

occurred in the same acacia. This suggests that nest-site selection in Yellow-olive Flycatchers might be flexible (i.e., in acacias, with wasps, or both) and/or may vary between individuals.

Finally, none of the non-acacia nests of either bird species were located in trees containing thorns. As such trees were common, their non-use could be an indication that the pairs that nest in acacias were selecting for the presence of the ants, not the thorns.

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Vocal responsiveness to chilling in embryonic and neonatal American Coots.—Although neonates of many avian species rapidly develop an ability to thermoregulate physiologically, heat provided by a brooding parent commonly augments the young bird's imperfectly developed endothermic capacity (Theberge and West 1973). Brooding contact between parents and young is stimulated by loud "distress" calls of the young (Gullion 1954, Kirkley and Gessaman 1990). Distress calls, a common response to social isolation, are also stimulated by chilling (Kaufman and Hinde 1961) and may play a role in neonatal temperature control by maintaining parental brooding (Kirkley and Gessaman 1990). Distress calls are also given in response to chilling by late-stage embryos of some species, and so could have a thermoregulatory function before hatching (Evans 1990a). Despite the apparent relevance

of embryonic and neonatal calls for thermoregulation, little is known about the effects of temperature on these calls or how vocal responsiveness to chilling changes with age during the time that thermoregulatory ability is developing. We examined aspects of this problem in the American Coot (*Fulica americana*), a marsh-nesting species in which the newly hatched precocial young commonly are exposed to chilling in air or water but have only a limited endothermic ability (Sutter 1988).

If calls are involved in thermoregulation, we hypothesized that chilling would elicit neonatal calling only at body temperatures below that of young given free access to a heat source and that calling would begin at a body temperature no lower than that at which facultative thermogenesis occurs (approximately 35°C during the first week, Sutter 1988). For embryos at the pipped egg stage, uncorrected chilling could delay hatching (Evans 1990b). We therefore predicted that distress calls would be elicited when late-stage embryos were chilled below normal incubation temperature. Vocal responses due to social isolation or to overheating may also occur (Kaufman and Hinde 1961, Kirkley and Gessaman 1990) but were not examined here.

Methods.—Egg temperatures from the start of pipping onwards were obtained at the Delta Marsh, Manitoba, by replacing one natural egg at each of five nests with an agar-filled egg having thermal characteristics similar to a fresh egg (Evans 1989). The artificial eggs were never rejected by the parents and appeared to be incubated normally. The egg at one nest was fitted with a calibrated temperature-sensitive transmitter (Minimitter model L) monitored with a remote receiver. The other four eggs were fitted with implanted thermistor probes wired to remote, calibrated temperature recorders (YSI and Grant Instruments Cambridge). Readings were taken at intervals of from 15 min to 1 h. All readings for a given nest were averaged, providing one data point per nest for subsequent analysis.

Eggs for laboratory study were incubated in a commercial incubator held at $37.8 \pm 0.5^\circ\text{C}$ and $60 \pm 5\%$ relative humidity. Young were group-reared in pens providing moistened commercial chick starter, water, and access to an incandescent heat lamp. Pipped eggs and young were chilled by individually placing them within a coil of copper tubing through which water at either the control (37.8°C) or cold (20.0°C) temperature was pumped from controlled water baths (see Evans 1990a for details of apparatus). Calls/min were counted with a sound-operated relay and event recorder. Coot embryos within pipped eggs, like newly hatched young, emit a graded series of calls ranging from soft contentment "twitters" to loud "distress" calls (Cosens 1981). The intensity setting of the relay was chosen by trial and error to achieve maximum separation between these calls so that only loud distress calls were recorded. Body temperatures at the end of each minute were obtained with a 0.4-mm diameter flexible thermocouple inserted about 1 cm into the cloaca of chicks or into the pip hole of pipped eggs. Temperatures were measured to the nearest 0.1°C with a Sensortek model Batt-12 thermometer.

Testing began with a 10-min pre-test at control temperature (37.8°C) to establish baseline vocal response levels. Water at the experimental temperature (20.0°C) was then pumped through the coil for 30 min. Chilling was followed by a 10-min post-test at the control temperature. Eight embryos were tested during the final day before hatching, when pip holes were well developed. Young were tested on the day of hatching (day 0, $N = 9$), day 3 ($N = 12$) and day 7 ($N = 11$). Pipped eggs and young were selected for testing on the basis of availability at the appropriate age, without reference to their use in tests at an earlier age. This procedure minimized the number of eggs collected while maintaining statistical independence of individuals within age classes. Preliminary analyses indicated that there were no effects ($P > 0.5$) of prior testing. Statistical comparisons of paired measures on each individual within age classes employed either Paired-*t* or, for non-normal data, non-parametric Wilcoxon matched pairs tests (Sokal and Rohlf 1969).

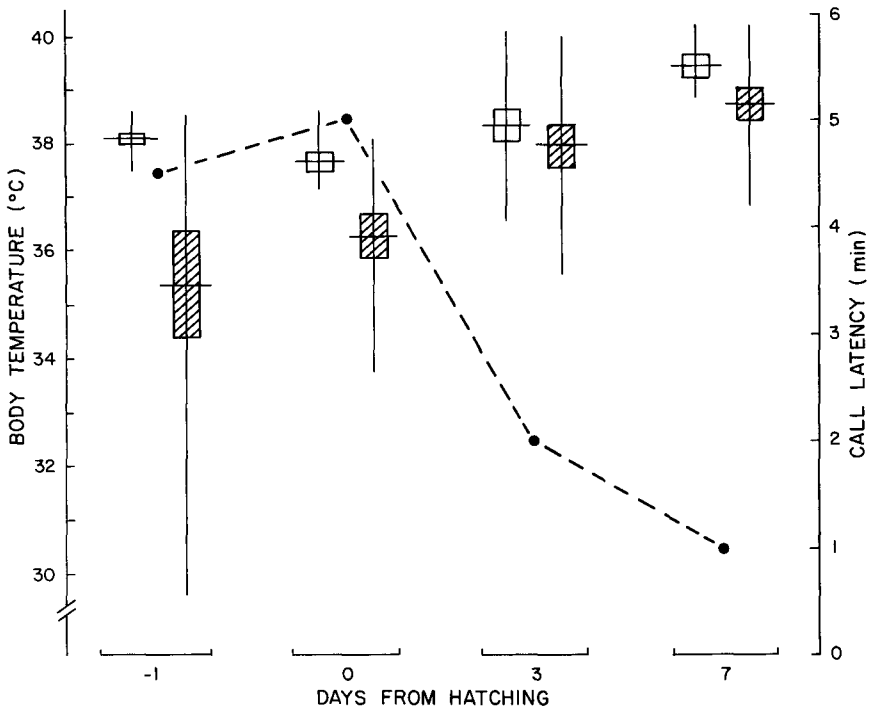


FIG. 1. Effects of chilling on body temperature and time to start calling (latency) in embryos at the pipped egg stage (-1 day), in young on the day of hatching (0 days), and at three and seven days of age. Body temperatures shown by horizontal lines (mean), bars ($\pm$ SE) and vertical lines (range). Open bars = last minute at control temperature before chilling started; hatched bars = minute during which calling began after onset of chilling. Solid circles and dashed lines indicate median time to begin calling after the onset of chilling.

Results.—An average of 148 ± 41 (SE) readings were taken at the five naturally incubated nests. Mean temperature was $35.0 \pm 0.5^\circ\text{C}$ (range = $33.9\text{--}36.0^\circ\text{C}$). During the pre-test period in the laboratory, body temperatures of pipped eggs and young at zero and three days of age were similar to the control incubation temperature of 37.8°C . Pre-test temperatures were about 1.5°C higher at seven days of age (Fig. 1, Table 1). During subsequent chilling, body temperature dropped steadily for all ages, reaching a mean of from 27.1°C for eggs to 35.0°C for seven-day-old young by the final minute (Table 1). There was at all ages a small but significant drop in body temperature between the final test minute and the first post-test minute at the warmer control temperature (Table 1). Body temperature then increased gradually throughout the remainder of the post-test period.

At each age, modal and median pre-test call rates were zero. During subsequent chilling, median time to begin calling (defined as the first minute in which at least five calls were given) was about five min for pipped eggs and newly hatched young, followed by a decrease down to one min by seven days of age (Fig. 1). Once calling began, it usually continued unabated until after the end of chilling at all ages. Embryos at the pipped egg stage began

TABLE 1
EFFECTS OF REWARMING CHILLED EMBRYOS AND YOUNG ON MEDIAN CALLS AND MEAN $\pm$ SE BODY TEMPERATURE
(SAMPLE SIZES IN PARENTHESES)

Period (min)	Pipped eggs (8)		Hatch day (9)		Three days (12)		Seven days (11)	
	Calls ^a	T _b ^b	Calls	T _b	Calls	T _b	Calls	T _b
Pre-test	0	38.1 $\pm$ 0.1	0	37.7 $\pm$ 0.2	0	38.4 $\pm$ 0.3	0	39.5 $\pm$ 0.2
Test: final	13	27.1 $\pm$ 0.2	21	30.4 $\pm$ 0.3	24	31.7 $\pm$ 0.5	25	35.0 $\pm$ 0.3
Post-test: 1	1.5	26.9 $\pm$ 0.2	11	30.1 $\pm$ 0.3	9	31.5 $\pm$ 0.5	9	34.8 $\pm$ 0.3
3	0	27.4 $\pm$ 0.2	0	30.6 $\pm$ 0.3	0	32.0 $\pm$ 0.5	1	35.1 $\pm$ 0.2
5	0	27.9 $\pm$ 0.2	0	31.3 $\pm$ 0.3	0	32.6 $\pm$ 0.5	0	35.5 $\pm$ 0.3
Statistic ^c	T = 0, t = 2.75		T = 3, t = 8.03		T = 0, t = 8.96		T = 1, t = 6.38	
P	<0.05		<0.02		<0.01		<0.01	
	<0.02		<0.001		<0.001		<0.001	

^a Per minute.

^b T_b = body temperature (°C).

^c Comparisons between final test minute and first post-test minute. T = Wilcoxon matched-pairs test, t = paired t-test.

calling only after their body temperature had dropped significantly below pre-test levels (Fig. 1, Paired $t = 2.49$, $P < 0.05$) to a level that did not differ significantly (unpaired $t = 0.19$, $P > 0.5$) from the mean natural incubation temperature of 35.0°C. Body temperature at the time calling began increased with age but was still significantly lower than pre-test levels in newly hatched young (Paired $t = 3.66$, $P < 0.01$). By three and seven days of age (Fig. 1), calling began when there was only a slight ($P > 0.05$) decrease in body temperature from pre-test levels.

There were significantly fewer calls given during the first post-test minute of rewarming than during the final minute of testing despite the continuing drop in deep body temperature at that time (Table 1). By the third post-test minute, median call rate had dropped to zero at all ages except seven days, where median rate was one call per min. Median call rate was zero for all ages by five min post-test.

Discussion.—The results support our prediction that calls of late-stage embryos would be stimulated at body temperatures below normal incubation temperature. We did not anticipate that calling would begin at, rather than below, incubation temperature, since such a response would appear to serve little or no thermoregulatory function. However, this unanticipated result may be more apparent than real. It is likely that the embryonic temperature of live pipped eggs during natural incubation would be slightly above the temperature we recorded in our artificial eggs (Drent 1970), thereby bringing the laboratory results into closer agreement with functional expectations. Calling by young coots occurred at temperatures above that at which facultative thermogenesis occurs (about 35°C, Sutter 1988). This sensitivity, if present under natural conditions, should enhance the thermoregulatory effectiveness of distress calling. Our prediction that young should call only after body temperature decreased below the level that they could maintain when given free access to a heat source was supported by hatch-day young but only marginally by older young. By three and seven days after hatching, the young were so sensitive to chilling that calling began when there was only a slight, nonsignificant drop in deep body temperature.

The rapid cessation of calling during the first post-test minute despite the continuing decline in deep body temperature at that time (Table 1) suggests that peripheral receptors are involved in cessation of calling. Peripheral receptors are known to be involved in the cessation of other thermoregulatory activities in birds (Bligh 1973). In the wild, the onset of warming after chilling would normally indicate that corrective parental action had been taken, thereby removing the need to continue calling even before deep body temperature had begun to increase.

Vocal responsiveness to chilling is the only thermoregulatory mechanism able to function while the embryo is trapped within the confines of the pipped egg. On the day of hatching, a strong vocal response to chilling still occurs, but movement of the young to a heat source becomes a more sensitive mechanism for maintaining core temperature. By the age of 3–7 days, vocalizing and movement appear to be equally sensitive to chilling, and both have a higher temperature threshold than facultative thermogenesis. Although it remains to be proven that calling to the parent is involved in coot thermoregulation, the sensitivity of the response to chilling indicates that it would be highly efficient in that capacity.

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Successful exchange of prairie-chicken eggs between nests in two remnant populations.—Declining fecundity may be a classic symptom of inbreeding depression, and is expected in isolated populations that have fallen below about 50 individuals (Franklin 1980, Shaffer 1981, Simberloff 1982, Brussard 1985). Sterility of males was suspected as a contributing factor in the extinction of the Heath Hen (*Tympanuchus c. cupido*) (Gross 1928). Currently, each of the three remaining populations of Greater Prairie-Chickens (*T. c. pinnatus*) in Illinois contains fewer than 50 individuals, and 28 years (1963-1990) of nest data for the Jasper County population show significant declines in egg fertility and egg success (hatched eggs/total eggs) (Westemeier, unpubl. data). The number of Illinois prairie-chickens declined from millions throughout the state about 1860 to estimates of 25,000, 2000, 500, and 76 in increasingly scattered population in 1933, 1962, 1972, and 1990, respectively (Westemeier 1985, unpubl. data).

Following a joint decision by the Illinois Dept. of Conservation (IDOC), Illinois Natural History Survey (INHS), Illinois Nature Preserves Commission, and Illinois Endangered Species Protection Board to address possible inbreeding depression in Illinois prairie-chickens, an effort was undertaken in 1990 to exchange clutches of eggs under incubation in Jasper and Marion counties. The objective was to enhance genetic variation in both gene pools by mimicking natural dispersal. The two populations, about 56 km apart, are supported by a total of 858 ha of intensively managed sanctuaries. Except for one intervening lek with four males in spring 1990, about 42 km from the Jasper population, former lek sites between