(*Speotyto cunicularia*) to a moving object when the object did and did not cast a conspicuous shadow.

We used a single Burrowing Owl for all tests. It was trapped about 5 km north of Davis, Yolo County, California. We chose this species because it is easily trapped and because it often feeds nocturnally upon terrestrial prey, including rodents, and therefore may exploit shadow cues (Thomsen, Condor 73:177–192, 1971).

The owl was kept in a plywood box that was a 91.4-cm cube with a 45.7 × 45.7-cm window centered on one side. The owl regularly used the perch in its box and faced toward the window. A red, 7-watt incandescent bulb inside the box provided illumination for viewing the owl's behavior.

Attached to the owl box on the windowed side was a second box, which contained the moving object and the shadow-casting and nonshadow-casting lighting systems. This box was open on the side that was adjacent to the owl box, so that the interior of this box was visible to the owl through the window. The moving object was a steel nut attached by monofilament fishing line to the top of this box. This object could be held outside the box and released to swing past the window.

The shadow-casting and nonshadow-casting lighting conditions were provided by one and four 7-watt incandescent bulbs, respectively. The single bulb was centered above the window. Each of the four bulbs was attached to a different edge of the windowed side of the owl box, and each was in a sanded acrylic container for diffusion of light. The single bulb cast a conspicuous shadow, the four bulbs cast four very inconspicuous shadows. The brightness of both shadow and nonshadow bulbs was adjusted to yield 0.01 ft-c. The room containing the apparatus was always dark.

We used human subjects to watch the responsiveness of the owl to the moving object. None was aware of the purpose of the experiment or that the owl was viewing the object under special lighting conditions. Each subject was told to report that the owl had detected the object if the owl moved coincidentally with the object's movement. Such movement usually consisted of abrupt visual fixation of the object by head movement. The conspicuousness of the head movement was increased by releasing the object only when the owl was not gazing directly at the window. Either a "yes" or "no" response was required for every trial.

The experimenter notified the subject at the beginning of each trial that the object was about to be released by pulling a string tied around the subject's wrist. The object was held outside its box between trials. During each trial it was released, allowed to swing across and back, then caught and held. Each subject watched the owl for 30 trials made at 30-sec. intervals.

Ten subjects were used for a total of 150 trials under each lighting condition. Lighting conditions were constant during each subject's trials and were alternated with successive subjects. We deleted five shadow and four nonshadow trials due to extraneous noises.

In the shadow conditions, the owl was judged to have detected movement in an average of 10.6 (range = 8–16) per 30 trials, whereas in nonshadow conditions detection occurred in an average of 6.4 (range = 2–11) per 30 trials. This difference was statistically significant ($t = 1.93$; df = 8; $p < 0.05$ in a one-tailed test). Hence, the owl responded to the moving object when it cast a shadow more than when it did not, even though illumination was equal in both conditions.

The results are not incompatible with the hypothesis that visual prey detection should be enhanced in lighting conditions in which shadows are cast (e.g., moonlight) relative to conditions in which shadows are not cast (e.g., twilight). We must of course exercise caution in extrapolating these results gathered from one owl under special conditions to other predators and prey. The following hypotheses should be considered with such caution in mind.

Shadows might be expected to constitute effective aids to prey detection for owls since these birds typically hunt from an elevated position. A prey individual plus shadow should subtend a larger visual angle when viewed from above than when viewed obliquely. Shadows might also be expected to constitute effective aids to prey detection in deserts for two reasons: (1) the paucity of cover in deserts increases the usefulness of vision for prey detection; (2) shadows should contrast most conspicuously with the light soil of arid regions.

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DAILY TEMPERATURE CYCLES IN BARRED, GREAT-HORNED AND SNOWY OWLS

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This paper reports preliminary data on daily rhythmic fluctuations in skin and deep body temperatures of captive owls, and is a by-product of research aimed at the development of radio-telemetric techniques suitable for continuous, simultaneous monitoring of certain physiological and behavioral activities of unrestrained birds in the wild. The work was carried out at the University of Minnesota's Cedar Creek Natural History Area, located in Anoka County, during the period February–April 1971.

MATERIALS AND METHODS

Four owls were obtained for the experiments. A Snowy Owl (*Nyctea scandiaca*) and a Barred Owl (*Strix varia*) were captured from the wild, and two Great Horned Owls (*Bubo virginianus*) were acquired from local zoos. Each owl was confined to a portable aviary, placed either outdoors or in the laboratory. During the experiments the birds were held in cages

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TABLE 1. Summary of the temperature monitoring schedule for four individual owls during the experimental period February–April 1971.

Species	Temperatures monitored		No. days temperatures monitored	No. hours over which data obtained	No. separate monitoring runs	Dates
	indoors	outdoors				
Strix varia		Body	7	63	6	March 3–10
Nyctea scandiaca	Body		2	16	2	March 24–25
		Body	15	167	11	Feb. 4–18
	Skin		6	116	1	March 24–29
Bubo virginianus (1)		Body	15	158	9	Feb. 10–24
Bubo virginianus (2)		Body	9	61	6	Feb. 15–23
		Skin	2	25	1	April 5– 6
	Body		2	12	1	April 5– 6
	Skin		5	77	2	April 5–10

measuring 60 × 60 × 120 cm. Ambient temperature indoors was held at 15°C; the photoperiod was 12 hours darkness and 12 hours light, with the lights on at 07:00 and off at 19:00 local time. Ambient temperatures outdoors ranged between –37°C and 20°C.

Body and skin temperatures were telemetered by radio transmitters. The body transmitters, including thermistors, were encased in paraffin and coated with dental acrylic formed into cylinders 15 mm in diameter and 30 mm long. The owls were persuaded, by force-feeding, to swallow the cylinders. The birds were fed lean beef, domestic pigeons, grouse and mink. The food was given at the time that the transmitter cylinder was inserted. An ingested rather than an implanted transmitter was used, since the experiments were designed so as to cause minimal disturbance to the birds. Although an ingested transmitter might deliver data that are more related to the bird's intake of food, it was thought that the risk of temperature deviation would be greater in an area of inflammation following surgery. As a further check, all temperature recordings that were made within two hours after a bird had been fed were precluded from analysis. The ingested transmitters were recovered and re-used after they had been cast as pellets by the birds. Skin temperature was monitored by a glass-probe thermistor taped to a featherless tract under the wing in the region close to the body. A flexible wire was used to attach the thermistor to a transmitter package that was attached to the owl by an antenna loop encircling the bird's body (see Nicholls and Warner 1968).

The ingested transmitter used an astable multivibrator to control the pulse repetition rate of a crystal-controlled oscillator. The pulse rate of the oscillator varied at an audio rate as determined by the resistance of the thermistor probe which varied with the body temperature. The signals were picked up by two antennae placed inside the cage, and processed through a radio receiver. The transistors in the astable multivibrator were a matched pair contained in a single case to reduce drift and errors. The audio output of the receiver was fed to a Hewlett-Packard Model 500 frequency meter. This meter was used with a X10 scale expand feature so that a full scale deflector covered about 1.5°C. The scale reading was continuously recorded on a Rustrak paper-chart recorder. In addition, the frequency was sampled and printed every 10 minutes by a counter-printer-timer to serve as a check on the drift of the frequency meter.

The skin temperature transmitter used a principle similar to that described by Fryer, Deboo and Wingett (1966). To eliminate drifts caused by battery voltage and ambient temperature variations, the on-to-off time ratio of a crystal-controlled oscillator was controlled as a function of temperature. The demodulator for this transmitter gated a 100 kHz oscillator on and off. This was relayed into the Hewlett-Packard 500 frequency meter, integrated and recorded with the D.C. Rustrak chart recorder. The accuracy of this system was also checked every 10 minutes by the counter-printer.

The telemeters were calibrated frequently between experiments, using a water bath and mercury thermometer. Over the range of body temperatures encountered, the output of the transmitters was linear. Least-squares regression was carried out in the calibrations. Since the regression equation was: Temperature (°C) = a + b (frequency, cps), the frequencies monitored from owls could be converted directly to °C.

RESULTS

Table 1 provides a summary of the temperature monitoring schedule. In the analyses of the data, use was made of temperature values obtained at 15 minute intervals. Temperatures of the owls during the first two hours after "feeding" of the transmitter or attachment of the skin probe were not included in the analyses, since handling of a bird caused its temperature to rise. Also omitted were all data recorded during observer-visits to the birds and for

TABLE 2. Overall average daily body temperatures of owls maintained outdoors.

Species	Mean body weight (g)	Body temperature (°C)				
		Mean	S.D.	Lowest	Highest	Range
Strix varia	748	39.52	0.25	38.79	40.40	1.61
Nyctea scandiaca	1916	38.54	0.31	37.99	39.95	1.96
Bubo virginianus (1)	1425	38.97	0.23	37.66	40.23	2.57
Bubo virginianus (2)		39.27	0.24	37.52	40.36	2.84

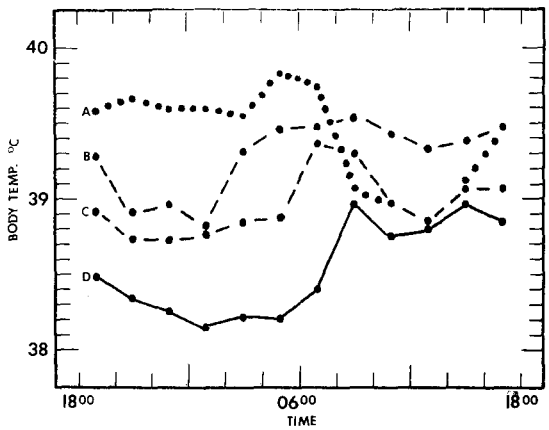

FIGURE 1. Average daily body temperature cycles in *Strix varia* (A), *Bubo virginianus* 1 (C) 2 (B) and *Nyctea scandiaca* (D) maintained outdoors.

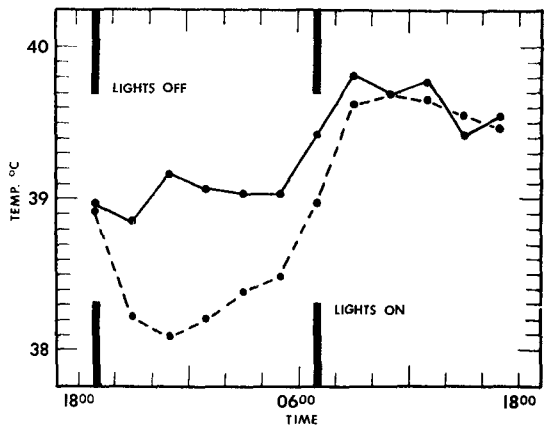

FIGURE 2. Average daily body (solid line) and skin (broken line) temperature cycles in *Nyctea scandiaca* maintained indoors.

one hour thereafter, since we found that the mere sight of a human was sufficient to cause an owl's temperature to rise by about 2°C. In short, the analyses of temperature records, and the techniques of measurement, attempted to reduce as much as possible disturbance of the subjects and effect of excitement and struggle on their temperatures. The temperature values reported here are averages of 15 minute records pieced together from many part- and whole-day runs when the birds were not disturbed.

Table 2 shows that the computed overall averages of the means of the daily body temperatures of the four owls while outdoors were similar, as were their ranges of temperature variation. Thus, deep body temperatures were maintained within the usual avian range, even though ambient temperatures varied between –37°C and 20°C.

Figure 1 shows that the thermal levels of the owls kept outdoors varied in relation to time of day. In *N. scandiaca*, the lowest deep body temperature occurred consistently during the dark phase, and the highest temperatures during the light phase of the daily cycle. The daily drop in body temperature occurred between 18:00 and 19:00 at about time of local sunset; a relatively sudden temperature rise of about 1°C occurred daily between 06:00 and 07:00 at about time of local sunrise (times of sunrise and sunset based on U. S. Naval Observatory Chart for Minneapolis). *Bubo virginianus* followed the same general pattern, but the changes were not as consistently timed or as marked as in *N. scandiaca*. This form of regular diel cycle was found to be reversed in *S. varia* (table 3).

In *N. scandiaca* kept indoors under constant ambient temperature and controlled photoperiod, skin and deep body temperatures, when monitored at the same time, each followed similar trends with the skin temperature averaging slightly lower (fig. 2). Both *N. scandiaca* and *B. virginianus* had depressed skin and body temperatures during the dark phase of the daily cycle (tables 4, 5). The temperature rhythms showed a pattern similar to that obtained from the birds when they were outdoors. Indoors, the birds responded to the lights being switched on (07:00) or off (19:00) by raising or lowering their body temperatures by about 1°C respectively.

DISCUSSION

Most previously published values of temperatures in birds have been based on either single or relatively few determinations gathered under a variety of means, which often involved handling of the birds or subjecting them to some other form of artificial excitation. As stressed by Dawson and Hudson (1970), there may be many factors that can influence the labile thermal levels of birds. The specification of a single temperature for a bird is of limited utility. Hence, we see no point in comparing "characteristic" temperatures for our birds with values obtaining for the same species by other workers. Even within the

TABLE 3. Comparison of body temperatures of owls maintained outdoors at light and dark periods of the daily cycle.

Species	Mean body temperature and S.D. at hours of cycle		*t* test
	08:00–16:00 (A)	20:00–04:00 (B)	
	°C	°C	
Strix varia	39.23 ± 0.23	39.61 ± 0.24	A < B at confidence 0.995
Nyctea scandiaca	38.88 ± 0.54	38.23 ± 0.48	A > B at confidence 0.990
Bubo virginianus (1)	39.08 ± 0.36	38.79 ± 0.35	A > B at confidence 0.975
Bubo virginianus (2)	39.42 ± 0.37	39.01 ± 0.56	A > B at confidence 0.975

TABLE 4. Comparison of body temperatures of owls maintained indoors at light and dark periods of the daily cycle.

Species	Mean body temperature and S.D. at hours of cycle 08:00–16:00 (A)	20:00–04:00 (B)	*t* test
Nyctea scandiaca	39.64 ± 0.33	39.03 ± 0.68	A > B at confidence 0.995
Bubo virginianus (2)	39.69 ± 0.21	38.35 ± 0.13	A > B at confidence 0.995

spectrum of our results, and under standard conditions, interspecific comparisons could be spurious. For instance, although our data appear to support McNab's (1966) contention 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," such a comparison is strictly not valid because our work and McNab's generalization did not take into account such real interspecific differences as relative efficiency of body insulation (cf. Gessaman 1972).

Within the daily temperature cycles of birds, the highest levels of body temperature occur during the active part of a bird's daily activity cycle, depending on whether the particular species is nocturnal or diurnal (Dawson and Hudson 1970). However, while it is generally accepted that daily rhythms and body temperature and metabolism can be correlated with daily locomotory activities, body temperature can be controlled by an independent circadian oscillator that neither depends on nor reflects higher metabolic rates or activity levels (see Aschoff 1967 and references therein cited). Within the daily cycles of body temperature as reported here for *S. varia* and *B. virginianus*, highest temperatures occurred during dawn and dusk. In *N. scandiaca* highest temperatures occurred during the light phase of the cycle. This correlates with what is known generally about each species, daily pattern of hunting, but critical field observations are lacking.

A resting component, indicated by a drop of metabolic activity, during the light period between dawn and dusk has been reported to occur in nocturnal owls (Graber 1962, Gatehouse and Markham 1970). In these species metabolic rates peaked at about dawn and dusk, and metabolic levels at night were higher than during the day. In the diurnally active Burrowing Owl (*Speotyto cunicularia*) body temperature regulated at about 1.5–2.0°C lower in the dark than during the normal photoperiod (Coulombe 1970). On this basis, one might conclude that the relatively elevated daytime body temperature of *N. scandiaca*, as reported here, was a reflection of the species' predominantly diurnal habits (Watson 1957, Nicholls 1968). Conversely, in the normally more nocturnally active *S. varia* (Nicholls in prep.) body temperatures were high at night and relatively low during the light period of the daily cycle. The somewhat intermediate condition as demonstrated by *B. virginianus* might be a reflection of the species' essentially crepuscular motor activity (Nicholls pers. comm.). Thus, the daily cycles of body temperature in the three species appear to be generally correlated with normal locomotor activity. This, however, is not to say that temperature and locomotor activity cannot be independent.

SUMMARY

Body and skin temperatures of captive owls (*Nyctea scandiaca*, *Bubo virginianus* and *Strix varia*) were measured with an automatic continuously recording telemetry system. Thermal levels of the owls varied in relation to time of day. In *N. scandiaca* the lowest deep body temperature occurred consistently during the dark phase, and the highest temperatures during the light phase of the daily cycle. The daily drop in body temperature occurred at about time of local sunset; a relatively sudden temperature rise of about 1°C occurred daily at about time of local sunrise. *Bubo virginianus* followed a similar general pattern, but the changes were not as consistently timed or as marked as in *N. scandiaca*. This form of regular diurnal cycle was reversed in *S. varia*.

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TABLE 5. Comparison of skin temperatures of owls maintained indoors at light and dark periods of the daily cycle.

Species	Mean skin temperature and S.D. at hours of cycle 08:00–16:00 (A)	20:00–04:00 (B)	*t* test
Nyctea scandiaca	39.59 ± 0.20	38.18 ± 0.34	A > B at confidence 0.995
Bubo virginianus (2)	39.71 ± 0.20	38.71 ± 0.21	A > B at confidence 0.995

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INCUBATION PATCH FLUCTUATIONS IN RED-WINGED BLACKBIRDS

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Most incubating passerine birds develop an incubation patch in the region of the ventral apterium. The patch loses feathers and becomes thicker and more vascular to serve as an area for better heat transfer to the incubated eggs.

Jones (1969, 1971) reviewed the literature on incubation patch development in birds. Selander and Kuich (1963) reported changes in incubation patch tissues of wild Red-winged Blackbirds (*Agelaius phoeniceus*) in some stages of nonbreeding and breeding. They experimentally induced feather loss and incubation patch development with hormone injections.

In my investigations of the incubation and parental behavior of Red-wings, I sought a detailed description of changes occurring in the incubation patch throughout the entire reproductive cycle. By separating the cycle into portions of nest building, egg laying, normal incubation, extended incubation, nestling care and fledgling care, I intended to determine the quantitative changes occurring in the stratum germinativum, dermis, blood vessels and fat cells in a sample size adequate to justify discussion of anatomical changes that occur. Observations of changes could then aid in interpreting the theories and observations that have been made with regard to hormonal, tissue and behavioral interactions (Jones 1971, Holcomb 1974).

I began studying Red-wings in 1963 but most data on tissues were collected in 1967 at Wooster, Ohio, and in 1968 and 1969 near Omaha, Nebraska. Birds were breeding in a variety of habitats including alfalfa and clover field, old weed fields, hedgerows, ditch banks, and marshes. Investigators visited nesting areas nearly every day beginning in March and ending in August. Males generally arrived back from migration in early March and females soon afterward. Pairing began in late March and continued through April and early May. Nero (1956a, b) described details of territory establishment and pairing.

When nesting occurred, from late April until mid-August, I attempted to discover nests during nest-building and then to visit these nests each day.

The normal incubation period of Red-wings is 11 days (Allen 1914). To prolong incubation, four artificial eggs of the same size and coloration as normal eggs were placed in nests.

Female Red-wings were collected in pre-breeding, breeding, and post-breeding seasons. The pre-breeding birds were designated as unpaired and were females flying about in flocks in March and April before pairing with a mate. Breeding females were designated as (1) paired with the male (collected in April and early May); (2) nest-building; (3) nest completed before egg-laying; (4) egg-laying, day 1–2; (5) egg-laying, day 3–4; and (6) incubation, day 1–3, 4–6, 7–9, 10–12, 13–15, 16–18, and 19–21. Most of the breeding females were collected in late April, May, or June, including those caring for nestlings or fledglings. Post-breeding females were all collected in August. When a female was collected, the ventral side of the body where incubation patch should develop was carefully examined to determine (1) extent of feather loss in all regions and (2) degree of apparent edema of tissues.

Four pieces (approx. 5 mm^2) of incubation patch were taken from each female; one piece each from the right and left anterior and right and left posterior portions of the incubation patch.

Approximately 2 mm of tissue in each square represented the abdominal feather tract area along the edge of the incubation patch. This served as a reference point for beginning observations when analyzing the histology of the incubation patch. Both front and rear sections were taken to determine if development of the patch was different in these regions. It was assumed that right and left portions would be the same and these two samples would insure having at least one good sample for analysis from both front and rear. Pieces of incubation patch were laid on dry paper towelling to which they adhered when placed in 10% formaldehyde. This prevented the tissue from rolling into a ball. After a few days, they were placed in 70% alcohol for storage, and any feathers present were carefully removed from the tissue with forceps.

The patch was sectioned at 5–7 μ and stained with haematoxylin and eosin. A mean of 30 serial sections of tissue was taken from each sample; three of these were selected at random for detailed examination. Starting at the edge of the incubation patch tissue in a section, at least 3 mm of tissue were available for study. From each of the three selected sections, the first, second, or third millimeter of tissue was chosen at random and used for the examination. In each bird, 3 mm of tissues were analyzed from both the front and rear portions of the incubation patch.

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