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## VOCAL RESPONSE OF EARED GREBE EMBRYOS TO EGG COOLING AND EGG TURNING

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**ABSTRACT.**—In a laboratory study, the vocal responses of Eared Grebe (*Podiceps nigricollis*) embryos to egg cooling and egg turning were examined. Nineteen late-stage, prepipping embryos were twice subjected to 10 min of egg cooling and 10 min of normal incubation temperatures. Experimentally cooled embryos vocalized more than embryos exposed to normal incubation temperatures. Cooled embryos produced more bouts of calls and fewer calls per bout than when exposed to normal incubation temperatures. Intercall intervals within bouts did not differ between warm and cold periods. Results of the egg-cooling experiment support the “care-soliciting signal” hypothesis. In a separate paired experiment, embryos vocalized more when turned than when at rest. Because grebe nests are composed of sodden materials, embryos that are about to hatch may signal their parents to turn the eggs, because positioning a pipped egg upside down may suffocate the embryo. Also, prepipped embryos may vocalize more frequently when turned as a signal to their parents that they are viable and will soon hatch. Eared Grebe embryonic vocalizations probably are multifunctional, with care-soliciting being one of their functions. *Received 22 April 1994, accepted 27 January 1995.*

EMBRYONIC VOCALIZATIONS appear to be common in precocial bird species but are rare in altricial species (Oppenheim 1972). In grebes, embryos of many species emit loud vocalizations that can be heard 2–3 m from the nest one to two days prior to pipping. External pipping may be delayed until only 3 h or less before hatching of the precocial grebe chick. Although most avian embryos do not vocalize until after they have pierced the inner-shell membrane, Pied-billed Grebe (*Podilymbus podiceps*) embryos are able to emit vocalizations while the inner-shell membrane is intact (Driver 1967). That these vocalizations occur despite the many en-

ergetic and gas exchange difficulties faced by embryos in pipped eggs (Whittow and Tazawa 1991) suggests that the vocalizations have an important function.

Eared Grebes (*Podiceps nigricollis*) incubate a clutch of three to four eggs (range 1–6) for 21 to 23 days, and peeping vocalizations can be heard 1 to 2 days before hatching. Vocalizations by Eared Grebe embryos influence the amount of time adults spend near the nest as well as other incubation behaviors such as the frequency of egg turning, nest building, and the amount of time parents are off the nest (Brua 1996). The traditional explanation for these vocalizations is that they signal to the parents the impending hatching of a chick and cause them to switch from incubation to brooding and feeding behavior (Norton-Griffiths 1969; Impekoven 1973, 1976; Templeton 1983; Brua 1996).

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A second possible function for embryonic vocalizations is parent-offspring recognition. Tschanz (1968) and Impekoven (1973) noted that incubating parents would rise, poke at the eggs, and call in response to embryonic vocalizations, and embryos sometimes would vocalize in response to parental vocalizations. They suggested that some form of parent-embryo communication was occurring. Tschanz (1968) experimentally demonstrated that Common Murre (*Uria aalge*) embryos were capable of learning their parents' vocalizations. In a more recent study, Van Kampen and Bolhuis (1991) determined that young chickens developed a stronger affinity for an auditory stimulus to which they had been previously exposed if a visual model was also present. Van Kampen and Bolhuis argued that visual stimuli are critical to auditory learning in chicks and that vocalizations primarily draw attention to and aid in recognizing visual stimuli. Thus, auditory learning alone may not function as a form of imprinting (Bolhuis 1991, Van Kampen and Bolhuis 1991, Bolhuis and Van Kampen 1992).

Vocalizations produced by incubating Eared Grebes include an advertising call, a nest defense call, a soft vocalization produced during exchange of incubation duties, and a food call. These calls are infrequent during incubation and are not given in response to embryonic vocalizations. Thus, there may be limited opportunities for vocal parent-offspring recognition. Buitron and Nuechterlein (1993) reported that newly hatched Eared Grebes responded readily to playbacks of food calls recorded from other parents. Their findings suggest little if any individual recognition of the food call by young. Most studies on birds have reported that parents do not recognize their offspring until there is some selective advantage to do so, such as when the broods begin to mix (Beer 1980). Because Eared Grebe chicks climb onto the back of the attending adult at hatching and are back-brooded and fed there for 10 to 12 days, there may be no immediate need for parent-offspring recognition by voice. After the back-brooding period, however, the young are free swimming, and parent-offspring recognition is likely.

Another possible function of embryonic vocalizations is parental acceptance of newly hatched young. Beer (1966) reported that Black-headed Gulls (*Larus ridibundus*) incubating vocalizing, pipped eggs were likely to accept chicks added to the nest, whereas adults incubating nonpipped eggs were likely to be more ag-

gressive. Impekoven (1976) reported similar results for Laughing Gulls (*Larus atricilla*). In Eared Grebes, stray chicks that come too close or try to climb onto nests usually are rejected (Brua pers. obs.). However, when peeping eggs or newly hatched young are in their nest, newly hatched chicks are often accepted (G. Nuechterlein and D. Buitron pers. obs.).

In some species, the respiratory movements of the embryo produce clicking sounds that are distinct from peeping (Driver 1965, 1967; Forsythe 1971). Clicking sounds have been shown to synchronize the hatching of precocial species, either by older embryos accelerating the hatching of younger ones, or younger embryos retarding the hatching of older ones (Vince 1964, 1966, 1968). Grebe young hatch asynchronously, however, and Driver (1967) reported that Pied-billed Grebe embryos do not produce a clicking sound. Also, clicking sounds are unreported in Eared Grebes. Schwagmeyer et al. (1991) demonstrated in a laboratory experiment that hatching intervals in Glaucous-winged Gulls (*Larus glaucescens*) could be shortened between the second and third egg of a three-egg clutch if the eggs were incubated in contact with each other compared with clutches in which eggs were incubated 10 cm apart. However, hatching intervals were not reduced in a concomitant field experiment.

Evans (1988) proposed the novel hypothesis that embryonic vocalizations in American White Pelicans (*Pelecanus erythrorhynchos*) act as "care-soliciting signals" in response to parental neglect during the period of asynchronous hatching. When parental behavior shifts from incubation to brooding, the remaining eggs are often subjected to lower and more variable incubation temperatures (Evans 1989, 1990a). By vocalizing, embryos may induce the attending parent to take corrective measures to restore normal incubation temperatures (Evans 1988, 1989).

In this study, we used nearly hatched Eared Grebe embryos to test Evans' hypothesis that embryonic vocalizations are given in response to adverse incubation conditions. Hatching in Eared Grebes is strongly asynchronous, embryonic vocalizations are well developed, and unincubated eggs cool rapidly in the sodden floating nests. Our first experiment measured the vocal response of Eared Grebe embryos to egg cooling. We tested the following specific predictions: (1) embryos exposed to egg cooling will call more frequently than embryos exposed

to normal incubation temperatures; and (2) embryos subjected to egg cooling will peep sooner than embryos held at normal incubation temperatures. The second experiment evaluated whether embryos vocalize in response to egg turning. The two main proposed functions of egg turning in birds (see Drent 1973, 1975) are: (1) prevention of adhesions of extra-embryonic membranes to the embryo; and (2) reduction of discrepancies of incubation temperature between edge and center eggs. Domestic chicken embryos increased the frequency of backthrust movements when they were turned (Impekoven 1976). Also, sudden turning or shaking produced vocalizations from Herring Gull (*Larus argentatus*) embryos (Goethe, cited in Vince 1969). However, few studies have investigated the responses of embryos to egg turning. Eared Grebe eggs are turned when the parent rises and reaches beneath them with its bill. Field observations indicate that eggs can be turned (up to 180°) or only nudged so that they are moved slightly (Brua pers. obs.). Our experiment quantified the embryo's vocal response to egg turning and examined whether Eared Grebe embryos were more likely to vocalize if they were turned.

#### METHODS

During the summer of 1990, Eared Grebe eggs were collected at mid-incubation and held at 37°C in a March Roll-x incubator. Because of the unusually short period between pipping and hatching (30–180 min), we used only nonpipped, vocalizing eggs for both experiments.

*Egg-cooling experiment.*—Procedures for the egg-cooling experiment followed closely those of Evans (1988). A cooling chamber was formed by coiling a 2-mm (inside diameter) copper tube in the shape of an Eared Grebe egg. One end of the coil was open, allowing entry of the egg into the chamber. When an incubated egg began vocalizing, we wrapped it loosely in aluminum foil to conduct heat more evenly over the egg. We then placed the egg into the chamber with the same orientation as in the incubator to minimize any possible effects of egg turning on the embryo. We performed the experiment in a separate room to eliminate any effects of other vocalizing embryos on the experimental embryo. Water siphoned continuously through the copper tube during a treatment. The control (warm-water) treatment contained 37°C water, the same temperature as the incubator. The cooling (cold-water) treatment contained 16°C water, a common ambient temperature during incubation. Eggs were allowed a 10-min acclimation period using 37°C water. The acclimation period was followed by

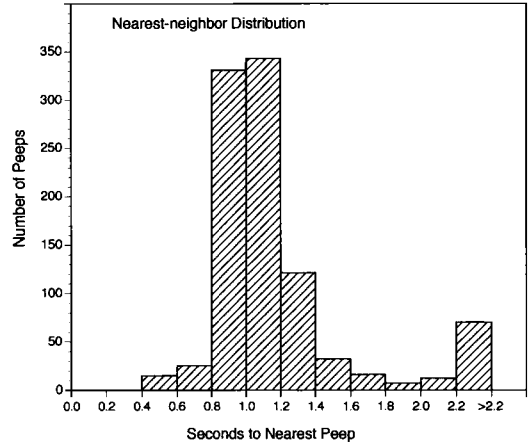


FIG. 1. Nearest-neighbor analysis of intercall intervals for peeping vocalizations given by 19 Eared Grebe embryos during warm control periods. Bimodal distribution was used to define bout length objectively.

four 10-min treatment periods conducted in the following order: warm, cold, warm, and cold. Vocalizations were recorded using a Sony dynamic microphone placed near the egg and a continuously running Sony TCM 5000 professional tape recorder. We tested 19 embryos in the experiment.

Tape recordings from the experiment were transcribed using a computer program that recorded the time of each vocalization. Because the total number of vocalizations for each period was distributed normally, a randomized complete-block ANOVA was employed for statistical analysis (SAS Institute 1988). Because the vocal-response latency values (time to first vocalization after start of treatment) were not distributed normally, a nonparametric Friedman two-way ANOVA was used to test vocalization latency differences among periods. Multiple comparisons tests were set at  $P \leq 0.05$  (Daniel 1990, Montgomery 1991).

We examined the vocalizations emitted during the last 5 min of the first warm and first cold periods for statistical differences. We used only the last halves of these periods to avoid sampling transition periods between treatment temperatures. For each embryo, we compared the mean intercall interval, the mean number of calls per bout (bout length), and the total number of bouts occurring during the warm and cold periods using a Wilcoxon matched-pairs signed-ranks test (Daniel 1990). We used nearest-neighbor analysis to measure intercall intervals. Here, we define bout length as the number of calls given in a series, with each call being separated by no more than 1.6 s (Fig. 1). We report  $\bar{x} \pm SE$ .

*Egg-turning experiment.*—A ramp was constructed with a slope of approximately 20°. On each side of the ramp, three pairs of holes were made, into which horizontal strips of plastic were inserted to prevent the egg from rolling down the incline. The distance

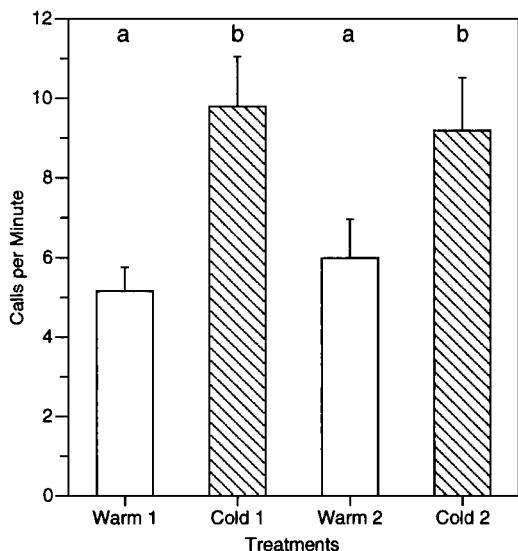


FIG. 2. Number of vocalizations ( $\bar{x}$ , SE) produced by 19 Eared Grebe embryos in response to warm- or cold-water treatments. Bars with different letters are significantly different (Duncan's multiple range test,  $P \leq 0.05$ ).

between each plastic strip was equivalent to one-half revolution of an egg. The ramp was placed in an open box and warmed with a light bulb to maintain an ambient temperature of 37°C (incubator temperature). Testing was done in a separate room to prevent experimental eggs from hearing other vocalizing embryos.

The experiment began by placing a vocalizing egg at the top of the ramp with the same orientation as in the incubator, and allowing it to acclimate for 5 min. The experimental treatment consisted of allowing the egg to roll down the ramp one-half revolution. We recorded the total number of embryonic vocalizations during a 1-min pretreatment (control) and a 15-s posttreatment period. The pretreatment period was initiated only after three consecutive minutes of no peeping. We then repeated the procedure. After another 3-min silent period and 1-min pretreatment period, the egg was allowed to roll one-half revolution, returning to its original position. Again, we recorded any vocalizations produced by the embryos. Twenty eggs were tested. Statistical analyses were performed using a Wilcoxon matched-pairs signed-ranks test.

RESULTS

*Egg-cooling experiment.*—Vocalization rates varied significantly among periods ( $F = 7.84$ ,  $df = 3$  and  $54$ ,  $P < 0.001$ ; Fig. 2). Duncan's multiple range test revealed that the comparisons between warm and cold treatments were signifi-

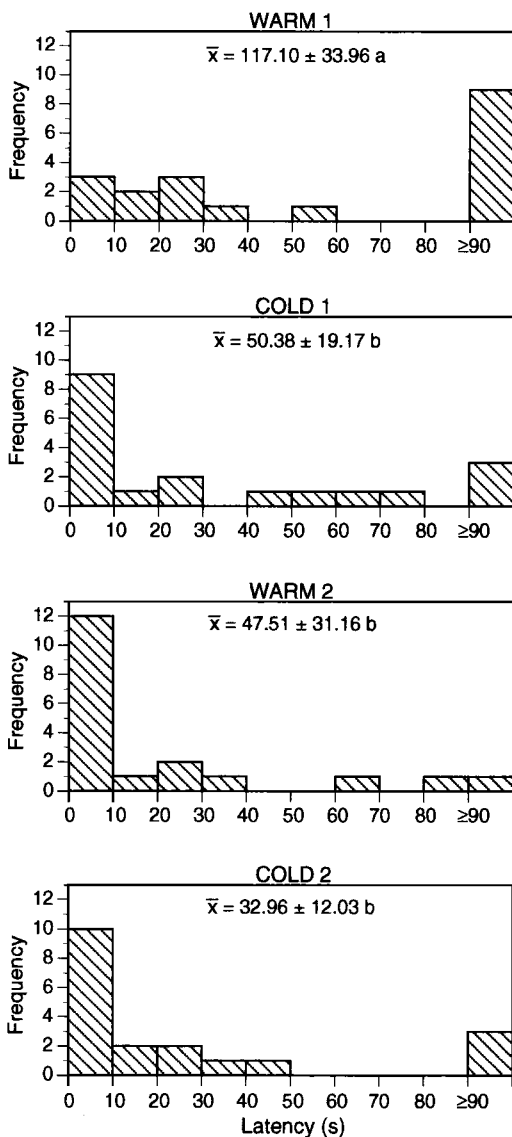


FIG. 3. Mean ( $\pm$  SE) and frequency distribution of latency time to first vocalization of 19 Eared Grebe embryos in response to warm or cold water treatments. Bars represent frequency in particular interval (0 to <10 s; etc.). Different letters following means indicate significant difference between periods (Duncan's multiple range test,  $P \leq 0.05$ ).

cantly different ( $P \leq 0.05$ ; Fig. 2). All embryos were likely to vocalize within the first minute of each period. However, vocal-response latency was significantly longer during the first warm period (a control involving a continuation of the warm acclimation period) than during the last three periods (each of which involved a

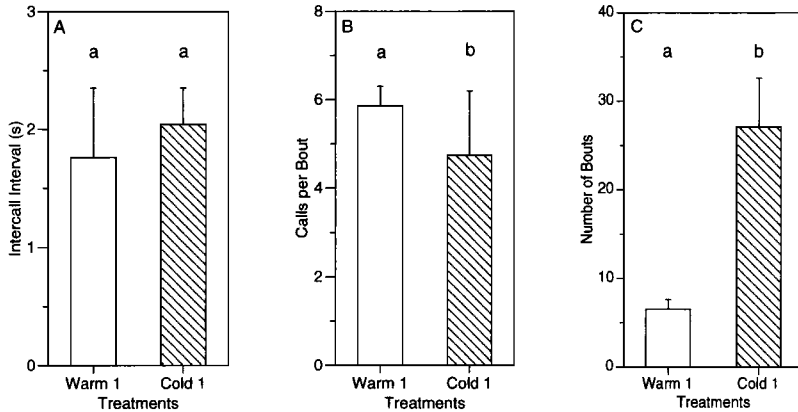


FIG. 4. Comparison between Warm 1 and Cold 1 treatments for three vocal parameters. Bar represents  $\bar{x}$ , SE for: (A) intercall intervals, (B) calls per bout, and (C) number of bouts. Different letters indicate significant difference between treatments for that parameter.

temperature change; Friedman two-way ANOVA,  $\chi^2 = 24.44$ ,  $df = 3$ ,  $P < 0.005$ ; Fig. 3). Frequency distributions of response latency times for the first period compared with subsequent cold and warm water periods showed that embryos most often peeped within 10 s of a change in water temperature (Fig. 3).

The difference in mean intercall interval between the warm ( $1.76 \pm 0.59$  s) and cold ( $2.04 \pm 0.31$  s) treatment approached significance ( $T = 36$ ,  $n = 16$ ,  $P = 0.052$ ; Fig. 4A). The mean number of calls per bout was greater during the warm ( $5.85 \pm 0.45$ ) than the cold ( $4.74 \pm 1.45$ ) treatment ( $T = 34$ ,  $n = 16$ ,  $P = 0.042$ ; Fig. 4B). Also, embryos produced more bouts of calls during the cold ( $27.0 \pm 5.64$ ) than the warm ( $6.44 \pm 1.17$ ) treatment ( $T = 14$ ,  $n = 16$ ,  $P = 0.002$ ; Fig. 4C).

*Egg-turning experiment.*—During posttreatment period 1, 13 of 20 embryos vocalized after rolling one-half a revolution down a ramp, whereas only 1 of 20 embryos vocalized during pretreatment period 1 (Fisher's exact test,  $P < 0.005$ ). The responses to the second rolling treatment were similar. After rolling back to their original positions, 9 of 20 embryos vocalized, whereas only one vocalized in pretreatment period 2 (Fisher's exact test,  $P = 0.004$ ).

For both test periods, embryos also emitted more vocalizations after being turned than when at rest (test 1,  $T = 1.5$ ,  $n = 14$ ,  $P < 0.001$ ; test 2,  $T = 4$ ,  $n = 10$ ,  $P = 0.007$ ; Fig. 5). Of the 13 embryos that produced vocalizations during the first test period, six did not emit any vocalizations when turned a second time. Only two

embryos vocalized during test period 2 but not during test period 1. The median number of vocalizations in test period 2 decreased significantly from test period 1 ( $T = 19$ ,  $n = 15$ ,  $P = 0.009$ ).

#### DISCUSSION

The results of our first experiment support the hypothesis that peeping vocalizations by embryos are elicited by egg cooling. Embryonic vocalizations may be a form of communication with parents to reduce the negative impacts created by egg cooling on the development and viability of the embryo. Long-term exposure of embryos to abnormally low incubation temperatures delays hatching in many species (see Lundy 1969). In a laboratory experiment that chilled embryos after pipping, Evans (1990b) reported significant delays in hatching time and an increase in hatching intervals in Ring-billed Gulls (*Larus delawarensis*). Also, Evans (1990c) determined that hatching intervals in American White Pelicans are prolonged when eggs are artificially chilled.

Spiers and Baummer (1990) quantified the degree to which long periods of exposure to cold temperatures slowed the development of Japanese Quail (*Coturnix coturnix*) embryos. A 1°C reduction in temperature reduced the wet mass of a 5-g, 16-day-old quail embryo by 0.35 g (7%), and a one-day delay in normal growth could result from a temperature drop of 2°C. Booth (1987) reported that Malleefowl (*Leipoa ocellata*) embryos used more energy and hatched with

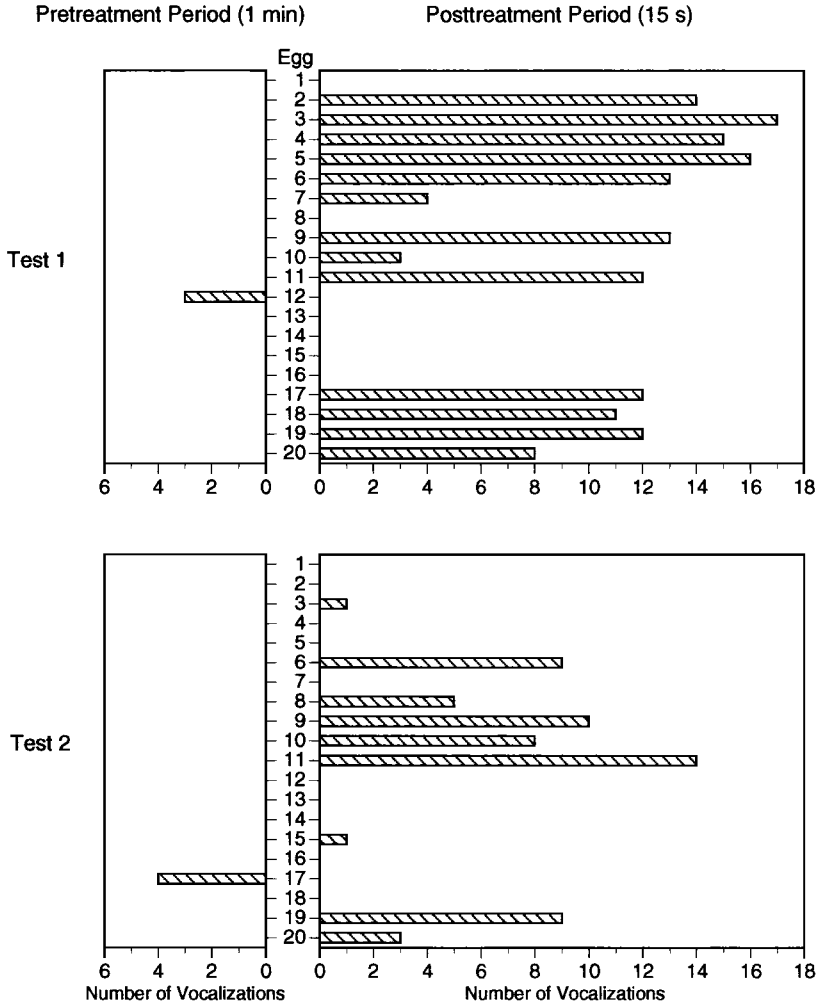


FIG. 5. Number of embryonic vocalizations given before and after egg turning. Two tests conducted on each of 20 Eared Grebe embryos. First test turned egg 180° and second returned the egg to its original position.

smaller energy reserves when incubated at low temperatures than when incubated at normal temperatures. After hatching, precocial birds use yolk reserves for both energy and nutrients for rapid growth (Peach and Thomas 1986). Thus, Eared Grebe embryos incubated at low temperatures may use energy normally reserved for body maintenance and growth.

Growth and energy costs may have important implications for late-hatching offspring of asynchronously hatching species, particularly those that exhibit obligate or facultative brood reduction. In Western Grebes (*Aechmophorus occidentalis*) and Pied-billed Grebes, for example, dominance hierarchies are established soon after hatching, with older siblings dominant to

younger siblings (Nuechterlein 1981, Forbes and Ankney 1987). Forbes and Ankney (1987) found that chick survival also decreased with increasing hatching intervals. If egg cooling has a physical impact on viability, later-hatching young may be at an even greater competitive disadvantage. Dominant chicks may limit access to food brought by their parents or access to their parents' limited back space during brooding (Nuechterlein 1981). Booth (1987) and Evans (1990b) have drawn similar conclusions in their studies.

Slow growth rates of late-developing embryos may lead to egg abandonment in grebes. Abandoned eggs of Eared and Western grebes often are fertile and within several days of

hatching (G. Nuechterlein and D. Buitron pers. obs.). Prinzing (1974, 1979) suggested that Eared Grebe embryos vocalized to prevent adults from abandoning the nest, and Simmons (1955) suggested a similar function for peeping in Great Crested Grebe (*Podiceps cristatus*) embryos. Although this "anti-abandonment" hypothesis was not tested directly, it is a special case of the care-solicitation hypothesis and seems very intuitive.

Experimental cooling of American White Pelican (Evans 1988, 1990d) and American Coot (*Fulica americana*) embryos (Bugden and Evans 1991) produced a significant increase in the number of vocalizations. In a later field study, Evans (1992) determined that American White Pelican embryos also emitted more calls per bout when the eggs were exposed than did covered embryos. In our experiments, Eared Grebe embryos detected rapidly any temperature changes and vocalized in response to them. The overall vocalization rate of Eared Grebe embryos nearly doubled during the cold-water treatments, but bouts became more disjunct, and chilled embryos produced significantly fewer calls per bout. American White Pelican embryos communicated their thermal status to their parents, and the parents often responded so that the thermal environment of the embryos improved (Evans 1990e, 1992). A system similar to that of American White Pelicans may exist for Eared Grebes, although this has not been tested experimentally.

Toward the middle of the incubation period, an avian embryo becomes fixed in position within the egg, and a mass asymmetry is created that causes the egg to maintain a position of equilibrium (Drent 1970). The position of equilibrium and the fixed position of the embryo within the egg allow for the pip hole to be formed uppermost in the egg (Drent 1973). Kovach (1968) speculated that an upward facing pip hole is selectively favored in domestic chickens because there is less interference of nest material with air flow and shell-cutting behavior.

Nests of Eared Grebes often are comprised of floating algae and sodden detritus. Therefore, the eggs usually are incubated under very damp conditions, often in shallow puddles of water in the nest, and embryos possibly would suffocate if the pip hole were turned down by the incubating parent. Perhaps the unusually short (1-3 h) pipped-egg stage of incubation in grebes

may relate to this danger. In response to being turned, Eared Grebe embryos emitted many more vocalizations than when at rest. Recently turned embryos also reduced the number of vocalizations when turned back to their original upright position. Possibly, a vocalizing embryo signals to the incubating adult that it is not in a position of equilibrium and should be turned. Similarly, pipped Bar-headed Goose (*Anser indicus*) embryos emitted distress vocalizations in response to being upside down, and the incubating parent responded by turning the egg, presumably so that the pip hole was again turned up (Wurdinger 1970, cited in Drent 1973, 1975).

Field observations of incubating Red-necked Grebes (*Podiceps grisegena*) indicate that individual eggs are rotated completely at least one time daily during early- to mid-incubation. If this is also true of Eared Grebes, the vocalizations by embryos 1-2 days before hatching may serve to signal the parents to stop such turning in preparation for the critical period of pipping. Alternatively, the grebe embryo may simply be signaling its parent that it is alive and about to hatch. Viable, nonpipped grebe eggs are occasionally abandoned, especially if only one egg has yet to hatch. Prepipped embryos also peep commonly when simply touched or jiggled, and this is possibly as effective as turning the egg 180° in eliciting embryonic vocalizations. Further laboratory experiments as well as field observations of parental behavior might be able to distinguish the anti-abandonment and anti-turning hypotheses, both of which are special cases of the care-solicitation hypothesis.

In conclusion, our data from the egg cooling and egg turning experiments are in accordance with the care-soliciting hypothesis of Evans (1988). Eared Grebe embryonic vocalizations appear to express reliably both the embryo's viability and its thermal environment, which likely results in greater parental attention to the nearly hatched embryo.

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