SOME ASPECTS OF TEMPERATURE RELATIONS IN SMALL OWLS

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THE owls, Strigiformes, and goatsuckers, Caprimulgiformes, are the only widespread groups of terrestrial birds in which most species are crepuscular or nocturnal. Members of these groups exhibit morphological modifications related to their modes of life, such as enlarged, specialized eyes and the asymmetrical ears of some owls. It is of interest to speculate on possible physiological modifications in metabolic rates and temperature regulation that can be correlated with nocturnal periods of activity. Birds active at night, when temperature is at its lowest, would possibly require less special augmentation of metabolic rate, as by shivering, than diurnal species. In addition they might have low rates of metabolism that would decrease energy requirements. Nocturnal species might be expected to be less tolerant of high ambient temperatures than diurnal ones that are active during the warmer parts of the daily cycle, and also to be less capable of withstanding extreme elevations of body temperature.

Two species of the family Caprimulgidae, the Poor-will (*Phalaenoptilus nuttallii*) and the Common Nighthawk (*Chordeiles minor*), have been carefully studied and both do indeed show unusually low rates of metabolism (Bartholomew et al., 1962; Lasiewski and Dawson, 1964). Both species also have highly effective systems of evaporative cooling that permit them to withstand high ambient temperatures with little elevation in body temperatures (Lasiewski and Bartholomew, 1966; Lasiewski and Dawson, 1964). As similar studies dealing with the physiology of small owls are lacking, I carried out investigations on several members of this group in conjunction with my study of the Elf Owl, *Micrathene whitneyi* (Ligon, 1968).

MATERIALS AND METHODS

I obtained three Whiskered Owls (*Otus trichopsis*), three Pigmy Owls (*Glaucidium gnoma*), and one of two Screech Owls (*Otus asio cineraceus*) in the Chiricahua Mountains, Cochise County, Arizona. The Whiskered and Screech Owls were taken from nests shortly before they fledged, the Pigmy Owls at 4 days of age. The other Screech Owl (*O. a. naevius*) and two Saw-whet Owls (*Aegolius acadicus*) were captured as adults near Ann Arbor, Michigan.

The owls were housed in wire-mesh cages in a room at the University of Michigan Museum of Zoology, where air temperature was maintained at 23°C and relative humidity ranged from 15 to 50 per cent. Photoperiods matched those prevailing for the latitude of Ann Arbor (about 42° N). The owls were fed laboratory mice with occasional supplements of live crickets obtained from a commercial hatchery. All the birds were in good condition throughout the experimental period. Those obtained as juveniles had completed the prebasic molt before investigations were begun, except the Pigmy Owls which were tested while in juvenal plumage. The owls captured as adults were also in fresh plumage.

All measurements were made during the day and food was withheld on the night preceding any test. Each bird was weighed to the nearest tenth of a gram prior to metabolic measurements.

For measurements of oxygen consumption each owl was placed in a new gallon paint can where it perched on a horizontal platform of ¼-inch wire mesh. Each chamber was equipped with fittings for tygon tubing connections and an airtight port for a thermocouple. The chambers were placed in a thermostatically controlled temperature cabinet. The air temperature inside each chamber was monitored with a thermocouple used in conjunction with a suitably calibrated Brown recording potentiometer. A Beckman paramagnetic oxygen analyzer (Model G-2) equipped with another chart recorder provided essentially continuous records of the oxygen consumption of individual owls. Air flowed from a low pressure line through a tube containing a water absorbent (Drierite) and then through a rotameter for measuring flow rate before entering the animal chamber. Values for oxygen consumption were calculated from flow rates and oxygen concentrations using the appropriate formula given by Depocas and Hart (1957). All values specified for oxygen consumption refer to dry gas at standard conditions of temperature and pressure (0°C and 760 mm Hg). CO_2 was removed before the air entered the analyzer.

The animals were placed in the chambers between 08:00 and 09:00 e.s.t. The first resting rates usually were taken about 2 hours later, well after the animals had come to rest. Metabolic measurements were taken at three or fewer ambient temperatures per day, and the animals were exposed to a given ambient temperature for at least 2 hours. Temperatures were presented to the owls in a direction away from the thermoneutral zone, i.e. starting at moderate temperatures and moving either to higher or lower temperatures in a stepwise fashion.

Evaporative water loss was determined by inserting a series of three U-tubes, filled with Drierite, into the exit air flow line from the metabolic chamber. Their change in weight over a carefully measured period of time was taken as the evaporative water loss. During determinations of evaporative water loss, metabolism was recorded every 2½ minutes, rather than every 10 minutes, as was the case at other times. The air flow for evaporative water loss experiments was 830 cc/min. Mineral oil was placed under the wire-mesh platforms to trap feces the birds voided.

Body temperatures were taken at the conclusion of a metabolic run by use of either a copper-constantan thermocouple or a mercury thermometer especially designed for small animal work. Continuous recordings of deep body temperature over a period of several hours also were taken, as discussed below.

Investigations of heat tolerance and of the effects of differing humidities on evaporative cooling were undertaken in a Hotpack room (ca. 7′4″ × 6′8″ × 4′0″) in which humidity and temperature were controlled. Values for the former were imprecise (e.g. setting of the wet and dry bulb controls for a relative humidity of 20 per cent resulted in values ranging from 19 to 26 per cent, as calculated from the actual wet and dry bulb temperatures, over the range of temperatures at which the birds were tested). Ambient and body temperatures were recorded continuously by thermocouples attached to a Brown recording potentiometer. The thermocouple recording ambient temperature was placed within 3 inches of the birds. Body temperatures were obtained by placing thermocouples through the cloaca into the large intestine and securing the wire leads to the bases of the rectrices with surgical clips. The birds were then placed in a small (10″ × 10″ × 10″) wire cage in the constant

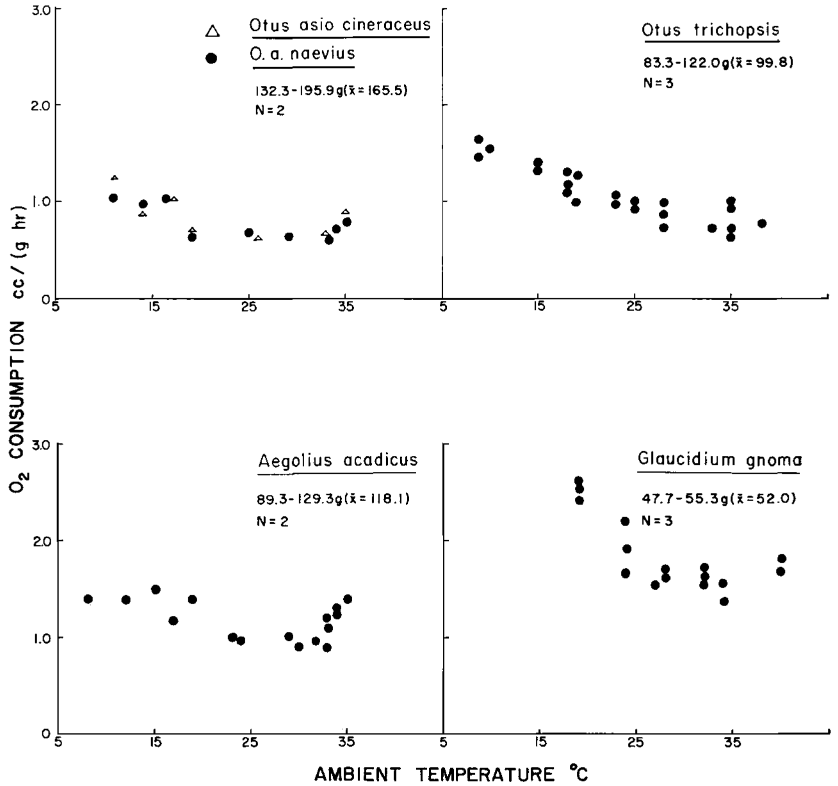

Figure 1. Resting rates of oxygen consumption of four species of small owls in relation to ambient temperature.

temperature room and their body temperatures were allowed to reach a stable level before ambient temperatures were increased. In each test I attempted to hold the humidity at a constant level while ambient temperature was varied. Responses to increased temperature at three humidity ranges were investigated: low (19–26 per cent); medium (47–58 per cent); and high (76–89 per cent). Vapor pressure deficits at these humidities, over the temperature ranges studied, were 38–54, 16–36, and 7–14 mm Hg respectively.

The effects of increasing temperature on behavioral and postural adjustments and on gular flutter were observed through a small window in the door of the Hotpack unit, through which the observer was inconspicuous to the owls. Rates of gular flutter were obtained both with an electronic stroboscope and by direct counting over a period timed with a stopwatch. To determine the rate of gular flutter stroboscopically it was necessary to enter the room with the owls. This usually delayed the initiation of flutter until body temperature was somewhat higher than that at which this activity usually began. The periodicity of flutter and the duration of each flutter session were recorded on a revolving kymograph drum by activating a signal magnet connected to an inductorium.

TABLE 1

MINIMAL LEVELS OF METABOLISM IN THE ZONE OF THERMAL NEUTRALITY

Species	Weight (g)	T_A (°C)	Metabolism (ccO_2/g hr)
Screech Owl	141.5	26	0.63
	191.5	19	0.63
Whiskered Owl	122.0	35	0.62
	119.0	35	0.70
Elf Owl	50.3	27	0.89
	45.4	35	0.99
	42.8	35	0.95
Pigmy Owl	55.3	35	1.36
	53.2	27	1.55
Saw-whet Owl	129.3	32	0.96
	122.1	33	0.87
	119.7	29	1.03

Gular fluttering appeared to be stressful to the owls in which it was studied, and during measurements of it ambient temperatures were increased fairly rapidly to minimize the total time birds were actively engaged in this activity.

Some data on Elf Owls, reported on elsewhere (Ligon, 1968), are included for comparative purposes.

RESULTS

Oxygen consumption.—Relationships of oxygen consumption to ambient temperature in the Screech, Whiskered, Saw-whet, and Pigmy Owls are illustrated in Figure 1. Table 1 gives minimal levels of metabolism of small owls. A least squares regression was fitted to the points obtained at lower temperatures for three of the species. The equations for the slopes of those species and the temperature ranges from which the slopes were derived are: *Otus asio*, $ccO_2/(g\ hr) = 1.58 - 0.043t$, 11–19°C; *O. trichopsis*, $ccO_2/(g\ hr) = 1.75 - 0.035t$, 9–25°C; *Aegolius acadicus*, $ccO_2/(g\ hr) = 1.55 - 0.022t$, 8–24°C.

Body temperature.—Body temperatures, taken at the conclusion of metabolic tests at various ambient temperatures, show considerable lability (Figure 2). Continuous recordings of body temperatures, taken over an extended period of time at a constant ambient temperature, show a similar body temperature-ambient temperature relationship. Noticeable hyperthermia developed at different ambient temperatures depending on the moisture content of the air.

Evaporative water loss.—Figure 3 illustrates the relationship of evaporative water loss to ambient temperature in the Elf and Whiskered Owls. Relative humidity within the metabolism chamber increases as ambient temperature rises, and the humidity level together with the ambient

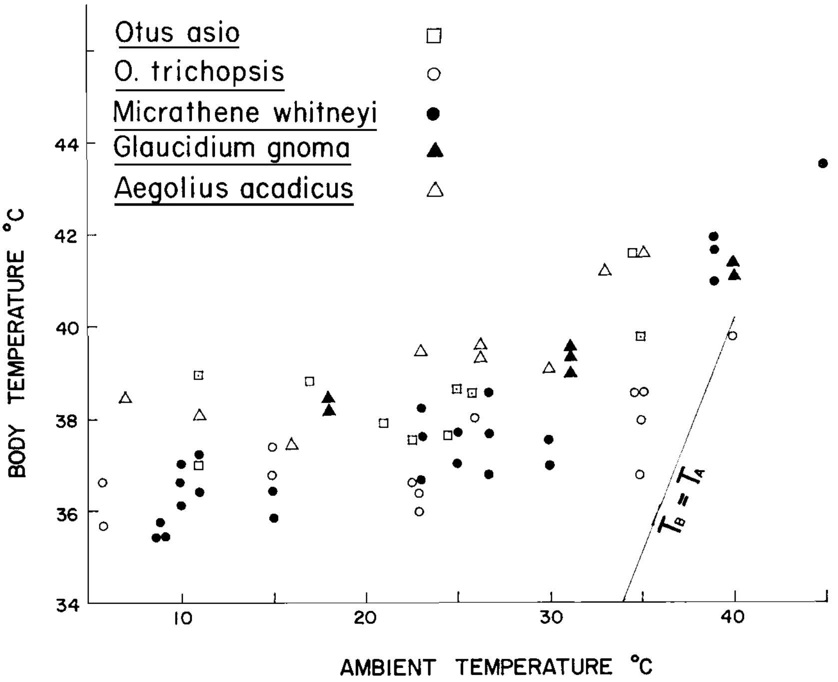

Figure 2. Body temperature of five species of small owls as a function of ambient temperature. Relative humidity at the highest ambient temperature was 14 per cent.

temperature acts to trigger active evaporative cooling. Relative humidities within the metabolism chambers were calculated using the equation given by Lasiewski (1964). Relative humidity was about 14 per cent at 45°C for the Elf Owl and was 11 per cent at 38°C in the Whiskered Owl. Other calculated humidity values were less. Additional evaporative water loss values were: Pigmy Owl, 2.5 and 4.9 mg H_2O/(g hr) at 35°C and 8.6 and 9.6 mg H_2O/(g hr) at 40°C; Screech Owl, 0.79 mg H_2O/(g hr) at 19°C and 1.16 mg H_2O/(g hr) at 33°C.

Responses to rising ambient temperatures.—Initial responses to rising ambient temperatures in the Screech, Whiskered, and Saw-whet Owls were similar to those described for the Elf Owl (Ligon, 1968:55–56). Responses of the Pigmy Owls to high ambient temperatures were not studied.

First there was a cessation of activity and compression of the body feathers, thus reducing the insulation provided by the plumage. The wings were then held away from the body and usually the eyes were closed. As body temperatures rose panting began, often with conspicuous dorsal-ventral movements of the abdomen. When body temperature continued

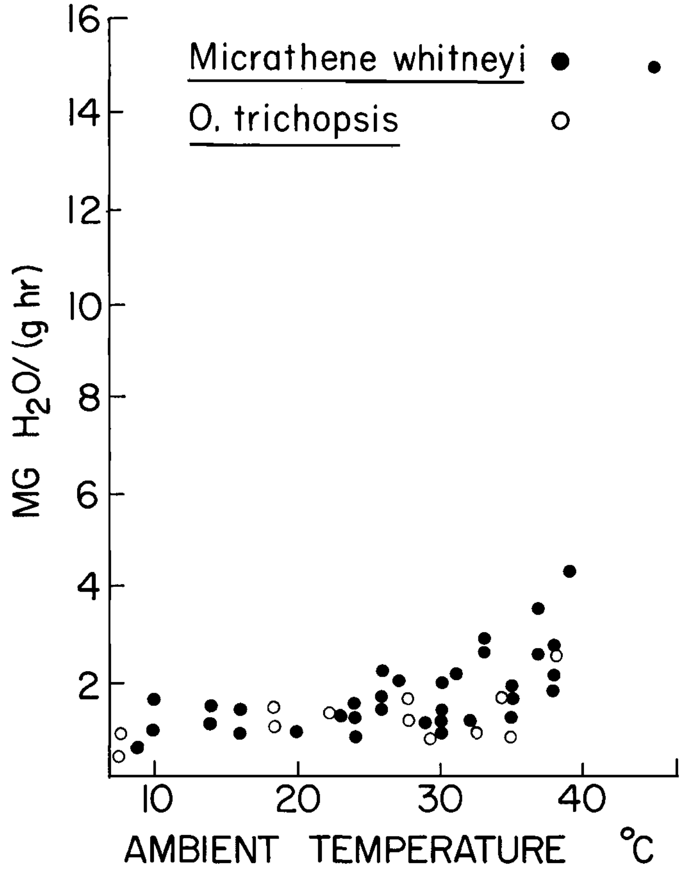

Figure 3. Evaporative water loss as a function of ambient temperature in the Whiskered and Elf Owls. Maximum relative humidity was 11 per cent at 38°C in the Whiskered Owl and 14 per cent at 45°C in the Elf Owl. Elf Owl data from Ligon (1968).

to rise, the Saw-whet and Elf Owls often became restless before initiating gular flutter, whereas the Screech and Whiskered Owls remained calm before fluttering began.

Body temperature of the Arizona Screech Owl and Whiskered Owls typically showed a relationship to increasing ambient temperature similar to that of the Elf Owl (Ligon, 1968). Ambient temperatures rose well above body temperatures at low humidities, body and ambient temperatures rose close together at moderate humidities, and body temperature paralleled but was above ambient temperature at high humidities. The more northern Screech Owl and the Saw-whet Owls were unable to maintain

TABLE 2
RATES OF GULAR FLUTTER AND PANTING IN INDIVIDUALS OF FOUR SPECIES OF SMALL OWLS

Species	Gular Flutter (flutters/min)	Panting (breaths/min)
Screech Owl	215–540	—
Whiskered Owl	150–386	68–128
Elf Owl	176–523	135–160
Saw-whet Owl	109–435	86

body temperature below a rising ambient temperature at any of the humidities to which they were exposed, presumably as a result both of their heavy insulation and less effective systems of evaporative cooling.

Rates of gular flutter are given in Table 2. The Whiskered and Screech Owls (including *O. a. naevius*) appeared to flutter with less effort than did the Elf or Saw-whet Owls. The mandibles moved slightly, if at all, in the former two species, and as the birds became more stressed the gular area occupied by flutter increased, as did the time spent in this activity, in a manner similar to the Poor-will (Lasiewski and Bartholomew, 1966). The Whiskered Owl demonstrated a slow flutter and a pumping of the gular area with the beak closed more often than did the other species. The Saw-whet Owls also varied both rate of flutter and area occupied by flutter as the birds became more stressed. In this species the lower mandible moved with every flutter, as was often true of the Elf Owl. In all species slow movements of the gular area before and after sessions of flutter were not uncommon and rate of flutter often slowed conspicuously before stopping. A sticky saliva or mucus accumulated in the mouths of all species during gular flutter, and strands could often be seen adhering to the palate and floor of the pharynx.

Upper lethal body temperatures.—Two Elf Owls died several hours after reaching body temperatures of 42.3 and 42.4°C respectively. The former had undergone a rise in body temperature to between 41 and 42°C for three 20-minute periods, each separated by more than 1 hour. The latter's body temperature was above 41.5°C for 18 minutes. The body temperature of another Elf Owl reached 43.6°C, but this bird suffered no ill effects (Ligon, 1968: 57). Two Saw-whet Owls that were heated to 42.9 and 44.3°C respectively died within 24 hours. In both cases body temperatures were at these maxima for no more than 10 minutes. Both suffered loss of coordination prior to death. Although I reduced ambient temperatures rapidly when it became apparent that the Saw-whets were severely stressed, there was a lag before body temperature ceased to rise (Figure 4) with fatal elevation of body temperature resulting. A Whiskered Owl that was

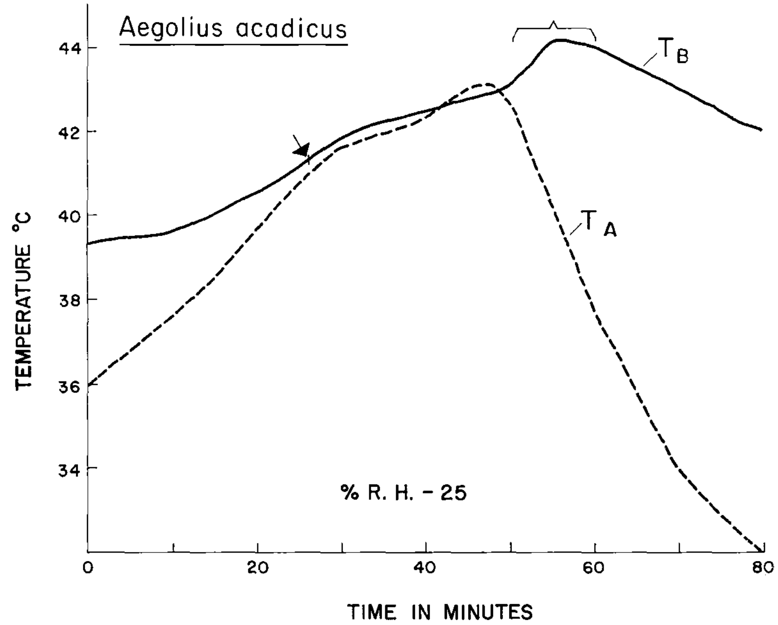

Figure 4. Cloacal temperature in the Saw-whet Owl, in relation to ambient temperature, at a relative humidity of about 25 per cent. The arrow indicates the point at which gular flutter began. The bracket indicates the period of extreme restlessness of the owl which contributed to a fatal elevation of body temperature.

heated to 42.2°C became very restless, but the ambient temperature was quickly lowered and it survived with no apparent damage.

Some of the fatal elevations in body temperature described above are considerably less than those tolerated with no ill effects by several other bird species (Dawson and Schmidt-Nielsen, 1964). The reasons for this intolerance in the owls studied are unclear.

Attempts to induce torpor.—I attempted to force a single Elf Owl into torpor. In a 3-day period of food deprivation, during which time metabolism was recorded at an ambient temperature of 7°C for three 8-hour periods, the bird suffered a 24 per cent loss in body weight (46.9 to 35.7 g). Although the owl appeared to be weakened by this treatment nothing indicated that it approached torpidity at any time. Metabolism remained high (2.44–2.94 $ccO_2/(g\ hr)$ and body temperature did not fall below 35°C.

On two occasions I placed individual Whiskered Owls in a Hotpack unit set at an ambient temperature of 15°C and withheld food for 4 days. Weights of the two owls dropped from 97.3 and 89.1 g to 81.4 and 75.8 g respectively. Body temperatures were 36–37°C at the end of 48 and 96 hours.

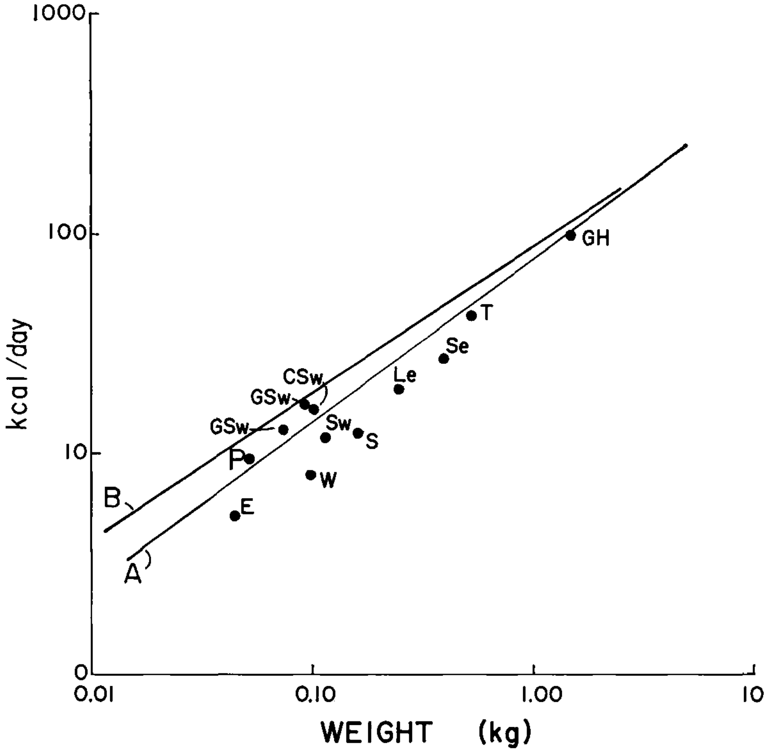

Figure 5. Relation between standard metabolic rate and body weight in owls. A, regression line of King and Farner (1961); B, combined passerine and nonpasserine regression line of Lasiewski and Dawson (1967). Coordinates are logarithmic. From the present study: Pigmy Owl (P), Saw-whet Owl (Sw), Whiskered (W), and Screech (S) Owls. From Ligon (1968): Elf (E). From Graber (1962): Long-eared Owl (Le), Short-eared Owl (*Asio flammeus*) (Se), and Saw-whet (GSw). From King and Farner (1961): Tawny Owl (*Strix aluco*) (T), Great Horned Owl (*Bubo virginianus*) (GH). From Collins (1963): Saw-whet Owl (CSw).

A Screech Owl was placed in the Hotpack unit, also at 15°C, for a 3-day period, with all food withheld. During this time its weight decreased from 129.6 to 98.6 g, a 24 per cent loss. As in the other species, no hypothermia was evident.

Discussion

Standard rates of metabolism.—Earlier (Ligon, 1968: 57) I determined a metabolism-weight curve (kcal/day $= 45.6$ kg$^{0.71}$) for some owls, using standard values I obtained of the Elf, Screech, and Whiskered Owls, plus that of the Long-eared Owl, *Asio otus* (Graber, 1962). More recently I obtained standard values for the Pigmy and Saw-whet Owls and these, together with published values for other owls, are plotted in Figure 5.

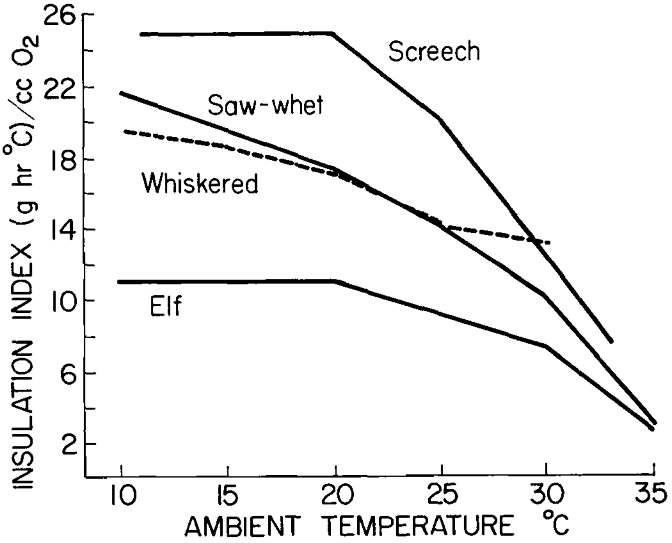

Figure 6. Index of insulation (T_B–T_A/O_2 consumption) in relation to ambient temperature for four species of owls. From Ligon (1968: 58).

Body temperature.—Body temperatures of the owls did not appear to be closely related to body size per se, contradicting the contentions of McNab (1966) that "Small birds have higher body temperatures than large birds because they have higher rates of heat production, relative to their weight, than do large birds, . . ." (see Table 1) and "The apparent correlation between the level of body temperature and the taxonomic group is really a correlation of weight and taxonomic group." These generalizations are based on data gathered by a variety of means, most of which do not reflect the labile nature of body temperature in birds, nor are the effects of the different methods used in obtaining the data considered.

Insulation.—An index of insulation, T_B–T_A/O_2 consumption (Musser and Shoemaker, 1965), is given in Figure 6. The Screech and Elf Owls maximize their insulation more rapidly than do the other two species, which combine increasing insulation and metabolism over a wide range of ambient temperatures, as West (1962) described for several species of passerines. This similarity of response in winter-captured wild birds (Saw-whet Owls) and cage-reared birds that had never encountered cold (Whiskered Owls) suggests that their responses to decreasing temperatures were not conditioned by the environment, as is the case in birds acclimated to low temperatures in the laboratory (West, 1962).

Insulation values were calculated in the manner described by Misch (1960) for the two species (Elf and Screech Owls) that maximized insulation. The insulation value for the Elf Owl (0.30 C × m^2 × hr × $kcal^{-1}$) is lower than all but one value listed by Misch, whereas the value obtained for the Screech Owl (1.00 C × m^2 × hr × $kcal^{-1}$) is higher than that of any species studied except the Gray Jay, *Perisoreus canadensis* (Veghte, 1964).

Effectiveness of evaporative cooling.—Effectiveness of evaporative cooling $\left(\frac{\text{Evaporative Heat Loss}}{\text{Heat Production}}\right)$ in the Elf Owl is about one-half that of the Poor-will, a species of similar body size, in part because metabolism during gular flutter is approximately doubled in the Elf Owl (Ligon, 1968: 59), whereas it is only slightly elevated in the Poor-will (Bartholomew et al., 1962). Effectiveness of gular flutter was not quantified in any of the other species of owls, but observations of their behavior suggest that the Screech and Whiskered Owls are capable of greater heat dissipation by this means than are the Elf and Saw-whet Owls, apparently because they are able to utilize a greater portion of the upper digestive tract as an evaporative surface (see Lasiewski and Bartholomew, 1966).

Unlike the caprimulgids that have been studied, the owls investigated here do not flutter at a constant rate. In addition, in some of the species the mandibles are moved with every flutter, increasing the energy expenditure of this system of cooling. I was unable to detect panting during periods of gular fluttering in the owls I studied. This is unlike the situation in the Great Horned Owl, where panting and gular flutter are simultaneous and synchronous (Bartholomew et al., 1968).

Based on responses to rising ambient temperatures, apparently selection for an effective system of evaporative cooling has been stronger in the caprimulgids studied than in many owls. The Poor-will and Common Nighthawk frequently roost and nest in open places directly exposed to the rays of the sun, whereas the small owls nest in cavities and choose day roosts in shaded trees or bushes or in cavities. Cavity temperatures of several Elf Owl nests and one Screech Owl nest were recorded continuously in late May and early June in Cave Creek Canyon of the Chiricahua Mountains. The maximum temperature recorded in an Elf Owl cavity was 40°C (Ligon, 1968: 49), while it was 32°C in the Screech Owl nest.

The ability to gular flutter is apparently characteristic of all owls. It is frequently observed in the Great Horned Owl and is a highly effective means of cooling in this species (Bartholomew et al., 1968). I have seen it in the Hawk Owl (*Surnia ulula*) and W. R. Dawson informs me that he has observed it in a captive Snowy Owl (*Nyctea scandiaca*). Elf Owls are capable of gular flutter at hatching (Ligon, 1968: 50).

Body and ambient temperatures at which initial gular flutter were recorded, at three humidity levels, are presented in Table 3. An inverse

TABLE 3
MEAN BODY AND AMBIENT TEMPERATURES AT WHICH INITIAL GULAR FLUTTER WAS RECORDED AT THREE HUMIDITY LEVELS

	Relative humidity (vapor pressure deficit)					
Species	20 (44)	N	50 (23)	N	80 (10)	N
Screech Owl						
T_A	39.9	3	37.3	3	35.7	3
T_B	41.7		40.9		39.5	
Whiskered Owl						
T_A	40.2	2	39.2	3	38.5	2
T_B	40.6		41.1		40.9	
Elf Owl						
T_A	40.8	3	39.3	6	38.8	3
T_B	38.7		38.7		40.6	
Saw-whet Owl						
T_A	41.7	2	40.7	2	35.4	2
T_B	41.2		41.5		41.6	

relationship apparently exists between two factors influencing the onset of gular flutter, ambient temperature and relative humidity.

In the Elf Owl the values of body and ambient temperatures at the onset of gular flutter are reversed at high and low humidities, suggesting the presence of temperature receptors in the gular area. At moderate ambient temperatures the temperature of the gular region is presumably depressed less at high humidities than at lower humidity levels because of reduced evaporation. This is suggested by a rise in body temperature at ambient temperatures as low as 34°C, when humidity is high (Ligon, 1968: 56). In warmer situations when the temperature of the gular area reaches about 41°C (whether by inhalation of air of that temperature at low humidities, or by a rise in body temperature at high humidities) flutter is initiated. The gular area of the Poor-will seems to have temperature receptors (Lasiewski and Bartholomew, 1966, Figure 4). Bartholomew (1966) also obtained indirect evidence for peripheral temperature receptors in the Masked Booby (*Sula dactylatra*).

Response to shortage of food.—Torpor in owls, first suggested by Johnson (1963) for the Flammulated Owl (*Otus flammeolus*), has not been demonstrated for any species. The Whiskered Owl, known to be resident in the mountains of southern Arizona (Phillips et al., 1964: 49), seems a likely species to exhibit torpor, if it exists in this group. As the southwestern mountains have cold spells with snow cover often persisting for several days, this species, which feeds primarily on arthropods, is probably subjected intermittently to extended periods of food shortage. However, I obtained no evidence suggesting that either the Whiskered Owl or the Screech and Elf Owls are capable of reducing their metabolism in response to food deprivation and lowered ambient temperatures. Banks (1964) likewise was unable to induce torpor in a Flammulated Owl that fasted for 96 hours.

Small owls do appear to have one trait enabling them to withstand periodic food shortages, namely the ability to undergo drastic fluctuations in weight. Collins (1963) illustrated this in the Saw-whet Owl, where he found weight differences of more than 100 per cent (54.2–123.5 g) among 11 specimens taken in the wild. Although sexual dimorphism must be considered in this case, a tolerance for drastic weight loss undoubtedly is important when food is scarce. The weights of my captive owls at the onset of attempts to induce torpor were similar to those of wild birds of the same sex; these birds withstood 25 per cent decreases in weight with no apparent ill effects.

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SUMMARY

Responses to varying ambient temperatures were investigated in four species of small owls: Screech, *Otus asio*; Whiskered, *O. trichopsis*; Pigmy, *Glaucidium gnoma*; and Saw-whet, *Aegolius acadicus*. Some data on the Elf Owl are also included. Minimal values of oxygen consumption within the zone of thermal neutrality ranged from 0.62 ccO_2/(g hr) in the Whiskered Owl to 1.36 ccO_2/(g hr) in the Pigmy Owl.

Body temperatures ranged from 35.4–42.0°C over an ambient temperature range of 6–40°C. No obvious correlation was noted between size and body temperature in these owls. Noticeable hyperthermia developed at differing ambient temperatures in different species and was influenced by the moisture content of the air. Attempts were made to induce torpor in three species; none was successful.

Insulation is high in the Screech Owl and low in the Elf Owl compared to other bird species in which it has been studied. It did not appear to be

maximized in the Whiskered and Saw-whet Owls at the lowest temperatures to which they were subjected. Instead, metabolism and insulation apparently increased together over a wide range of decreasing ambient temperatures.

Rate of gular flutter ranged from a minimum of 109 flutters/min in the Saw-whet Owl to a maximum of 540 flutters/min in the Screech Owl. Unlike the caprimulgids in which gular flutter has been studied, the rate of flutter varies in these owls. Within a species the highest panting rates sometimes approached the slowest flutter rates.

The responses of the Elf Owl in experiments dealing with the interrelationships of temperature and humidity suggest the presence of temperature receptors in the gular area or upper respiratory tract.

Owls appear to be less able to survive great elevations in body temperature than many other species of birds. Four owls (two Elf, two Saw-whet) died after having been subjected to body temperature elevations of 42.3–44.3°C for periods of 10 to 20 minutes.

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