at present does not diminish the significance of *Pristiguana*, but highlights the need for new fossil material and more osteological studies of Recent lizards.

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Hypothermia of Broad-Tailed Hummingbirds during Incubation in Nature with Ecological Correlations

Abstract. *The first continuous recordings of natural hypothermia, and the only evidences of hypothermia during incubation, were obtained from temperature sensors embedded in synthetic hummingbird eggs placed in the nests. Resorting to this energy-conserving process was infrequent and could be correlated with reduced opportunity for energy intake.*

The energetics of hummingbirds are of special interest because of high ratios of surface (heat dissipating) to volume (heat producing) (*1*), intense metabolism (*2*), and slight insulation (*3*). The energy reserves of a hummingbird must be sufficient to meet the costs of nocturnal maintenance and the resumption of foraging at daybreak. A limited energy supply can be conserved by entry into hypothermic torpor, wherein the normal 38° to 43°C range in body temperature is "abandoned" and heat production is reduced during the nocturnal fast (*4, 5*).

Previous information on torpor of hummingbirds has come for the most part from the laboratory, where the nutritional state of captive birds has been questioned (*6, 7*). There is a paucity of quantitative records of torpid birds under natural conditions. Thus patterns of entry and the factors causing them had been unknown.

All previous recordings of nocturnal nest temperatures have shown that female hummingbirds do not become hypothermic during incubation. The maintenance of a high thermal gradient from nest to environment is especially remarkable in the cold nights of mountain climates (*8*). From continuous monitoring of nest temperatures and environmental data, we have found the first evidence of torpor in incubating female hummingbirds. The torpor can be correlated with weather conditions that posed chilling demands upon marginal energy reserves.

Nest temperatures of the broad-tailed hummingbird (*Selasphorus platycercus*) were recorded in the vicinity of Gothic, Gunnison County, Colorado (elevation 2900 m in the Elk Mountains), in the summers of 1971 and 1972. Thermistors and thermocouples were embedded in synthetic eggs of Silastic medical elastomer (Dow-Corning 382) and connected to recording potentiometers. The temperatures recorded were toward the hen's end of the temperature gradient from bird to air. This also provided a time account of the hen's absences from the nest, which showed as cooling "spikes" (displacements in the trace).

On 8 June 1972, three nests were being monitored. Two of the nests, located approximately 1 km apart, showed the same pattern (Fig. 1). The lower temperatures and solar irradiation for this day, compared with days preceding and following (Fig. 2), resulted from heavy, steady rain during the periods of 0830 to 0945 and 1520 to 1710. The amount of rain was not recorded at Gothic, but 5½ km to the south (Crested Butte) there was 1.6 cm of rain. During the rain, the two females remained on the nests, missing several normal, periodic, feeding sorties characteristic of the daytime (cooling spikes, Fig. 1, a and b). Approximately 21 and 12 percent of the normal activity daylengths of 14.75 to 15.25 hours, respectively, were unavailable for feeding. There were 18 and 7 percent fewer departures from the nests than normal for the day. Despite continuation of foraging 15 and 18 minutes later than normal that evening, this must have decreased the total energy intake significantly.

The night of 8 June was clear and cold. At 0100, the temperature of the synthetic egg in nest 1 began a steady decline from 31° to 6.5°C (readable to ± 0.2°C). At 6.5°C the temperature stabilized, remaining as if regulated, while the air temperature in Gothic continued a slow decline to − 1°C (readable to ± 1°C) on the valley floor. The minimum temperature at the nest site before sunrise was + 2°C (readable to ± 0.5°C). The body temperature of the female hummingbird, though unrecorded, was probably slightly higher than the 6.5°C "egg" temperature. Air velocities during the period of hypothermia were 0 to 4 km hr^{-1}, mostly under 1½ km hr^{-1}.

Since the females move relative to the orientation of the sensor "eggs," one could argue that the cooling cycles (Fig. 1, a and c) represent cooling of "egg" from movement rather than hypothermia of the hen. However, the "eggs" cooled much faster when the female departed to feed, even in the mildness of midday. The nocturnal cooling was more gradual despite a colder environment, an indication that a larger mass, hen plus clutch, was cooling as a unit. This and the consistency of the pattern and the timing of the gradual arousal convince us that the females had been hypothermic.

At nest 5 entry into torpor began later, about 0245. This later recourse to torpor correlates with the fact that the bird missed the smaller percentage of daytime feeding (12 percent as compared to 21 percent for nest 1), which suggests a physiological mechanism analogous to a fuel gauge. At first glance the series of cooling spikes preceding entry into hypothermia may suggest the "test drops" of a ground squirrel entering hibernation (*9*), but the cooling rate was rapid, like a nest departure, rather than the unique gradual cooling observed in the torpor cycle that followed. Hence this female may have attempted to feed in the open wet meadow during the night, as if to preclude the need for torpor.

The stabilization of egg temperature at about 6.5°C during hypothermia in both nests is of particular interest. The torpid state was thought originally to be an abandonment of control, in conformity with environmental temperature (*5, 6, 10*). However, at least three species of hummingbirds regulate a body temperature of 10° to 20°C during torpor. When the environment was cooler, the metabolism was directly proportional to the temperature difference (*11*). The Andean hill star (*Oreotrochilus estella*) maintains 7°C on the cold Andean high plateau, the minimum body temperature from which spontaneous arousal has been observed (*12*). Such regulation in torpor has not been reported for temperate species, which are more likely to be exposed to low temperatures, at which irreversible cold damage could only be prevented by a regulated torpor. The nest recordings in the present study seem to support further the idea that hypothermic torpor should be regarded as a regulated process.

The hypothermia was terminated by steady exponential rises in "egg" temperatures which started about 1 hour before normal departure at nest 1, and ¾ hour before normal at nest 5. Normal "egg" temperatures were attained before sunrise. The first foraging trips were 7 minutes early at both nests, when compared to the previous day, but within the range of variation for first departure during incubation. Ordinarily, after a homeothermic night, the first departure of the birds from the nests was 5 to 20 minutes before sunrise on a clear morning, later on overcast days. The time of the first trip appears to be determined by light intensity, in turn a consequence of tree canopy and cloud cover.

In continuous recordings of 161 hummingbird incubation-nights during the summers of 1971 and 1972, we found no other instances of torpor during incubation, although we have recorded this in two nests containing chicks (see below). One egg in nest 5 hatched and the chick developed apparently normally for 11 days, so that the period of torpor was probably not seriously detrimental to the developing embryo. The other egg was infertile. The nest was abandoned 5 July after the chick died. Nest 1 was abandoned on 10 June, either because of "overstudy" or predation (one egg missing).

There are records of eggs cooling during the incubation of other species of birds without damage (*13*). However, if the duration of incubation is a function of time spent in normothermy, torpor should retard development. Thus, frequent resort to torpor could be involved in the longer incubation periods of hummingbirds nesting high in the Andes (*14*).

A similar cooling cycle occurred the first night after hatching in nest 14,

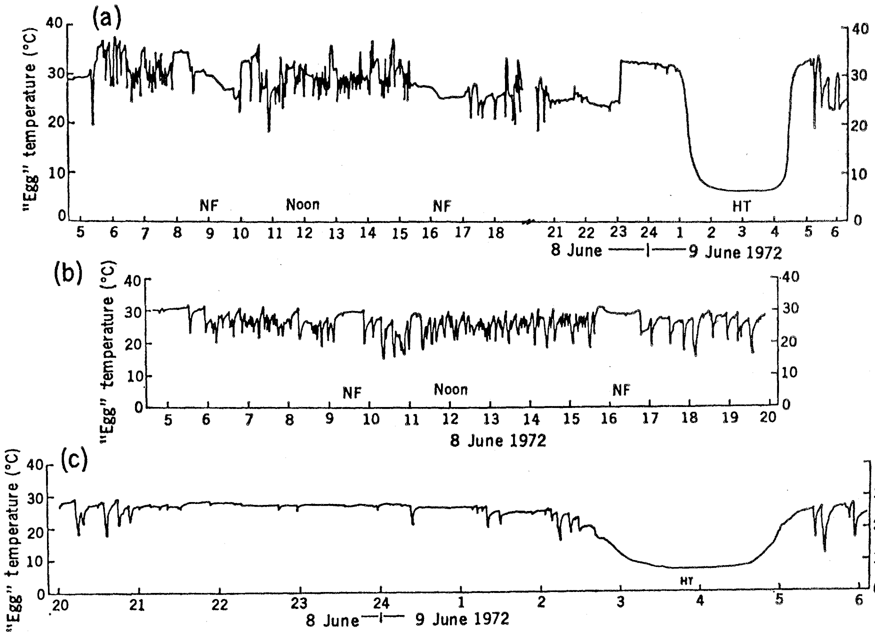

Fig. 1. Temperatures in the nests of broad-tailed hummingbirds obtained from Silastic eggs containing a thermocouple (a) or thermistor (b and c). (a) Nest 1, Copper Creek: the hen did not leave the nest to feed (NF), 0830 to 0945 and 1520 to 1710. The chart drive failed about 1850 and was restored about 2030. The abrupt temperature rise soon after 2300 was probably due to a change in body position so that the artificial egg came into better contact with the female. Hypothermia (HT) began at 0100 and appeared to be regulated from about 0210 to 0405, with normal temperature regained by 0500. (b) and (c) Nest 5, wet meadow: periods of missed feeding trips (NF), about 0910 to about 0950 and about 1545 to 1645, were shorter than in nest 1, as was the period of hypothermia, 0245 to 0500 (HT).

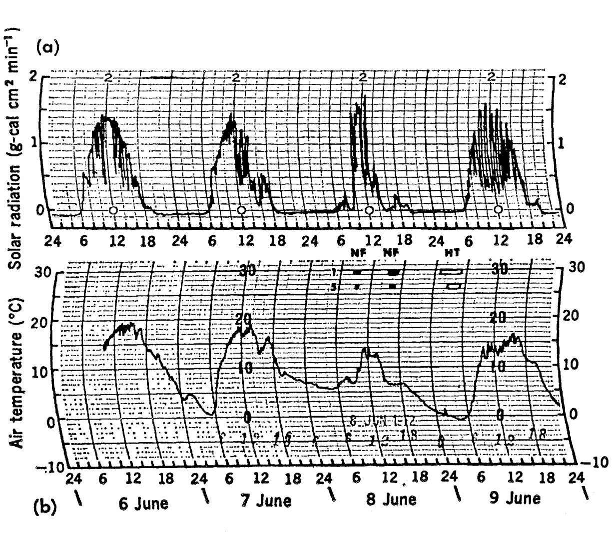

Fig. 2. Meteorological conditions which resulted in hypothermia of nesting hummingbirds. NF, nonfeeding periods; HT, period of hypothermic torpor (same notation as in Fig. 1) for nests 1 and 5, respectively. (a) Solar radiation for 8 June was generally less, the period of higher midday radiation restricted between the heavy rainstorms (*16*). (b) The air temperature was lower and the period of midday warming brief on 8 June. Temperatures at or below freezing were recorded at various locations in Gothic the following predawn (*16*).

on the night of 5 July when the minimum air temperature was 3°C. This was not preceded by inclement weather that would have confined the hen to her nest. However, the synthetic egg and recorder had been installed in the afternoon of the previous day, just after the first egg hatched. Possibly because of the disturbance, the frequency of nest departures for the remainder of the day was 22 percent less than for the same time period the following day, not followed by torpor. Thus a similar pattern of reduction of foraging can be suggested as the cause for resorting to hypothermia. Both chicks from this nest fledged normally. When the local nectar supply was declining at the end of the season, hypothermia occurred twice in a fourth nest (containing chicks), as indicated by the same temperature patterns as those in Fig. 1, a and c.

The pattern of these first observations of hypothermia during nesting and the correlations with reduced opportunity for feeding suggest that the duration of the hypothermia is consistent with the relation between food intake and duration of torpor observed for rodents in the laboratory (*15*). Because arousal and reattainment of normal body temperature appears to be timed for a first-light search for more food, it must be the onset of torpor that is geared to the extent of depletion of energy reserves, an interaction between "biological clock" and "biological fuel gauge."

Tiny hummingbirds, nesting in the chilling nocturnal climate of the Rocky Mountains, are succeeding in near-marginal energetic conditions. A reduction in feeding opportunity by inclement weather or by demands of nest protection may lead to an energy crisis. Unlike man, the nesting hummingbird reduced the rate of depletion of energy reserves, rather than crying for "more!"

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Nonvisual Photic Responsiveness in Newly Hatched Pigeons (Columba livia)

Abstract. *Overt behavioral arousal was elicited by light stimulation in pigeon hatchlings. The sensitivity is* not *mediated via the retina or by direct stimulation of the brain, but rather it is most likely a dermal sensitivity.*

The effects of unconventionally mediated sensory stimulation upon the behavior of organisms have always been as interesting as they are mystifying. There have been several reports in the literature of extraretinally mediated effects of light on avian circadian and reproductive cycles, for example, *Zugunruhe*, fat deposition, and testicular growth (*1*). These effects of light stimulation on behavior are of a relatively long latency and lack a direct indicator of the relation between the stimulus and immediate behavior. More direct effects on behavior have been observed in studies with chick embryos in which light stimulation alters the motility patterns (for example, number of movements and temporal distribution of activity) of 4- to 9-day-old embryos (*2*). This early sensitivity occurs prior to any evidence of visual function (*3*).

In the course of our investigation of the onset of visual function in the altricial pigeon embryo, as indicated by the pupillary reflex (*4*), we discovered a nonvisually mediated response to light stimulation in newly hatched pigeons. We were attempting to devise an overt behavioral measure of visual responsiveness (in order to amplify our earlier findings), and intermittently presented hatchling pigeons with 5 seconds of light stimulation. The characteristic response we observed consisted of a squab raising its head and vigorously waggling it from side to side. Often these movements would be accompanied by wing fluttering and leg extensions, which resulted in raising the body from the substrate. On occasion we also noted vocalization. This entire behavioral pattern is similar to the normal feeding pattern of newly hatched doves and pigeons (*5*). The pattern can also be elicited by gentle bilateral tactile stimulation of the bill (*6*), which is roughly analogous to the procedure employed by the parent pigeon.

As a routine control procedure for possible nonretinally mediated photic sensitivity, we covered the eyes of the hatchlings to make certain that the behavioral responses we were observing were in fact visual. Under these conditions, with the eyes covered, the squabs continued to respond to the light onset, and we began to investigate the actual nature of this curious and unexpected responsiveness.

For this purpose, fertile pigeon eggs were incubated in a forced draft incubator at 37.5°C and 60 to 70 percent relative humidity. They were turned automatically eight times daily. Within 6 to 24 hours after hatching, the birds were observed individually in a Plexiglas observation box (temperature and humidity controlled as above). The hatchling was placed in a small plastic container (6.5 by 6.5 cm) located 20.0 cm directly below the stimulus light (500-watt photoflood lamp, General Electric No. EBV2). Two glass heat filters and a petri dish filled with a saturated copper sulfate solution, acting as a further heat filter, were positioned between the Plexiglas and the lamp. The temperature in the plane of the