird could be followed continuously.

<div align="center">RESULTS</div>

Oxygen consumption.—With two exceptions, the metabolic values obtained for the Common Nighthawk pertain to individuals that were regulating body temperature. The relation of oxygen consumption by these individuals to temperature is illustrated in figure 1. They seem to lack a well defined thermoneutral zone (range of ambient temperatures over which a standard rate of metabolism is adequate for temperature regulation), metabolism decreasing with increasing temperature to about 35° C. and then slowly increasing above this level. The oxygen consumption at 35° C., which approxi-
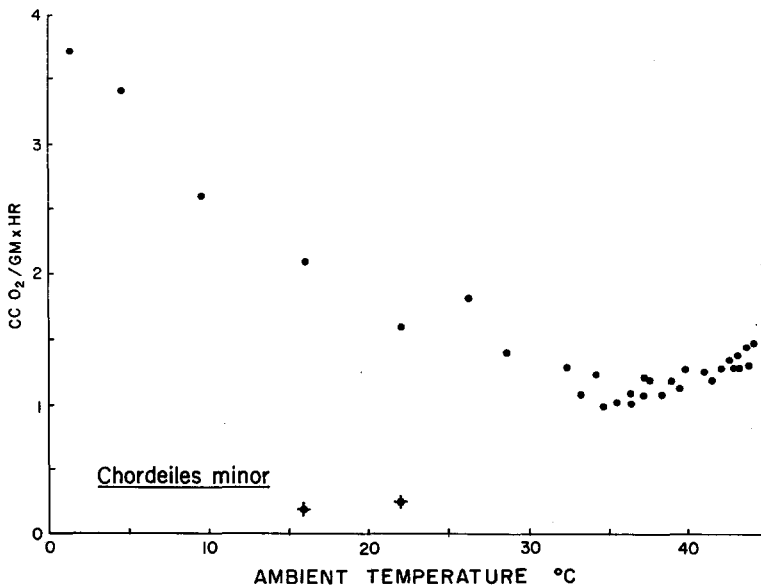

FIG. 1. The relation between oxygen consumption and ambient temperature in the Common Nighthawk. Plain shaded circles represent homothermic birds resting in the dark. Torpid birds are designated by +.

mates 1.1 cc. O_2/gm. hr., has been taken as the standard metabolic rate of the Common Nighthawk.

The relation of oxygen consumption to temperature appears curvilinear between 22° and 35° C. This suggests that both adjustment of heat production, the primary means of temperature regulation at cold temperatures, and adjustment of mechanisms for heat conservation occur in this temperature range. Below 22° C. the available data describe an essentially straight line having a slope of -0.11 cc. O_2/gm. hr. ° C. This line extrapolates to zero metabolism in the vicinity of 38° C., which is in the range of body temperatures observed in nighthawks resting at moderate or cool ambient temperatures (see fig. 5).
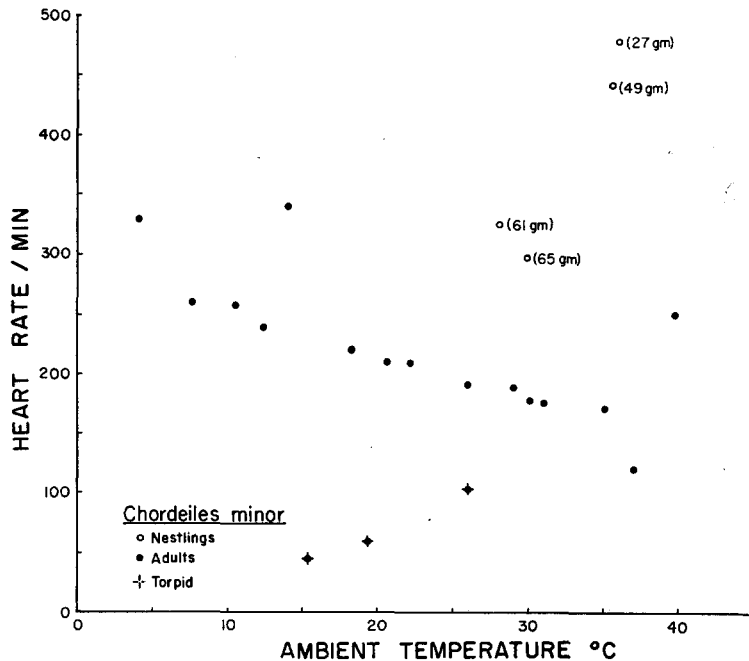

FIG. 2. The relation between heart rate and ambient temperature in *Chordeiles minor*. Nestlings are indicated by unshaded circles, while adults are designated by shaded circles. A + over the shaded circle indicates a torpid bird.

The slope of the straight line which can be fitted to the data on oxygen consumption for temperatures above 35° C. is only 0.04 cc. O_2/gm. hr. °C. The rise in oxygen consumption in this range is primarily associated with activity serving to augment evaporative cooling.

Two values were obtained for the oxygen consumption of a torpid nighthawk. As noted subsequently, this animal only became torpid after maintenance on a reduced diet that had resulted in severe loss of weight. Its oxygen consumption in this condition amounted to less than a sixth that of nontorpid individuals resting at the same ambient temperatures.

Heart rate.—Three types of data were obtained on heart rates of nighthawks (fig. 2). The first concerns individuals studied at moderate ambient temperatures prior to reaching the weight range characteristic of mature birds. Even with allowance for

a slight difference in the temperature at which measurements were performed, the rates for 27- and 49-gm. individuals are conspicuously higher than those for 61- and 65-gm. ones. In turn, the rates for these latter birds are higher than those for birds of mature weight studied at similar temperatures. Although a trend of this type could be anticipated on the basis of general knowledge of metabolism-weight relationships in birds, the actual differences in heart rate among the nighthawks of different ages are too large to be entirely accounted for by the differences in size. Differences in insulation and metabolic activities related to growth may also be involved.

The second type of data available on heart rates of nighthawks concerns the relation of this function to ambient temperature for birds within the weight range of mature birds. In general an essentially linear, inverse relation seems to exist between heart rate and temperature. On a percentage basis, the slope of the line which can be fitted to these data is much shallower than that for the relation of oxygen consumption to temperature below $22°$ C. The line for the former relation extrapolates to zero heart rate at a temperature markedly above $40°$ C.

The third type of data available on heart rates concerns values for a torpid individual. Since body temperature was close to ambient temperature in this bird, it is not surprising that a direct relation is indicated between heart rate and ambient temperature. Torpidity markedly lowers cardiac activity, with heart rates for the torpid individual ranging from half to less than a quarter those for euthermic animals at the same ambient temperatures.
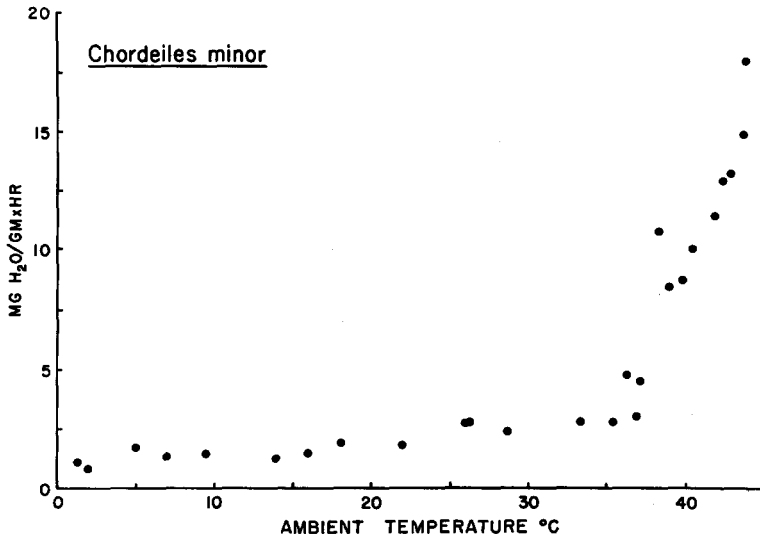

FIG. 3. Evaporative water loss as a function of ambient temperature in the Common Nighthawk.

Evaporative water loss.—The relation of evaporative water loss by the Common Nighthawk to ambient temperature is illustrated in figure 3. Between $1.2°$ and approximately $35°$ C., loss by this route increases at the rate of only 0.01 mg. H_2O/gm. hr. $°$ C. Above $35°$ C. it increases at a much more rapid rate, 1.4 mg. H_2O/gm. hr. $°$ C. A nearly five-fold increase occurs in evaporative water loss by the nighthawk between $35°$ and $44°$ C.

In hot environments, Common Nighthawks, like other caprimulgids on which obser-
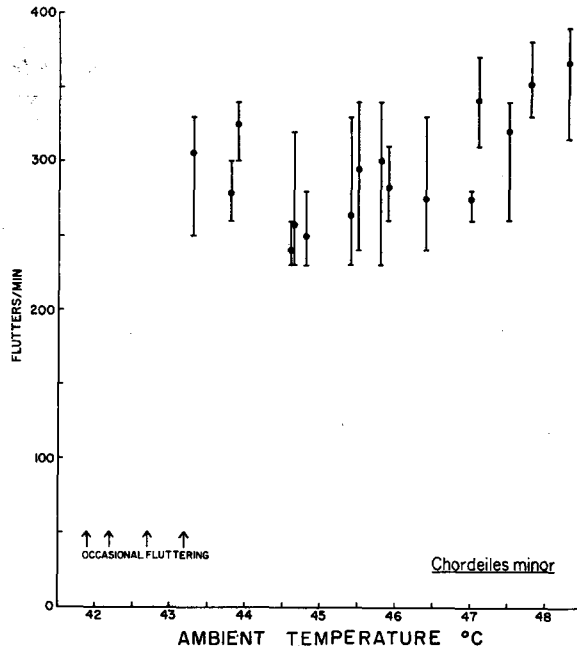
FIG. 4. The relation between the frequency of gular flutter and ambient temperature in the Common Nighthawk. Flutter rates were determined stroboscopically. Vertical lines represent the range of values obtained for an individual at that temperature and the mean value is indicated by a shaded circle.

vations have been made (see Cowles and Dawson, 1951; Bartholomew, Hudson, and Howell, 1962), appear to effect evaporative cooling primarily by fluttering the gular area (fig. 4). This activity occurs intermittently between 41.9° and 43.2° C. Above 43.2° C. it is continued for longer periods. Surprisingly, the rate at which the gular area is fluttered appears largely independent of temperature between this temperature and 47° C. Even at temperatures above 47° C. there is only a faint suggestion of an increase in the rate of this activity. The gular flutter response is not limited to adults but is fully developed when the chick hatches from the egg.

Body temperature.—With three exceptions, the values presented for body temperatures (fig. 5) pertain to nontorpid nighthawks. When such individuals rest in the dark at cool or moderate temperatures (ca. 2° to 35° C.) they tend to maintain body temperature within a range of several degrees (ca. 34° to 40° C.) rather than at a single level. Less individual variation is apparent at temperatures above 35° C., where body temperature rises about 0.4° C. per 1° C. rise in ambient temperature. A line fitted to the data crosses the isothermal line at 41° C. above which nighthawks remain cooler than the environment.

As noted previously, some nighthawks were forced into torpor following serious losses in body weight equivalent to 28 to 34 per cent of their initial weight. The three values of torpid body temperatures pertain to the individual on which measurements of metabolism and heart rate were made. All closely approximate ambient temperature (fig. 5). This particular bird was the only nighthawk that spontaneously aroused from
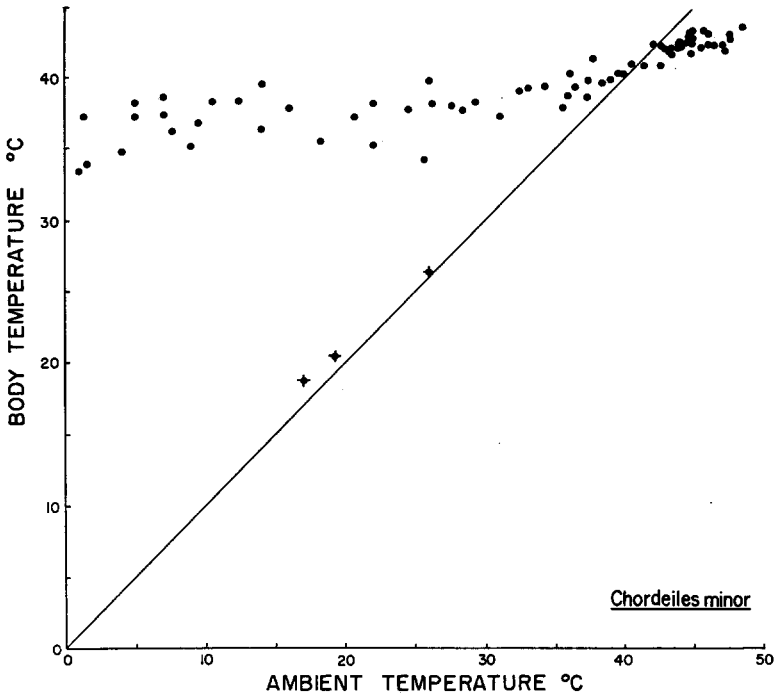
FIG. 5. Body temperature as a function of ambient temperature in *Chordeiles minor*. Torpid birds are indicated by +.

torpidity. Of the three other nighthawks that became torpid, one died when the ambient temperature was changed from 16° to 11° C., and the other two were unable to arouse spontaneously and died when they were artificially re-warmed.

Standard metabolism.—The Common Nighthawk is the third caprimulgid for which standard (or basal) metabolic rate has been determined, the Pauraque (Scholander *et al.*, 1950) and the Poorwill (Bartholomew, Hudson, and Howell, 1962) having been studied previously. All three of these species have lower standard metabolic rates than passerine birds of comparable weight (table 1). Insufficient information is available to allow direct determination of whether or not their rates also fall below those of nonpasserines. However, it is of interest to note that the standard metabolic rate of the Common Nighthawk deviates less than 20 per cent from the value estimated for a bird of comparable size by extrapolation of a weight-metabolism curve constructed by King and Farner (1961) for a group of predominantly nonpasserine birds weighing more than 125 gm. (table 1). Moreover, the values for the standard metabolic rate of the Pauraque actually exceed those estimated by this procedure. However, that of the Poorwill falls considerably below the value estimated for a bird of its size (table 1). This variation in the weight-metabolism relationships of three species of caprimulgids suggests that factors other than size play a role in the determination of the standard metabolic rate in this family of birds. The nature of these factors remains to be demonstrated.

Thermal conductance.—In the thermal range over which temperature regulation proceeds principally by adjustment of heat production (below 35° C. in *C. minor*; see p. 480), the slope of the line fitted to metabolic values adjusted for surface area

provides a convenient index of maximum insulation in the species studied, being inversely proportional to it. The value of the slope is termed thermal conductance, with higher values indicating less effective insulation. Thermal conductance approximates 2.2 kcal./hr. °C. m^2 in the Common Nighthawk (surface area was computed using the formula $m^2 = 0.1\ W^{0.67}$, where W is weight in kg.), a value appreciably higher than that of the Poorwill (Bartholomew, Hudson, and Howell, 1962) which approximates 1.6 kcal./hr. °C. m^2. Thermal conductance (expressed as cc. O_2/gm. hr. °C.) generally appears to vary inversely with size in smaller homeotherms (Lasiewski, 1963), and the reason for the Poorwill's having more effective insulation than the nighthawk is not clear. It is of interest to note that the Poorwill winters in southwestern United States and northwestern México, where it encounters cool and even cold weather, whereas the Common Nighthawk passes this season in tropical areas of South America.

TABLE 1

STANDARD (BASAL) METABOLIC RATES OF VARIOUS BIRDS

Species	Weight (gm.)	Basal metabolic rate (cc. O_2/gm. hr.)	Reference
Common Nighthawk (*Chordeiles minor*)	60–85	1.1	Present study
Pauraque (*Nyctidromus albicollis*)	43–48	1.5–2.3	Scholander *et al.*, 1950
Poorwill (*Phalaenoptilus nuttallii*)	40	0.8	Bartholomew, Hudson, and Howell, 1962
Blue Jay (*Cyanocitta cristata*)	81	1.9	Misch, 1960
Evening Grosbeak (*Hesperiphona vespertina*)	50–65	2.5	Dawson and Tordoff, 1959
Gray Jay (*Perisoreus canadensis*)	62–65	2.5–2.9	Scholander *et al.*, 1950
Hypothetical bird	70	1.3[1]	
Hypothetical bird	48	1.5[1]	
Hypothetical bird	40	1.5[1]	

[1] Predicted by extrapolation of curve fitted by King and Farner (1961) to data on birds weighing more than 125 gm.

Relation of oxygen consumption and heart rate.—The available data on both oxygen consumption and heart rate of *Chordeiles minor* permit calculation of values for the oxygen pulse (oxygen consumed per unit weight per heart beat) at several metabolic levels (table 2). In euthermic birds these values tend to increase as metabolic rate increases with decreasing temperature. This indicates that a rise in stroke volume (volume of blood expelled from the left ventricle per beat) and/or in the utilization coefficient for oxygen (amount of oxygen withdrawn in the tissues from a unit volume of blood) must accompany the observed increase in heart rate. The oxygen pulse of the Poorwill (Bartholomew, Hudson, and Howell, 1962) also rises as metabolism is increased with decreasing ambient temperature (table 2). However, the actual values for this species represent only about two-thirds the corresponding ones in the Common Nighthawk. The oxygen pulses of both of these birds markedly exceed the values which have been reported for several lizards (3–4×10^{-5} cc. O_2/gm. beat) weighing from 30 to 500 gm. (see Dawson, 1960; Dawson and Templeton, 1963; Bartholo-

mew and Tucker, 1963). Only the single torpid nighthawk on which observations were made had an oxygen pulse closely approaching the reptilian level.

Evaporative water loss.—Measurements on resting birds of more than a dozen species have made possible the construction of a curve which summarizes in a reasonably satisfactory manner the general relationship between rate of evaporative water loss at 25° C. and body weight in animals weighing from 20 to about 150 gm. (Bartholomew and Dawson, 1953). The Lesser Nighthawk (40 gm.) was included among these species, and its rate falls very close to the curve. However, the rate obtained in the present study for the larger Common Nighthawk at 25° C. exceeds the value predicted from this curve for a bird of similar weight by more than 25 per cent. The reason for this discrepancy is not clear. It may be related to the fact that the metabolic rate of this caprimulgid at 25° is well above the standard or basal level (see fig. 1) in contrast to the situation in most birds of comparable size, in which this temperature is well within the zone of thermal neutrality.

TABLE 2

OXYGEN PULSE OF CAPRIMULGIDS AT VARIOUS AMBIENT TEMPERATURES

Species	Oxygen pulse (cc. O_2/gm. beat)			State
	10° C.	20° C.	30° C.	
Common Nighthawk	1.8×10^{-4}	1.3×10^{-4}	1.1×10^{-4}	Euthermic
Common Nighthawk		5.1×10^{-5}		Torpid
Poorwill	1.1×10^{-4}	8.7×10^{-5}	7.3×10^{-5}	Euthermic

TABLE 3

EVAPORATIVE WATER LOSS IN RELATION TO METABOLISM IN THE COMMON NIGHTHAWK

Ambient temp. (° C.)	(a) O_2 consumption (cc./gm. hr.)	Estimated max. production of H_2O in metabolism* (mg./gm. hr.)	(b) Evap. H_2O loss (mg./gm. hr.)	b/a (mg. H_2O/cc. O_2)
5	3.3	2.2	1.3	0.39
10	2.7	1.8	1.5	0.56
15	2.1	1.4	1.7	0.81
20	1.8	1.2	1.9	1.06
25	1.4	0.9	2.2	1.57
30	1.2	0.8	2.4	2.00
35	1.1	0.7	3.0	2.72
40	1.2	0.8	9.3	7.74

* In the estimate, it is assumed that the birds are utilizing carbohydrate, which yields 0.13 gm. of water per kcal.

Evaporative water loss gradually declines with decreasing temperatures below 35° C., despite a simultaneous rise in the rate of oxygen consumption (table 3). The reasons for this curious response are obscure. A similar relation is evident at temperatures below the zone of thermoneutrality in a number of small birds: House Wren, *Troglodytes aedon* (Kendeigh, 1939); House Sparrow, *Passer domesticus* (Kendeigh, 1944); Yellow Bunting, *Emberiza citrinella,* and Ortolan Bunting, *E. hortulana* (Wallgren, 1954); several species of hummingbirds (Lasiewski, 1964); Poorwill (Bartholomew, Hudson, and Howell, 1962) and Black-rumped Waxbill, *Estrilda troglodytes*

(Lasiewski, Hubbard, and Moberly, 1964). Whatever its basis, the reduction of evaporative water loss at cool temperatures has obvious advantages for the heat and water economies of these birds. It appears that water lost through evaporation by the Common Nighthawk at 5° and 10° C. is more than offset by the calculated production of metabolic water. However, the situation is reversed at higher temperatures (table 3).

Evaporative water loss by the Common Nighthawk per unit metabolism is summarized in table 3. It ranges from 0.4 mg. H_2O/cc. O_2 at 5° C., to more than 7.7 at higher temperatures. The value for 25° C. is higher than that observed in the Cardinal (*Richmondena cardinalis*), 0.9 mg. H_2O/cc. O_2 (Dawson, 1958), but is essentially identical with that observed for the Poorwill at this temperature (Bartholomew, Hudson, and Howell, 1962).
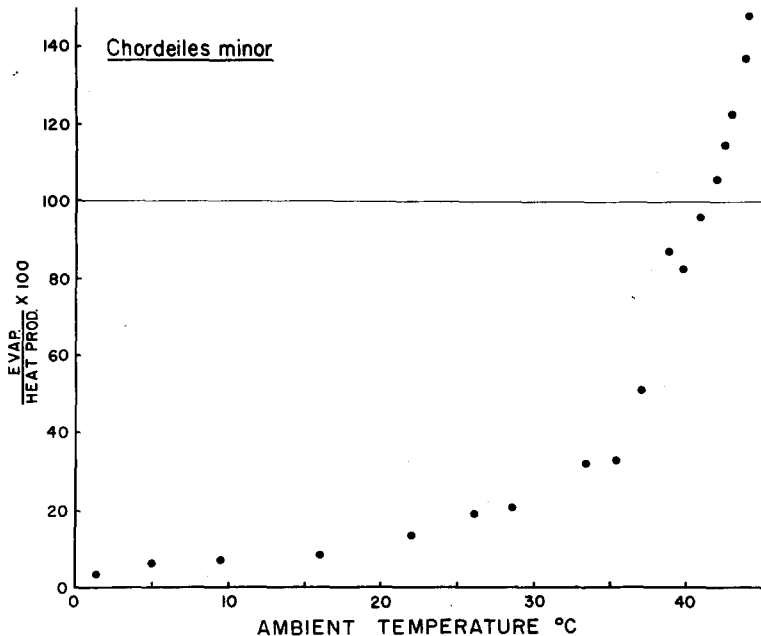

Fig. 6. The relation between heat dissipated through evaporative cooling and heat produced by metabolism as a function of ambient temperature in the Common Nighthawk.

Evaporative cooling.—The effectiveness of evaporative cooling in the Common Nighthawk can be estimated from data on oxygen consumption and evaporative water loss. The conversion of these data to caloric terms involved the assumptions that the use of 1 cc. of oxygen represents the production of 4.8 cal. and that evaporation of 1 mg. of water dissipates 0.58 cal. The proportion of heat production dissipated by evaporation is summarized in figure 6. This proportion rises sharply from about 30 per cent at 35° C. to 100 per cent at 41° C. The continued rise above 41° C. indicates that this bird can dissipate not only all of the heat it produces metabolically but also some or all that it gains from the environment. This is borne out by measurements of body temperature which indicate that this nighthawk remains cooler than its environment at ambient temperatures above 41° C. The relation between heat produced and heat dissipated for the Common Nighthawk is almost identical with that for the Poor-

will (Bartholomew, Hudson, and Howell, 1962). These two caprimulgids differ conspicuously from passerines in their capacities for evaporative cooling at high temperatures, for members of the latter group can dissipate only a fraction of the heat they produce at higher temperatures (Kendeigh, 1939, 1944; Wallgren, 1954; Dawson, 1954, 1958). The effectiveness of the caprimulgids at high temperatures stems from their ability to evaporate quantities of water through gular fluttering without a large increase in metabolism. In both the Poorwill and the Common Nighthawk, the rise in metabolism with temperatures above 35° C. is very gradual and never reaches a very high level. In passerines, which utilize panting as a means of increasing evaporative water loss, the rise in metabolism above the upper critical temperature is pronounced. The small extent of the increase of metabolism in caprimulgids suggests that their mechanism of heat dissipation is more economical from the standpoint of heat production than that of the passerines. At 40° and 44° C., the Common Nighthawk requires no more than 8.7 and 18.1 per cent, respectively, of the heat it produces evaporatively to offset the heat production associated with gular flutter and related activities (table 4). The true figures may actually be lower, for a portion of the use in metabolism at 40° and 44° C. may be associated with the slightly higher body temperature noted at these air temperatures (fig. 6). In the Cardinal it was estimated that about 40 per cent of the heat dissipated by evaporative cooling is required to offset the heat produced in activities leading to augmentation of the rate of evaporation (Dawson, 1958).

TABLE 4

NET EFFICIENCY OF EVAPORATIVE COOLING IN THE COMMON NIGHTHAWK

Ambient temp. (° C.)	(a) Metabolic cost of evap. cooling[1] (cal./gm. hr.)	Evap. cooling (cal./gm. hr.)	Percentage of evap. cooling required for dissipating a	Net efficiency of evap. cooling (per cent)
40	0.48	5.51	8.7	91.3
44	1.68	9.28	18.1	81.9

[1] Determined by subtracting basal metabolic rate from rate at temperature indicated. It is probable that part of the difference is associated with the slightly elevated body temperatures existing at 40° and 44° C. Therefore the true net efficiencies are probably higher than shown.

The absence of a strong thermal dependence in the frequency of gular flutter (fig. 4) is a striking feature of the response of the Common Nighthawk to heat. Perhaps it indicates that a specific resonant frequency exists at which gular fluttering can proceed with relatively little expenditure of energy. It is important to note that although the flutter frequency was fairly uniform, the length of time the birds engaged in this activity was temperature dependent. At lower temperatures (42° to 43° C.), these animals increased evaporative water loss by opening the mouth and occasionally fluttering the gular area. As the environmental temperature increased, the periods of gular fluttering became longer, until at higher temperatures, the birds were engaged in this activity almost continuously.

   Temperature regulation.—The variability of body temperature in Common Nighthawks that had rested in the dark (fig. 5) is similar to that observed in various passerines under comparable conditions (see Dawson, 1958; Misch, 1960). However, the general level of temperature maintained by these caprimulgids in environments between 1° and 34° C. is a couple of degrees lower than that characteristic of these other birds. In environments warmer than 34° C., nighthawks undergo a rise in body temperature, despite their unusually effective evaporative cooling. Such a rise is beneficial in adjust-

ment to hot environments, if prevented from proceeding to an injurious level, since it reduces the difference between the body and ambient temperatures and thereby lessens the need for evaporative cooling. Moreover, the stored heat which brings it about can be dissipated by heat transfer when conditions ameliorate, rather than by expenditure of water in evaporation.

The extensive resistance of the Common Nighthawk to heat is probably of greatest importance for birds protecting eggs or young from solar radiation. In this species eggs are frequently laid in exposed situations where heat can be intense, for example on tar and gravel roofs of buildings in the Ann Arbor area or in open fields, and such protection is essential. Gular flutter and related responses allow attentive birds to contend successfully with severe heat loads.

Torpidity.—The starvation required to induce torpidity in the Common Nighthawk and the failure of three of the four individuals which became torpid to arouse suggest that this condition normally plays no role in the biology of this highly migratory species. This is in contrast to the case of the smaller and somewhat more sedentary Poorwill. The difficulty with which torpidity is induced in the Common Nighthawk also contrasts sharply with the situation in the smaller Lesser Nighthawk. Perhaps the readiness with which goatsuckers become torpid is inversely related to size. It would be of interest to determine whether or not large species such as the Tawny Frogmouth (*Podargus strigoides*) can enter and arouse spontaneously from torpor.

SUMMARY

The effects of ambient temperature on physiological responses of six Common Nighthawks (*Chordeiles minor*) were studied. The standard metabolic rate for this species approximates 1.1 cc. O_2/gm. hr. and is essentially identical with those predicted for birds of this size range (60 to 85 gm.) by the King-Farner equation. Below 35° C., metabolism increases with decreasing ambient temperature, and the best estimate of thermal conductance in the zone of chemical regulation is —0.11 cc. O_2/gm. hr. °C. Above 35° C., metabolism increases at the rate of 0.04 cc. O_2/gm. hr. °C., and this rise in oxygen consumption is primarily associated with activity serving to augment evaporative cooling.

Evaporative water loss increases with increasing ambient temperature, with values ranging between 1.1 and 2.8 mg. H_2O/gm. hr. at 1.2° and 35.5° C., respectively. Above 35° C., evaporative water loss increases rapidly with ambient temperature, reaching 17.9 mg. H_2O/gm. hr. at 44° C. The effectiveness of evaporative cooling in *C. minor* was estimated from data on oxygen consumption and evaporative water loss. At 44°, these birds may dissipate through evaporation 1.5 times the heat produced by metabolism, and the relation between heat produced and heat dissipated in the Common Nighthawk is almost identical with that for the Poorwill.

An essentially linear, inverse relation exists between heart rate and ambient temperature in homeothermic nighthawks, with values ranging from 125 beats per minute at 37° C. to 330 beats per minute at 4° C. At cool to moderate ambient temperatures (ca. 2° to 35° C.), nighthawks tend to maintain their body temperatures within a range of several degrees (34° to 40° C.) rather than at a single level. A line fitted to the body temperature data crosses the isothermal line at 41° C., above which nighthawks remain cooler than the environment.

Common Nighthawks have the physiological capacity to enter into and arouse from torpor, but only after prolonged starvation. It seems unlikely that torpor plays any significant role in the ecology of this species.

At ambient temperatures above 41° C., nighthawks increase evaporative cooling through gular flutter, without a large increase in metabolism. The absence of a strong thermal dependence in the frequency of gular flutter suggests that a specific resonant frequency exists at which gular fluttering can proceed with relatively little expenditure of energy. Although the flutter frequency is fairly uniform, the length of time the birds engage in this activity is dependent on temperature, with longer periods of gular flutter occurring at higher temperatures.

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