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EMBRYONIC VOCALIZATIONS AND THE REMOVAL OF FOOT WEBS FROM PIPPED EGGS IN THE AMERICAN WHITE PELICAN¹

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Key words: American White Pelican; embryonic vocalizations; incubation; foot webs; communication; development.

The American White Pelican (*Pelecanus erythrorhynchos*) normally incubates a clutch of two eggs under the foot webs (Schaller 1964, Knopf 1979, pers. observ.). This mode of incubation is similar to that employed by several other members of the Pelecaniformes, including the Brown Pelican (*P. occidentalis*, Schreiber 1977), gannets, and boobies (Sulidae, Nelson 1978). In the Sulidae, Nelson has noted that with the onset of pipping, the incubating parent moves the webs below the eggs, presumably so the embryo will not be injured by the parent should weight be applied to the cracked and weakened shell. White pelicans also remove their foot webs from the eggs when they pip (pers. observ.).

Pelicans, along with sulids and presumably other members of the order, although altricial, are able to vocalize strongly during the pipped egg stage. This raises the possibility (Nelson 1978) that embryonic calls may play a functional role in bringing about the removal of the webs from newly pipped eggs. An exper-

imental test of this hypothesis for the American White Pelican was the objective of this study.

METHODS

Pelicans were observed at a colony of over 1,000 nests located on an island in East Shoal Lake, Manitoba, Canada. A blind was erected about 5 m from the edge of the colony 1 week before the onset of pipping. Nests within viewing range of the blind were examined quickly each morning and a sample of those containing either two unpipped eggs or one pipped and one unpipped egg were marked with small color-coded plastic flags. A miniature microphone (Realistic, Model 33-1052) was enclosed in thin plastic and laid between the eggs on the nest floor at four nests containing one pipped and one unpipped egg. Microphone leads were run back to the blind for subsequent monitoring with a Uher 4000 Report tape recorder. The nests were monitored, both visually and audibly, for a total of 5.33 hr.

To test experimentally for effects of pipped egg vocalizations on parental incubation behavior, a small (9.5 cm diameter) loudspeaker covered with plastic and a protective screen was buried immediately under the center of the nest cup and covered with about 1 cm of nest material, usually a mixture of fine gravel and dead vegetation. Nests ($n = 10$) selected for playbacks contained two unpipped eggs, but were always within a portion of the colony showing evidence of actual or

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imminent hatch at other nests, thus ensuring that the birds tested would themselves be approaching, though not yet at, the pipped egg stage of the incubation cycle. For playbacks, I used a continuous tape loop containing embryonic calls recorded from a nest with a pipped egg. A given playback sequence began with a 1-min silent control (pretest) period, followed immediately by a 1-min playback (test) period. Each test period was followed by a second 1-min silent control (posttest) period. While the loudspeakers were in place, the entire playback sequence was repeated a second time. Inter-test intervals at individual nests ranged from 15 to 109 ($\bar{x} = 75.5$) min. Statistical comparisons employed the Friedman two-way ANOVA by ranks and Wilcoxon's matched-pairs tests.

RESULTS

Examination from the blind of nests where incubation mode could be determined indicated that 36 of 41 (88%) parents with two as yet unpipped eggs held them under the webs. The locations of the five nests where the webs were not above the eggs were noted and examined the next day. Each of these five nests contained a pipped egg at that time, indicating that pipping was imminent when the original observations were made. Parental foot webs were no longer on the eggs at 25 of 32 (78%) nests containing one pipped and one unpipped egg when these nests were first observed from the blind. Webs were subsequently removed, prior to my exit from the blind, at six of the remaining seven pipped egg nests.

The calls emitted by embryos during the pipped egg stage were brief, loud, harsh squawks. Emission of these calls was almost incessant when I examined nest contents each morning. Calling was also frequent during normal incubation at each of the four monitored nests (mean call rate = 112, range = 60 to 260 calls/hr). Calls at these nests were given either singly or in bouts ranging up to 75 calls/bout (median = 5 calls/bout, $n = 57$ bouts). Calls at the monitored nests did not appear to result from vocal interactions with the usually silent parents.

The response of an incubating parent to a sequence of embryonic calls was similar throughout the pipped egg stage and, when playbacks were used, before pipping had begun. The typical response pattern consisted of looking down combined with a partial raising of the wings and an oblique raising of the front of the body above the feet and eggs, followed by a side-to-side swaying of the body as the feet were alternately lifted and set down in a shuffling-on-the-spot gait. This distinctive behavior will be referred to as "shuffling." At experimental nests, pretest levels of shuffling were low, reflecting the general low level of this form of behavior prior to the onset of pipping. Shuffles increased markedly during the 1-min playback periods (from 0.0 to $11.1 \pm SE = 1.9$ foot movements/bird), then returned rapidly to low levels (2.2 ± 0.8 , $\chi^2 = 16.2$, $P < 0.001$) when the playback sound was discontinued. The second set of tests yielded essentially the same results as the first set (pretest = 0.0, test = 12.8 ± 2.0 , posttest = 1.8 ± 0.6 , $\chi^2 = 15.8$, $P < 0.001$).

As the parent shuffled, the webs slipped down to the bottom of the nest, often to a position partially un-

derneath the eggs. The eggs, which were typically side by side when the webs were on top, usually came to rest with one partially or completely in front of the other, between the parent's legs. Shuffling was sometimes accompanied by turning on the nest (16 instances of turning during 39 observed shuffle sequences, experimental and observational nests combined), and by pushing back on the eggs with the bill (19 occurrences during the 39 shuffle sequences). These behaviors appeared to facilitate removal of the webs. The parental response sequence normally ended with settling down and covering the eggs.

DISCUSSION

A switch from incubating eggs under the foot webs to removal of the webs and subsequent incubating or brooding of pipped eggs and new young between the legs appears to be typical of American White Pelicans. The playback tests demonstrated that vocalizations commonly heard from pipped eggs facilitate this change in parental behavior, as previously suggested for members of the Sulidae (Nelson 1978). Whether removal of the webs from pipped eggs reduces their risk of injury from the parent (Nelson 1978), or is simply an early manifestation of a brooding pattern that would almost certainly have to occur once the young were hatched, remains unknown.

During the playback experiments, removal of the webs from above the eggs invariably occurred as a result of leg and foot movements associated with a shuffling sequence. It is therefore important to note that a behavior sequence essentially identical to shuffling, with temporary removal of the webs from the eggs, also occurs when an incubating parent turns the eggs during the normal course of incubation (pers. observ., cf. Schaller 1964). Shuffling and removal of the webs is thus not a response uniquely elicited by embryonic vocalizations. The main differences between the two contexts appeared to be the greater immediacy and permanence of web removal, and the frequent (>50%) occurrence of shuffling in the absence of billing the eggs in response to embryonic vocalizations.

The strong and early development of calling, combined with the continuance of these calls throughout the remainder of the incubation period and well into the posthatch period (pers. observ.), raises the possibility that calls of embryos and young pelicans may have some other function in addition to facilitating removal of the foot webs from pipped eggs. Synchronizing of the hatch within a clutch is one important function for embryonic sounds in some species (Vince 1969), but pelicans exhibit a decidedly asynchronous hatching pattern within the clutch (Knopf 1980, Cash and Evans 1986). More plausible is the possibility that embryonic calls provide recognition cues to the parents (Impeken and Gold 1973) or influence their adjustment to caring for the young, in particular bringing food (Nelson 1978). It is relevant to both of these hypotheses that the embryonic calls are distinctively different from begging calls employed by young when soliciting food from the parent (pers. observ.). If embryonic calls functioned primarily as early recognition and food soliciting signals, it seems surprising that the

begging calls used immediately after hatching would not also be used in the egg.

Behavioral thermoregulation, potentially achieved when calls from a cold embryo or hatched chick elicit enhanced incubation or brooding by the parent has also been suggested (Evans, in press) as a possible function of embryonic calls in white pelicans. Cooling is a potent stimulus eliciting calling by embryos of this species. When a return to warmer conditions is made contingent upon such calling in a laboratory context, the embryos are able to behaviorally thermoregulate against otherwise continuous cold stress for periods of up to at least 5 hr (Evans, in press). The tendency for parents to push the eggs back while shuffling and then resettle over them, as observed in this study, is consistent with this functional interpretation.

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LITTORAL FORAGING BY RED PHALAROPES DURING SPRING IN THE NORTHERN BERING SEA¹

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Key words: Bering Sea; foraging behavior; Phalaropus fulicaria; Red Phalarope; St. Lawrence Island; surf feeding.

Phalaropes demonstrate considerable plasticity in their choice of foraging habitats. The Red Phalarope (*Phalaropus fulicaria*) alternates use of pelagic environments in winter and migration (Taning 1933, Stanford 1953, Briggs et al. 1984) with wet tundra habitats during the breeding season (Kistchinski 1975, Mayfield 1979,

Ridley 1980). Foods available and taken in littoral zones of the Arctic Ocean in fall have been identified (Conners and Risebrough 1978, Johnson and Richardson 1980), but otherwise little attention has been devoted to the transition between the marine and terrestrial periods of the Red Phalarope's life history. We report phalarope use of littoral areas during spring in the northern Bering Sea at Kongkok Bay, St. Lawrence Island, Alaska. In addition, we describe phalarope foraging tactics and foods available in the surf zone, emphasizing this form of littoral foraging as an opportunistic and facultative feeding strategy.

STUDY AREA AND METHODS

This study was conducted at Kongkok Bay (63°24'N; 171°49'W) on the southwestern side of St. Lawrence Island (Fig. 1). The island here contains the southern end of the Poovoot Range, an area of primarily rocky

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