DIFFERENTIAL EFFECTS OF CHICK VOCALIZATIONS AND BILL-PECKING ON PARENTAL BEHAVIOR IN THE RING-BILLED GULL

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Abstract.—In a series of field experiments, adult Ring-billed Gulls attending either blindfolded or surgically muted chicks were observed in order to ascertain whether various patterns of parental behavior would be adversely affected by the failure of the chicks to peck the parent's bill or to vocalize. Adults attending chicks that were blindfolded either at hatching or 3 days later appeared normal in all patterns of parental behavior. Adults attending chicks that had been muted at hatching showed normal attentive and protective behavior but were markedly deficient in providing the chicks with food. Muting chicks after they had interacted normally with their attendant adults for 3 days resulted in no major departures from normal parental behavior, including the rate of feeding the chicks.

These results indicate that parent Ring-billed Gulls do not require specific stimulus input in the form of bill-pecking or vocalizations by their chicks to continue exhibiting parental attentive and protective behavior. This behavior, which is largely a gradually modified extension of that shown in the incubation phase, evidently can be further maintained by more general visual and (or) tactile input from chicks. Moreover, the bill-pecking of chicks apparently is neither essential nor sufficient to incite normal parental food-provisioning behavior. On the other hand, this provisioning behavior does appear to depend temporarily on auditory reception of the vocalizations of chicks located in the nest. Once instigated, however, its further maintenance no longer requires this form of auditory input. *Received 23 June 1978, accepted 30 November 1978.*

The avian breeding cycle consists of an intricately timed procession of behavior patterns and external situations that culminate in the production of independent offspring. In proceeding through the various phases of its cycle, a breeding individual engages in activities that both advance its reproductive progress and provide information from the external situation concerning this progress. Social interactions invariably enter into this information flow. Early in the cycle, communication between mates is continually occurring as each attunes its behavior to the other's state of progress. Where durable pair bonds are formed, mates continue to communicate as the cycle proceeds past the sexual phase to the care of the eggs and then the young. The hatching of the chicks opens a new avenue of communication wherein parents and offspring interact to promote the latter's growth and survival. Although this new avenue arises rather suddenly, parents quickly make appropriate behavioral adjustments in response to stimulus input received from their chicks. This input is the focus of the present paper, which reports data collected during a long-term study of the reproductive behavior of the Ring-billed Gull (*Larus delawarensis*).

As is typical of Larids, the Ring-billed Gull features a monogamous pair bond and a lengthy period of parental care, cooperatively carried out by both members of the pair. The species breeds in dense colonies in which individual pairs establish a territory of 1–4 m^2 and proceed therein to build a nest and to incubate the clutch of usually three eggs. The behavior of parents early after the chicks hatch has been described in detail for this and other species (Paludan 1951, Goethe 1953, Tinbergen 1953, Beer 1966, Emlen and Miller 1969). It is characterized in general by persistent territorial defense and by gradually declining brooding with periodic rising, inspecting the nest contents, and resettling. Within a few hours after the chicks hatch, the parents begin to feed them by regurgitating and presenting food. These food deliveries continue at variable intervals until the chicks become independent several weeks later.

The behavior of the chicks during this same early period has also been thoroughly examined (Moynihan 1959, Evans 1970). Initially the semi-precocial chicks are relatively immobile, remaining in the nest for 3–4 days before traversing to other locations on and, later, beyond the territory. They begin vocalizing even before leaving the shell and soon after hatching begin pecking at conspicuous visual objects, including the parent's bill. The action components of the pecking and the stimuli eliciting it have received intensive study (Tinbergen and Perdeck 1950; Weidmann and Weidmann 1958; Hailman 1962, 1967). This bill-pecking often is seen in conjunction with feedings and, as its common label of "food-begging" implies, is considered important in inciting the parent to deliver food. The chicks also vocalize while pecking as well as at other times (Tinbergen 1953, Hailman 1967), however, and the relative importance of the pecking and vocalization in evoking food delivery has not been ascertained. Conceivably, either or both might also provide input affecting other patterns of parental behavior. We examined these matters in a series of field experiments wherein we presented adults with chicks that were either blindfolded to prevent bill-pecking or surgically muted to prevent vocalizing. We then observed the adults to determine whether their parental behavior deviated from normal.

Materials and Methods

The data presented here were collected during 1970–1977 in several breeding colonies in eastern Washington. The colonies, consisting of 2,000–6,000 adults each, were located on islands in the Columbia River about 40 km north of Pasco, in the Potholes Reservoir near the city of Moses Lake, and in Sprague Lake near Sprague.

Observations were made with 7× binoculars and 15–45× spotting scopes from elevated positions on rocky outcrops, sand dunes, or 4–10-m towers located beside the colonies. Observed events were either noted directly or recorded vocally on cassette tape recorders for later transcription into notebooks.

Chicks were blindfolded by gluing, with liquid collodion, a 15-mm disc of stiff canvas to the down surrounding each eye. The disc, gray in background color and decorated with black dots to resemble a chick's eye and head spots, required only a minute or two for application at the nest. Data from nests where chicks lost a blindfold were eliminated from analysis.

A surgical technique, originally described by Gottlieb and Vandenbergh (1968) and previously applied on gull chicks in the field (Miller and Emlen 1975), was used to render chicks voiceless. Briefly, the method consisted of anesthetizing a chick with ether, exposing its syrinx through a small incision in the inter-clavicular fossa, applying a thin layer of liquid collodion to the exposed syringeal membranes to prevent their vibration, and sealing the incision with collodion. The operation required only about 15 min, with the chick recovering from the anesthesia within a half hour. In about 80% of the cases, we succeeded in completely muting the chick, as indicated by its failure to vocalize when later administered a mild pain stimulus that elicits abundant calling by normal chicks. Only completely muted chicks were used in the experiments.

Following the operation and recovery, muted chicks showed no obvious departure from normal behavior other than their lack of vocalizing. To control for possible nonvocal abnormalities that might be detected by an adult, however, sham operations were performed on other chicks. These chicks were treated in the same way as muted chicks except that the collodion was applied to the trachea just anterior to the syrinx, thus leaving vocal capability unhindered as verified through observations after surgery.

All surgery was performed during late evening in an improvised laboratory nearby, where all chicks for the experiment were held overnight. If the chicks had already been occupying experimental nests, normal chicks were placed into the nests as overnight substitutes to reduce chances of adults deserting the nests.

To avoid complications of variable brood sizes arising from differential mortality or disappearance of chicks within multiple-chick broods, the observed nests were standardized at hatching with a single hatchling chick per nest, using chicks obtained from other nests in the colony. Depending on the experiment, the chicks were either all normal ones or some had already received blindfolds or surgery. Each of the nests selected for observation contained eggs in late stages of incubation but without pip-holes through which foetal vocalizations could be heard. These eggs were replaced by two infertile eggs in addition to the single chick, the inserted eggs serving simply to entice the adults to resettle quickly on the nest following standardization manipulations. All chicks were leg-banded and all nests posted with numbered markers for individual identification.

EXPERIMENTAL DESIGN

Four experiments were conducted, the first two with blindfolded chicks and the last two with muted chicks. Data in each experiment were gathered from at least two seasons, in each of which one or more replicate samples of nests containing blindfolded or muted chicks were observed along with control chicks.

The first experiment was performed on adults during the first 1½ days posthatching. For this experiment, blindfolded hatchlings were placed into 30 nests at the time of standardization, 17 of the chicks being tethered in the nest to prevent their wandering. Normal, nonblindfolded hatchlings, used to provide control data, were similarly placed into 26 nests, 17 of these chicks also being tethered. After placement, all the nests were observed for 13–15 h during the next 1½ days, after which the blindfolds and tethers were removed.

The second experiment ascertained whether the parental behavior of adults that had attended normal chicks for the first 3 days after hatching would subsequently be affected by blindfolding the chicks. In this experiment, normal chicks were placed into 40 nests during standardization and allowed to interact undisturbed with the attendant adults for 3 days, whereupon 21 of the chicks were blindfolded and tethered in their nests and 19, also tethered, were left without blindfolds to provide control data. All nests were observed before blindfolding for 5½–9 h on day 3, and afterward for 11½–12½ h before the blindfolds and tethers were removed at 4½ days.

The third experiment examined the behavior of adults attending muted chicks during the first 3 days posthatching. For this experiment, 66 nests received a muted hatchling, 23 nests received a sham-operated hatchling, and 114 received an untreated normal hatchling at the time of standardization. No chicks were tethered. The nests were then observed for 4–7 h on the first day and for 7–9 h on each of the next 2 days.

The fourth experiment ascertained the effects of muting normal chicks after their attendant adults had interacted with them for the first 3 days after hatching. Normal chicks were placed into 42 nests during standardization and left undisturbed for 3 days, at which time 26 of the chicks were devocalized, 8 received sham operations, and 8 were left normal. Again, no chicks were tethered. The nests, which before treatment had been observed for 7½–8 h on day 3, were subsequently observed for 7½–9 h on day 4 and, in most cases, for 8–10 h on each of days 5 and 6.

During observations, particular attention was directed to the incidence of parental feedings. Nests under observation were continuously scanned, and the occurrence and time of every feeding at individual nests were recorded. The length of a feeding bout varied from within a minute to about 15 min. Occasionally, an adult would regurgitate and briefly present food several times within a short interval. Rather than specify these as separate feedings, we considered them a single feeding if the interval between successive presentations was 15 min or less.

When seen, nest reliefs were also recorded as to occurrence and time. Because these often can occur quickly, many of them undoubtedly went unobserved, but the data gathered allowed comparison of the minimum frequency of nest reliefs. Also noted, but without quantitative measurement, were more general patterns of parental behavior involved in maintaining the territory and attending, brooding, leading, and defending chicks.

RESULTS

EXPERIMENT 1

Upon returning to their nests following chick placement, adults encountering blindfolded hatchlings readily accepted them. Several of the chicks without a tether strayed away before the return of the resident adults and became lost or were killed by nearby adults. Of the 17 chicks tethered to prevent such straying, only 1 (6%)

TABLE 1. Food presentations at nests where adults were tending either a blindfolded or nonblindfolded (normal) chick as observed for 13–15 h on the first 1½ days posthatching.

Chick condition	Number of nests observed	Number of nests where presentations were seen	Median number of presentations/h (and 95% confidence limits)[a]
Blindfolded	27	24 (89%)	.32 (.22–.54)
Normal	25	23 (92%)	.39 (.23–.39)

[a] Blindfolded chick condition does not differ significantly from normal condition; $P \leqq .34$, one-tailed Mann-Whitney U test.

was rejected by the resident adults, a proportion identical to the single rejection of the 17 tethered normal chicks.

During the next 1½ days, the behavior of adults with blindfolded chicks appeared typical of this early posthatching stage. Persistent sitting on the nest, interrupted at irregular intervals by rising, inspecting beneath, and resettling, ensued in a manner similar to that at nests with normal chicks. More obvious indication of parental attentiveness was observed on several occasions when a blindfolded chick without a tether wandered from the nest. Often, the attending adult either called toward the chick, while making exaggerated brooding movements over the nest, or moved to the chick and settled on it. In some cases the adult repeatedly regurgitated food and presented it while moving back toward the nest in a manner resembling the actions of parents when later leading their chicks.

Attempted feedings were observed at all but three of the nests with blindfolded chicks, and overall the frequency of such attempts did not differ from the feeding frequency at nests with normal chicks (Table 1). Notably, even if an adult had to change direction on the nest, it presented food toward the chick's head despite the chick's lack of bill-pecking and associated head movements.

EXPERIMENT 2

The blindfolding of chicks after the third day posthatching also resulted in no marked deviations in the behavior of attendant adults. Immediately following the blindfolding and tethering of the chicks, many of the adults exhibited intensified brooding and frequent rising-resettling in apparent response to the struggling of the chicks against their tethers, but the enhanced activity of both chicks and adults soon subsided. Subsequent observations during the next 1½ days revealed no abandonments or other signs of reduced parental attentiveness. The frequency of observed nest reliefs (1 every 7.3 h) was similar to that observed at nests retaining normal chicks (1 every 7.1 h). At all but two of the nests, the adults continued to present food to the now blindfolded chick (Table 2). The frequency of these presentations declined slightly from that observed on day 3 before blindfolding, but it remained close to the also slightly reduced feeding frequency at nests with normal chicks. Overall, the cessation of bill-pecking and other visually oriented actions did not appear to disrupt parental behavior to any appreciable extent.

EXPERIMENT 3

Of the 66 muted hatchlings introduced into nests, only 33 (50%) survived the first few hours, while 10 (15%) were rejected by pecking and 23 (35%) unaccountably died or disappeared. Losses of normal and sham-operated hatchlings occurred at a significantly lower incidence ($P \leqq .05$, one-tailed Chi-square tests). Of the 114 nor-

TABLE 2. Food presentations by adults at nests where the chick either was blindfolded at the end of the third day posthatching or was left without blindfolds (normal).

Day posthatching	Chick condition	Number of nests observed	Number of nests where presentations were seen	Median number of presentations/h (and 95% confidence limits)[a]
Day 3 (observed 5½–9 h)	Normal (before blindfolded)	21	20 (95%)	.44 (.33–.73)
	Normal	19	18 (95%)	.44 (.33–.73)
Day 4–4½ (observed 11½–12½ h)	Blindfolded	21	19 (90%)	.35 (.26–.48)
	Normal	19	17 (89%)	.35 (.24–.56)

[a] Blindfolded chick condition does not differ significantly from normal condition on day 4; $P \leq .37$, one-tailed Mann-Whitney U test.

mal chicks, 75 (66%) survived, 7 (6%) were rejected, and 32 (28%) were lost unaccountably. Of the 23 sham-operated chicks, 17 (74%) survived, 1 (4%) was rejected, and 5 (22%) were lost unaccountably. The excessive loss of muted chicks did not relate to any particular reaction by resident adults as they responded to the chicks but rather seemed to result from a higher incidence of rejecting the chicks outright, refusing to approach and sit on the nest, and failing to emit attractive calls to chicks that had strayed from the nest.

At nests where the muted chicks survived placement, subsequent territorial maintenance and parental attentiveness did not grossly differ from that at nests with sham-operated or normal chicks. The pattern of persistent sitting and periodic rising-resettling appeared normal, although subtle departures might have been undetected in the absence of quantitative measures. The minimum frequency of nest reliefs (1 every 9 h) was similar to that at nests with sham-operated chicks (1 every 10 h) and with normal chicks (1 every 8.5 h). Hence, overall parental protective and attentive behavior seemed largely unaffected by the lack of chick vocalizations.

Despite their close attentiveness, however, adults tending muted chicks were strikingly deficient in providing the chicks with food. On the first day following placement, only four feedings of muted chicks were seen at the 28 nests under observation. By the end of observations on the third day, only 13 (46%) of these chicks had been observed receiving food, whereas 14 (93%) of the sham-operated chicks and 62 (98%) of the normal chicks had been seen receiving food.

Daily data on feedings are summarized in Table 3. At nests with normal chicks, feedings usually were seen within a few hours after placement and averaged one feeding every 4.2 h of observation on the first day. They subsequently underwent significant increases in frequency to one every 2.4 h on day 2 and to one every 1.9 h on day 3 ($P \leq .02$, two-tailed Wilcoxin matched-pairs signed-ranks tests). A similar increase during this early posthatching period has been previously shown in other studies (Emlen and Miller 1969, Evans 1970). The incidence of feeding sham-operated chicks was similar to that of normal chicks in all respects. After averaging one feeding every 5.4 h on the first day, the frequency rose to 1 every 2.4 h on the second day and 1 every 2.1 h on the third. In contrast, muted chicks were not fed nearly as often, averaging a scant 1 feeding every 35.9 h on the first day, 1 every 6.7 h on the second, and 1 every 8.7 h on the third.

As an additional test to confirm that the low frequency of feeding was ascribable to the failure of muted chicks to vocalize, normal chicks 1–2 days old were placed

TABLE 3. Feedings at nests where adults were tending either a muted, sham-operated, or normal chick during the first 3 days posthatching.

Day posthatching	Chick condition	Number of nests observed	Number of nests where feedings were seen	Median number of feedings/h (and 95% confidence limits)[a]
	Muted	28	4 (14%)	.00 (.00–.00)
Day 1 (observed 4–7 h)	Sham-operated	15	10 (67%)	.15 (.00–.32)
	Normal	64	40 (62%)	.20 (.14–.25)
	Muted	22	11 (50%)	.05 (.00–.29)
Day 2 (observed 7–9 h)	Sham-operated	14	12 (86%)	.42 (.20–.67)
	Normal	63	60 (95%)	.40 (.29–.43)
	Muted	13	7 (54%)	.07 (.00–.24)
Day 3 (observed 7–9 h)	Sham-operated	12	12 (100%)	.55 (.25–.59)
	Normal	56	55 (98%)	.50 (.40–.62)

[a] Muted chick condition differs significantly from normal condition and from sham-operated condition on each of the 3 days; $P \leq .001$, one-tailed Mann-Whitney U tests.

on day 4 posthatching into 11 nests previously containing muted chicks that had died on the second or third day. The adults at seven of these nests had never previously been observed feeding the muted chicks. During 8 h of observation following this introduction of normal chicks, feedings were observed at all 11 nests, and overall, averaged 1 feeding every 1.8 h (median of 0.50 feedings per h with 95% confidence limits of .29–.75; confidence limits derived according to Campbell 1967). This immediate elevation in feeding rate is further evidence that the earlier feeding deficit resulted from lack of auditory input to the adults from their muted chicks.

Observations of muted chicks as they interacted with attending adults revealed no indication of any nonvocal abnormalities other than later signs of weakness brought on by insufficient food intake. Following their placement, they, as well as sham-operated chicks, appeared to be as active and to bill-peck as vigorously and frequently as normal chicks. Any surgical effects on nonvocal behavior apparently were minor and, as evidenced by the near normal rate of feeding sham-operated chicks, of little consequence to parental food-provisioning.

TABLE 4. Chick survival at nests where adults were tending either a muted, sham-operated, or normal chick during the first 3 days posthatching.

Day posthatching	Chick condition	Number of chicks in sample[b]	Accumulated number of chicks fate unknown	Accumulated number of known mortalities	Number of known survivors[a]
	Muted	32	3 (9%)	7 (22%)	22 (69%)
Day 1	Sham-operated	15	0 (0%)	1 (7%)	14 (93%)
	Normal	64	1 (2%)	0 (0%)	63 (98%)
	Muted	31	3 (10%)	15 (48%)	13 (42%)
Day 2	Sham-operated	15	1 (7%)	2 (13%)	12 (80%)
	Normal	59	1 (2%)	2 (3%)	56 (95%)
	Muted	29	4 (14%)	23 (79%)	2 (7%)
Day 3	Sham-operated	15	1 (7%)	4 (27%)	10 (67%)
	Normal	54	5 (9%)	4 (7%)	45 (83%)

[a] Muted chick condition differs significantly from normal condition on each of the 3 days ($P \leq .001$) and from sham-operated condition on day 2 ($P \leq .01$) and on day 3 ($P \leq .001$); one-tailed Chi-square tests.

[b] Decreases with successive days in some samples arose from some nests being eliminated because the adults adopted an additional chick or emigrated with the chick from the territory and could not be located.

TABLE 5. Feedings at nests where the chick either was muted, received a sham operation, or was left untreated (normal) at the end of the third day posthatching.

Day posthatching	Chick condition	Number of nests observed	Number of nests where feedings were seen	Median number of feedings/h (and 95% confidence limits)[a]
Day 3 (observed 7½–8 h)	Normal (before muted)	26	26 (100%)	.50 (.37–.62)
	Normal (before sham-operated)	8	8 (100%)	.50 (.12–.87)
	Normal	8	8 (100%)	.59 (.22–1.00)
Day 4 (observed 7½–9 h)	Muted	26	24 (92%)	.42 (.25–.53)
	Sham-operated	8	8 (100%)	.49 (.33–1.00)
	Normal	8	8 (100%)	.45 (.25–.67)
Day 5 (observed 8–10 h)	Muted	16	15 (94%)	.25 (.12–.44)
	Sham-operated	6	6 (100%)	.34 (.11–.87)
	Normal	5	3 (60%)	.17 (.00–.50)[b]
Day 6 (observed 8–10 h)	Muted	14	14 (100%)	.40 (.20–.50)
	Sham-operated	3	3 (100%)	.60 (.20–1.40)[b]
	Normal	3	3 (100%)	.25 (.25–.75)[b]

[a] Muted chick condition differs significantly from normal and sham-operated conditions (combined) on day 4 ($P \leqq .05$) but not on day 5 ($P \leqq .48$) or day 6 ($P \leqq .26$); one-tailed Mann-Whitney U tests.
[b] Numbers in parentheses are total range; sample too small for deriving confidence limits.

The effect of inadequate feedings of the muted chicks was quite apparent in their low rate of survival (Table 4). By the end of the first day's observations, 7 (22%) of the 32 muted chicks checked for survival were known to have succumbed. The mortality rate then rose rapidly to 48% and 79% by the end of days 2 and 3, respectively. Only 2 (7%) of the muted chicks were known to be alive at the end of the third day. Sham-operated chicks fared much better, as 67% survived the 3-day period, a proportion slightly but not significantly lower than the 83% survival of normal chicks ($P \leqq 0.14$, one-tailed Chi-square test).

EXPERIMENT 4

Muting chicks after 3 days of interacting normally with their attendant adults evoked no substantial change in parental behavior during the 3 days of observation following muting. No rejections or abandonments were observed, nor were any signs apparent of reduced attentiveness, as the adults remained near their now muted chicks. Feedings (Table 5) continued in all cases except one, where the chick disappeared after 9 h of observation. On the first day following devocalization, the feeding frequency dropped slightly, although significantly, from that of the preceding day ($P \leqq .01$, one-tailed Wilcoxin test). It declined even further on the next day, then rose again during the last day of observations. At the fewer nests with sham-operated and normal chicks, however, a similar pattern of fluctuation and overall decrease in feeding frequency was also observed. Other studies have independently revealed a decline in feeding rate during the later part of the first week (Emlen and Miller 1969, Evans 1970), as apparently fewer but larger deliveries of food are brought to the chicks.

Records kept on survival (Table 6) further indicated that the reduced frequency of feeding muted chicks was not grossly abnormal. Only 4 (16%) of the chicks died during the 3 days following muting, as compared to 1 (12%) sham-operated chick and 1 (14%) normal chick. The 14 muted chicks still being watched on the third

TABLE 6. Chick survival at nests where the chick either was muted, received a sham operation, or was left untreated (normal) at the end of the third day posthatching.

Day posthatching	Chick condition	Number of chicks in sample	Accumulated number of chicks fate unknown	Accumulated number of known mortalities	Number of known survivors[a]
Day 4	Muted	25	3 (12%)	2 (8%)	20 (80%)
	Sham-operated	8	1 (12.5%)	0 (0%)	7 (87.5%)
	Normal	8	1 (12.5%)	1 (12.5%)	6 (75%)
Day 5	Muted	25	3 (12%)	4 (16%)	18 (72%)
	Sham-operated	8	2 (25%)	1 (12.5%)	5 (62.5%)
	Normal	8	1 (12.5%)	1 (12.5%)	6 (75%)
Day 6	Muted	25	4 (16%)	4 (16%)	17 (68%)
	Sham-operated	8	2 (25%)	1 (12.5%)	5 (62.5%)
	Normal	7[b]	1 (14%)	1 (14%)	5 (71%)

[a] Muted chick condition does not differ significantly from normal and sham-operated conditions (combined) on any day; $P \leq .32$, one-tailed Chi-square tests.
[b] Sample size decreased because adults and chick at one nest emigrated from the territory and could not be located.

day of observations were later checked for survival on the sixth day after muting, and all were alive and appeared healthy. Hence, any reduction in feeding rate owing to vocal impairment was not so severe as to cause excessive mortality.

DISCUSSION

Our experimental approach in this study was one of selectively eliminating a particular kind of potential stimulus input from chick to parent while leaving other stimulus variables and surrounding circumstances as natural as procedures would permit. The elimination of the chick's bill-pecking through blindfolding was not entirely selective, of course, as other visually oriented actions of the chick were also eliminated, and any deviation from normal behavior by the attendant adult would have to be interpreted accordingly. The elimination of auditory input by surgically muting the chick embodied all variants of chick vocal patterns and thus precluded evaluation of the importance of any particular pattern. It was selective, however, to the extent that only a single source of sound input to the adult was eliminated and in this regard was preferable over the alternative method of surgically deafening the adult, whose subsequent behavior could be adversely affected not only by the surgery but also by the total deprivation of auditory input. Of course, the surgery for muting the chick could affect its nonvocal behavior in such a way as to produce abnormal visual or tactile input to the adult, a possibility that we examined by means of sham operations and found to be negligible.

Some departure from natural circumstances necessarily was caused by our experimental intervention in standardizing nests and in treating chicks. The standardizing of nests with only one chick each possibly resulted in some quantitative differences in parental behavior, such as a lower feeding frequency (see Henderson 1975), as compared to that of adults tending more typical broods of 2–3 chicks. Hence, although our quantitative figures seem valid for comparing different treatment conditions, on an absolute basis they may not represent a larger brood situation.

Quite apart from brood size, the standardization method involved the abrupt introduction of chicks into nests during disturbed adult uprise. Upon returning to the nest after the disturbance the adult undoubtedly responded less positively to the chick than if the adult had been sitting calmly while the chick hatched beneath. Our intrusion probably contributed much to the losses incurred at the time of chick placement, but at nests with surviving chicks it likely had only a brief effect on the adult after settling back on the nest. Likewise, any adverse effects from our intrusion into the colony for chick treatment at the end of the third day posthatching would likely end shortly after the return of the adult.

STIMULUS INPUT FROM CHICKS AND PARENTAL TENACITY

The persistence with which a parent Ring-billed Gull protects and tends its chicks is a direct indicator of overall parental tenacity. At first, the protective and attentive behavior is an extension of that already occurring in the preceding incubation phase wherein adults are aggressively defending the territory and continuously providing warmth and physical protection to the nest contents. After the chicks hatch, these nest-oriented activities persist for 2–3 days, whereupon their focus shifts to the chicks themselves as the latter become more mobile and spend more time away from the nest (Emlen and Miller 1969, Evans 1970). The persistence of these activities depends upon continual stimulus input, for destruction of the eggs or chicks leads to a rapid deterioration of parental stability followed by desertion of the nest or brood site (Emlen and Miller 1969). During incubation, the critical input is largely through tactile reception, augmented by visual input from the eggs (Poulson 1953, Beer 1961, Baerends et al. 1970). The hatching of the chicks drastically changes the stimulus situation as the tactile and visual features of the nest contents suddenly become more complex and dynamic, and new auditory input is received. As the posthatching phase progresses, more gradual changes ensue as the chicks grow and undergo developmental changes in behavior.

In view of the complexity and diversity of potential stimulus input from chick to parent, we did not highly suspect the singular action of pecking the parent's bill to be critical for continued parental tenacity, and indeed, its elimination either at the time of hatching or 3 days later did not result in any signs of deteriorating parental attentiveness or protection. Auditory input from the chick was more suspect, in that auditory signals feature prominently in many aspects of avian breeding behavior. Even here, however, elimination of this input at hatching or 3 days later had no substantial adverse effect on parental attentive or protective behavior. Hence, this behavior appears to be effectively maintained by other stimulus input received through the visual and (or) tactile modalities.

STIMULUS INPUT FROM CHICKS AND PARENTAL FOOD-PROVISIONING

Whereas the protective and attentive behavior shown by parents to their chicks can be considered an extension, with gradual modification, of foregoing behavior patterns, parental food-provisioning is a new activity that begins with the appearance of chicks in the nest. It can be prematurely induced by substituting chicks for the eggs a week or two earlier than the normal hatching time (Miller 1972), and it immediately ceases if the chicks die or are replaced with eggs (Emlen and Miller 1969). It obviously is instigated, therefore, by stimuli received from active chicks through one or more sensory modalities.

Significance of bill-pecking.—The pecking that a chick delivers to its parent's bill could provide both tactile and visual stimulation inciting food regurgitation. Our results, however, indicate that it is not an essential stimulus for either the instigation or later maintenance of parental food-provisioning. Chicks prevented by blindfolds from bill-pecking received offers of food as frequently as did normal chicks (Tables 1 and 2). On the other hand muted hatchlings, quite capable of bill-pecking and often observed vigorously doing so, were scarcely fed at all (Table 3), indicating that the pecking in itself is insufficient for stimulating parents to begin delivering food at a normal rate. Whether these results apply equally to parents with and without breeding experience remains unanswered, as the breeding experiences of adults in our samples were unknown. They do, however, signify that some caution should be exercised in labelling the bill-pecking as "food-begging" insofar as such a label is meant to imply that the pecking itself provides the primary stimulation for parental food-provisioning.

Rather than through any effects on the parent, the significance of the bill-pecking perhaps relates more directly to the ingestive function of this motor pattern. A hatchling gull chick pecks at a wide array of conspicuous visual objects, not all of which constitute a food source (Goethe 1937; Hailman 1961, 1967). Pecks directed to the parent's bill could help assure that the chick initially discovers and subsequently learns its normal source of food. Such a trial-and-error effect is indicated by Hailman's (1961, 1967) analysis of the ontogeny of this pecking in Herring and Laughing gull chicks (*Larus argentatus* and *L. atricilla*).

Significance of chick vocalizations.—As mentioned earlier, the vocalizations emitted by chicks as they hatch constitute a new source of potential auditory input to the parent. Just how well the adult can hear these vocalizations as it covers the chicks on the nest is uncertain, but following hatching, sitting adults increase their rate of rising and inspecting beneath (Beer 1966), thereby enhancing auditory reception of the vocalizations. The results of our third experiment (Table 3) indicate that reception of these calls is critical for instigating normal parental food-provisioning. Although appearing normal in other patterns of parental behavior, adults tending muted chicks either failed to feed them or did so at such a low frequency that the chicks could not survive. Without the auditory input, the stimulation received through other modalities was evidently insufficient for inciting parents to deliver food regularly. Whether this other stimulation is necessary for the auditory input to be effective is a question that we are investigating further.

Notably, adults tending muted chicks failed to feed them adequately despite the nearby presence of normally vocalizing chicks that had hatched in adjacent nests, some as close as 0.3 m and well within hearing distance of a human. Thus, many of the vocalizations of these nearby chicks should have been audible, but the adults apparently were not affected, indicating that their responsiveness to chick vocalizations is selectively restricted to a localized source beneath them in the nest. This selectivity is to be expected in a densely populated nesting colony where each breeding adult must tune its behavior to its own reproductive progress.

Once provisioning behavior has been initiated, its further maintenance could become independent of the stimuli initially essential for its instigation. In the evolving relationship between chick and parent, complex changes occur in both. As the chick grows, its changing physical features and behavior alter the nature and extent of stimulus input received by the parent, which in turn must modify its responsiveness accordingly. Such modification is indicated by the results of our fourth experiment (Table 5). In contrast to its earlier dependence on chick vocalizations, food-provisioning continued at a near normal rate at nests where chicks were muted at the end of the third day. Normally, chicks this age still frequently vocalize and thus continue to provide potentially available auditory input. Conceivably, such input is still essential but the responsiveness of the parent is no longer selective as to source, so feedings of the muted chicks continue through the effects of vocalizations of nearby chicks. A second possibility that seems more likely, however, is that once establishing the routine of regularly feeding their chicks, parents require less overall input from them than when food-provisioning is earlier instigated. With this overall reduction, auditory input from chicks evidently decreases in importance, as probably does tactile input, as brooding activity declines. Hence, the essential input would be provided mainly by visible features of the chicks or, redundantly, by either these features or vocalizations, one providing the necessary input in the absence of the other.

In terms of monitoring its reproductive progress and responding to received stimulus input to advance this progress further, the Ring-billed Gull appears to depend highly on auditory input as it reaches a stage in its breeding cycle where a rather sudden, drastic change occurs in its external reproductive situation. According to our results, the auditory input received from chicks at this stage is temporarily crucial in order for the adult to respond with food-provisioning behavior sufficient for advancing the cycle to further stages where the external situation changes more gradually and such auditory input decreases in importance.

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