THE DEVELOPMENT OF A VOCAL THERMOREGULATORY RESPONSE TO TEMPERATURE IN EMBRYOS OF THE DOMESTIC CHICKEN

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ABSTRACT.—We examined the vocal responsiveness of chicken (*Gallus gallus*) embryos at the pipped egg stage to determine if they were able to regulate their thermal environment by soliciting heat from a surrogate parent. There was no overall effect on vocalizations of exposure to 20° C or 45° C relative to the normal incubation temperature of 37.8° C. There was, however, a general trend towards increased calling as the time of hatching approached. There was also some indication that embryos tested in the late stages of hatching (ringing) vocalized more in the cold, then became relatively silent when rewarmed. When cold-challenged embryos were given 2 min of rewarming (surrogate brooding) in response to their calls body temperature was slightly but significantly elevated above cold only exposed controls. Unlike previously reported anecdotal evidence suggesting a strong vocal response to cold, our results suggest chicken embryos show only weak incipient vocal response to temperature that begins to increase late in incubation and becomes fully functional only after hatching. Unlike other species tested to date, the developmental progression of behavioral and metabolic thermoregulation appear to be tightly linked in this species. *Received 27 Feb. 1998, accepted 5 Oct. 1998.*

The embryos of many avian species are capable of vocalizations prior to hatch (Freeman and Vince 1974; reviewed in Evans 1988a). Embryonic vocalizations may facilitate the transition from incubating eggs to brooding and feeding young (Impekoven 1973; Templeton 1983; Evans 1988a, b), may function as antecedents to post-hatching social behavior (Tuculescu and Griswold 1983), or may function in soliciting care from parents. The embryos of several species respond to cold by increasing vocalizations (Evans 1990a; Bugden and Evans 1991; Evans et al. 1994, 1995; Brua et al. 1996). These vocalizations affect parental behavior and may elicit more attentive incubation (Evans 1989, 1990b, 1992; Brua 1996).

When cold-induced vocalizations trigger rewarming by a surrogate parent in altricial pelicans and semiprecocial gulls, cold-challenged embryos can vocally regulate their body temperatures at relatively safe levels (Evans 1990a; Evans et al. 1994, 1995). In these species such vocal behavioral thermoregulation evidently precedes their ability to thermoregulate endothermically; altricial and semiprecocial species show no apparent metabolic response to cooling before hatching (Matsunaga

et al. 1989, Kuroda et al. 1990). However, in precocial species there is evidence that gradual cooling of late stage embryos brings about a small but measurable incipient endothermic response (Freeman 1964, Tazawa et al. 1988, Kuroda et al. 1990). The relationship between the emergence of endothermy and the timing of a vocal response to cold in precocial species is unknown. We examined this issue in the precocial domestic chicken (*Gallus gallus*).

Chicken embryos are capable of vocalizations 2–3 days prior to hatch, but these vocalizations become more frequent during the final 24 hours before hatching (Gottlieb and Vandenbergh 1968, Dawes 1981, Tuculescu and Griswold 1983). In response to the loud calls ("distress calls", Collias 1987) of embryos, hens will vocalize or move around on the nest (Tuculescu and Griswold 1983). Following the maternal response the embryos become silent or emit soft trill calls ("pleasure calls", Collias 1987).

Study of the vocal response of chicken embryos to cold has produced variable results. Early investigation suggested that a pipped egg that was alternately cooled and warmed would give "distress" calls or "pleasure" calls in close correspondence to the temperature changes (Collias 1952). Subsequent studies have shown decreased vocal activity (Oppenheim and Levin 1974), increased vocal activity (Evans 1988a), and inconsistent vocal

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responses (Dawes 1981). Some evidence also suggests that chicken embryos increase their rate of vocalization during exposure to high temperatures (Oppenheim and Levin 1974).

This study was designed to systematically reassess the vocal response of late stage chicken embryos to temperature. We examined the effects of temperatures both above and below the normal incubation temperature, and the effectiveness of call-induced rewarming bouts in the regulation of temperature during cold challenge.

METHODS

White Leghorn Chicken eggs were incubated in a forced air commercial poultry incubator (Perersime Model no. 1) that maintained conditions within a suitable range (37.8 ± 0.5° C and 65 ± 5% relative humidity). Only externally pipped eggs, which are known to be capable of vocalizations (Tuculescu and Griswold 1983), were selected for study.

Effects of continuous chilling and heating.—To examine the vocal response of embryos to low or high temperature, pipped eggs were placed singly, pip hole up, within an environmental chamber that consisted of a coil of copper tubing surrounded by insulating Styrofoam. The temperature in the chamber was controlled by pumping water from controlled water baths (±0.5° C) through the coil surrounding the egg. Testing began with a 10 min pre-test at the control temperature (37.8° C). The coil temperature was then changed to the experimental (20° C or 45° C) or left at the control temperature (37.8° C) for 30 minutes. This was followed by a 10 min post-test period at 37.8° C.

The body temperature of the embryo was measured with a thermocouple placed approximately 1 cm directly into the pip hole. The thermocouple was surrounded by deep lying portions of the embryo's body, away from the outer shell. It was held in place by porous adhesive tape ("Micropore") applied to the exterior of the shell. The body temperature of the embryo and the coil temperature were recorded to the nearest 0.1° C every 30 s by a data logger [Grant Instrument (Cambridge) Model 1203]. Calls with a minimum intensity of 78 dB (2.5 cm from the pip hole, B-fast scale) were recorded by a microphone set in the plexiglass lid of the chamber, connected to a sound operated relay and an Esterline Angus event recorder.

Vocal regulation of temperature during cold challenge.—The apparatus was similar to that described above except that calling of the embryo triggered a period of rewarming (illustrated in Evans 1990a). The embryo faced a continuous cold challenge at 20° C until 5 calls were given. The fifth call then triggered a 2 min period of rewarming with water at 37.8° C being pumped through the coil surrounding the egg. This period of rewarming was followed by a return to default chilling at 20° C until another bout of calling was initiated. If an embryo called in response to each successive period of cold challenge it would in effect be capable of regulating ambient, and hence body temperature (Evans 1990a, Bugden and Evans 1997). Control embryos were placed in the same apparatus and held at a constant 37.8° C throughout. Calls in the control situation triggered a mock warming bout where the same timer and pumps were activated as in the cold challenge situation but the water circulating through the coil remained at 37.8° C. All temperatures were recorded as in the first experiment. An Esterline event recorder recorded both individual calls and the warming and mock warming bouts. Control and cold challenge tests lasted for 1 hour on separate samples of eggs.

To determine when during the pip-to-hatch interval the vocal response to cold might develop, the timing of pipping, hatching, and testing were recorded at 4 h intervals. Short term exposure of pipped eggs to moderate cold can delay hatching in domestic chickens (Evans 1990c). Testing of the eggs at 20° C in this experiment thus could potentially affect the timing of their hatching and so distort the interpretation of the developmental onset of the vocal response to cold. To control for this possibility, the pip-to-hatch intervals of cold challenged and control embryos were compared with a separate sample of embryos (untested control embyros) that were not tested and left to hatch normally in the incubator. Statistical tests were done with STATISTIX (version 4.1, Analytical Software, IBM platform).

RESULTS

Effects of continuous chilling and heating.—Seven chicken embryos exposed to a 30 minute period of chilling at 20° C experienced a fall in body temperature of 8.0 ± 0.3° C (mean ± SE) from 36.9 ± 0.2° C at the start to 28.8 ± 0.3° C at the end of the exposure period. These embryos had a mean calling rate of 10.2 ± 6.8 calls per minute. This result was skewed by two highly vocal embryos that were nearly hatched (ringing stage, Freeman and Vince 1973) by the end of the test. The remaining five embryos were completely silent during their exposure to cold, resulting in a median call rate of 0.0 calls per minute. The body temperature of embryos held at the control temperature of 37.8° C shifted by 0.5 ± 0.1° C, from 37.0 ± 0.2° C to 37.5 ± 0.2° C. None of the 7 control embryos reached the ringing stage and all were relatively quiet during the test period with a mean calling rate of 0.1 ± 0.04 (median of 0.1) calls per minute.

Body temperature of seven embryos exposed to 45° C rose by an average of 4.1 ± 0.3° C, from 36.3 ± 0.2° C to 40.4 ± 0.4° C. Call rate averaged 1.2 ± 0.7 calls per minute

with a median of 0.5 calls per minute. While 2 of these embryos were in the ringed stage, their call rates (1.7 and 0.5 calls/min) were similar to the overall average call rate for this group. A Kruskal-Wallis one way nonparametric ANOVA showed no overall differences in calling rates of chicken embryos at the three temperatures ($H = 4.14$, $P > 0.05$, df = 2).

Vocal regulation of temperature during cold challenge.—Thirty-three embryos were tested under cold challenge experimental conditions (20° C) and 34 were tested as warm-only (37.8° C) controls. There was no significant difference in the time from pipping to the time of hatching in cold challenged, control, and 12 untested control embryos (One way ANOVA: $F_{2,76} = 1.34$, $P > 0.05$). For additional analyses embryos were grouped according to time between testing and hatching. There were 8, 13, and 12 embryos tested under cold challenge and 13, 12, and 9 embryos tested as warm only controls for three developmental categories 0–2.5, 2.5–7.5 and >7.5 h before hatching. The vocal response of cold challenged embryos was greater than that of the warm only controls in all developmental categories (Fig. 1). However, *a priori* two-sample *t*-tests between cold experimental and warm controls showed no significant difference in any of the developmental categories (0–2.5: $t = 0.93$, $P > 0.05$; 2.5–7.5: $t = 0.44$, $P > 0.05$; >7.5: $t = 1.63$, $P > 0.05$).

Within 2.5 h of hatching, the mean number of warming or mock warming bouts increased in both the cold challenged embryos and in the warm only controls (Fig. 1). Since cold exposure produced no significant difference in vocal response, all data were combined for further comparison of vocal response with respect to time before hatch. Embryos vocalized significantly more frequently as the time of hatching approached (Kruskal-Wallis ANOVA: $H = 11.10$, $P < 0.01$, df = 2).

The pattern of calling during the 2 min rewarming and mock rewarming bouts provided an additional measurement of the response to temperature (Table 1). Because of a 6 s delay of the chamber to temperature changes, cold challenged embryos were still experiencing temperatures well below the incubation/control temperature of 37.8° C at the start of each rewarming period. Cold challenged embryos
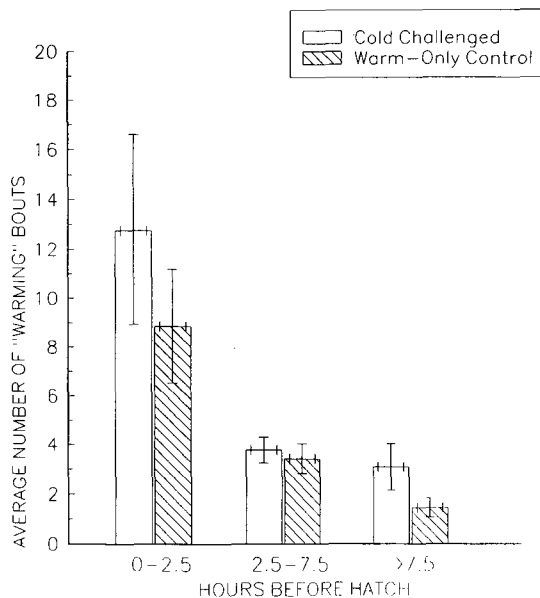

FIG. 1. Mean (±SE) number of vocally generated warming (cold challenged) and mock-warming (control) bouts at three pipped-egg developmental stages (cold challenge *n* equals 8, 13, and 12; warm-only control *n* equals 13, 12 and 9 for 0–2.5, 2.5–7.5 and >7.5 h before hatching respectively).

in the two groups vocalized more often than controls at this time, significantly so in the 2.5–7.5 h age group (Table 1). By the final minute of rewarming, the cold challenged embryos were almost silent, but this was also true for most of the control embryos whose temperatures had not changed. Control embryos that were less than 2.5 hours from hatch were an exception. These embryos vocalized at a relatively high rate during the final minute of the rewarming bout and maintained a call rate significantly greater than the experimental embryos.

Body temperatures maintained by experimental embryos during vocal regulation tests increased by about 1° C as hatching time approached, but this increase was not statistically significant (Fig. 1, Table 2). Body temperatures of experimentals were significantly lower than those of control embryos held at 37.8° C (Table 2), reflecting the general low level of call-induced rewarming periods in the experimentals. Body temperature of the experimental embryos by the end of 30 min of testing was significantly higher (29.9 ±

TABLE 1.   Median number of calls per minute given by chicken embryos in pipped eggs at the start and end of vocally-generated rewarming (experimental) and mock rewarming (control) bouts. Listed are medians of calls given per embryo per bout (1st and 3rd quartiles in parentheses).

Stage (h before hatch)	First 20 s		Final minute	
	Experimental	Control	Experimental	Control
<2.5	9.6 (6.1–11.8)	6.6 (2.0–17.4)	0.2 (0.0–2.2)	3.1 (1.0–8.7)[a]
	$n = 8$	$n = 12$	$n = 8$	$n = 12$
2.5–7.5	9.0 (4.7–13.1)	3.0 (0.0–6.9)[a]	0.0 (0.0–1.4)	0.5 (0.0–2.3)
	$n = 12$	$n = 11$	$n = 12$	$n = 11$
>7.5	3.0 (1.7–5.3)	3.0 (0.0–6.0)	0.0 (0.0–0.5)	0.0 (0.0–0.5)
	$n = 8$	$n = 7$	$n = 8$	$n = 7$
H[b]	7.03	3.61	1.13	10.67
df	2	2	2	2
P	<0.05	>0.05	>0.05	<0.01

[a] Experimentals and controls differ significantly ($P < 0.05$: Mann–Whitney U test).
[b] H, Kruskal–Wallis ANOVA statistic, distributed as χ^2.

0.4° C, all stages combined; $t = 2.28$, $P < 0.05$, df = 23) than embryos that were exposed to constant chilling for 30 min in experiment 1 (28.8 ± 0.3° C). This suggests a slight warming effect of vocalizations in experiment 2.

DISCUSSION

Exposure of chicken embryos to continuous cold (20° C) and continuous hot (45° C) environments did not significantly increase their rates of vocalization. The embryos remained relatively silent in spite of exposure to environmental temperatures that altered body temperature to a level which, if continued, would be expected to result in death of the embryo (Webb 1987). While the embryos were clearly capable of vocalizing, the close correspon-

dence of calling and temperature suggested in the literature (e.g., Collias 1952) was not evident. Only two cold challenged embryos, in the process of ringing prior to hatching, showed a strong vocal response. The vocal regulation experiments also showed an increase in vocal response in chilled embryos that were near to hatching (Fig. 1) but this trend was also seen in control embryos that were not exposed to cold. Tuculescu and Griswold (1983) have also noted a general increase in the rate of vocalization in the few hours just prior to hatching.

Despite increased vocalization rates as hatching approached, cold challenged chicken embryos in the vocal regulation apparatus were not able to elevate their body temperatures to safe, near normal incubation temper-

TABLE 2.   Median body temperature of chicken embryos during experimental and control vocal regulation test. Listed are medians of the average body temperature maintained during the one-hour test period (1st and 3rd quartiles in parentheses).

Stage (h before hatch)	Body temperature of embryos (°C)		
	Experimental	Control	P[b]
<2.5	31.5 (30.0–35.5)	37.8 (37.2–38.0)	<0.002
	$n = 7$[a]	$n = 7$[a]	
2.5–7.5	30.5 (30.0–31.0)	38.1 (37.8–38.3)	<0.001
	$n = 13$	$n = 12$	
>7.5	30.4 (29.4–30.1)	37.6 (36.9–38.1)	<0.001
	$n = 12$	$n = 9$	
H[c]	2.79	4.61	
df	2	2	
P	>0.05	>0.05	

[a] Excludes 1 experimental and 6 control embryos that displaced the thermocouple during ringing.
[b] Comparison of experimentals and controls at each stage—Mann–Whitney U test.
[c] H, Kruskal–Wallis ANOVA statistic, distributed as χ^2.

ature, at least under the conditions employed here (Table 2). This contrasts strikingly with a significant increase in vocal regulatory capability of hatched domestic chicks given 2 min periods of rewarming in response to cold-induced calling on the day of hatching (Bugden and Evans 1997). The finding that body temperature after 30 min of testing of vocal regulation in 20° C cold challenged embryos was significantly different than cold only exposed embryos in experiment 1 is consistent with the presence of some incipient effects of vocally elicited rewarming bouts. Our results thus raise the possibility that the marginally higher rate of calling in cold challenged embryos, especially as they neared hatching (Fig. 1), may represent the beginnings of a prehatch vocal thermoregulatory response to cold.

Examination of the patterns of calling (Table 1) suggests that immediately before hatch (<2.5 h), rewarming was associated with decreased calling in experimental (cold challenged) embryos, while the calling of control embryos during the final minute of the 2 min mock rewarming period continued at a significantly higher level. This difference is also suggestive of an incipient vocal response to temperature by chick embryos during the final hours before hatching. An increase in vocal response to temperature as the time of hatching approaches has also been noted during vocal regulation studies in semiprecocial Ring-billed Gulls (*Larus delawarensis*; Evans et al. 1994) and Herring Gulls (*Larus argentatus*; Evans et al. 1995).

The subtle beginnings of the vocal response to temperature found here parallels the incipient development of endothermy in late stage chicken embryos. The prehatching endothermic response is not robust. It has been noted only when exposure to cold was limited to gradual cooling of late stage embryos (Tazawa et al. 1988). Incipient endothermy is thought to be limited initially by conductance of O_2 through the eggshell (Tazawa et al. 1989) and then by the embryo's limited endothermic power (Tazawa et al. 1988, Whittow and Tazawa 1991). While these physiological results suggest that incipient endothermy occurs during the latter stages of embryonic development, the dramatic increase in oxygen consumption at the time of hatching (Kuroda et al. 1990, Whittow and Tazawa 1991) indicates

that endothermy becomes functional at that time (Freeman 1971, 1983). Our present results suggest that there is a similar incipient vocal thermoregulatory response of late stage embryos to cold that becomes fully functional at or soon after hatching (Tuculescu and Griswold 1983, Espira and Evans 1996, Bugden and Evans 1997). The developmental onset of vocal and metabolic thermoregulation thus appear to be closely linked in precocial domestic chicks.

In contrast to domestic chicks, the vocal thermoregulatory system of altricial pelicans and semiprecocial gulls is well developed prior to hatch (Evans 1988a, 1990a; Evans et al. 1994, 1995). Altricial and semiprecocial species evidently do not show any endothermic response before hatch (Matsunaga et al. 1989, Kuroda et al. 1990, Whittow and Tazawa 1991) suggesting that behavioral and metabolic thermoregulation are developmentally uncoupled in these species, unlike the apparent linkage in the domestic chicken.

Pelicans and gulls both exhibit asynchronous hatching, and later hatching eggs potentially experience significant levels of incubation neglect as the parents attend to the chicks that have already hatched (Evans 1990d, Lee et al. 1993, Evans et al. 1995). Although chickens display some level of hatching asynchrony (mean of 15 h in Burmese Junglefowl; Meijer and Siemers 1994), the chicken is not known to neglect its eggs and will normally remain on the nest for the first 12–24 h after hatching (McBride et al. 1969, Miller 1978, Meijer and Siemers 1994). A vocal response to cold thus may not be a functionally useful behavioral response for chicken embryos. After hatching, the situation changes dramatically when mobile chicks are potentially exposed to colder ambient temperatures, especially during foraging bouts (McBride et al. 1969, Sherry 1981). At that time calling to solicit brooding warmth becomes an important part of their behavioral response to cold (Kaufman and Hinde 1961, McBride et al. 1969, Sherry 1981). Taken together, results to date suggest that in precocial chickens, vocal and endothermic thermoregulation both show incipient, but largely nonfunctional, development prior to hatching and are both turned on rapidly as the chicks hatch and thermoregulation becomes a highly adaptive capability.

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