

## DEVELOPMENT OF INDIVIDUAL CALL RECOGNITION IN YOUNG RING-BILLED GULLS (*LARUS DELAWARENSIS*): AN EFFECT OF FEEDING

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**Abstract.** Individual recognition has been documented in young gulls, but less is known of the relevant developmental mechanisms. Since parents normally emit mew calls during feeding of the young, I tested the hypothesis that feeding with individually distinctive mew calls constitutes one such mechanism. Experimentally trained birds provided support for the hypothesis. Initially high approach and vocalization levels were maintained to the reinforced call, while responses to the other call declined, as did responses to both calls in untrained controls. Comparison with other species suggests that this developmental pattern is adapted to the natal social environment. In gulls, food is a potentially important mechanism influencing call 'meaning' (Smith 1977) between parents and offspring and between mates during courtship feeding.

Young gulls (Laridae) have a semi-precocial mode of development characterized by potentially mobile young that tend to stay in the vicinity of the nest, where they are fed by their parents (Nice 1962). Where nest densities are high, as they are in large colonies of ring-billed gulls (*Larus delawarensis*) (Evans 1970a), there exists a high potential for brood mixing. Studies with colour-marked young show, however, that such brood mixing is not common, due at least in part to an early development of individual recognition between parents and young (Evans 1970a; Miller & Emlen 1975). The entire range of potential cues mediating such individual recognition in gulls has yet to be studied in detail, but there is growing evidence that an ability of the young to recognize the individually distinctive voices of their own parents constitutes one important mechanism, in ring-billed gulls (Evans 1970a) and in other species (reviewed in Beer 1970; Evans 1977a).

Although the existence and probable adaptive importance of individual recognition of a parent's voice by a young gull have now been documented, the developmental mechanisms responsible for the ontogeny of voice recognition have received less attention (Beer 1970). To date, at least two potential mechanisms, one acting before hatching, the other after hatching, have been identified experimentally. In the laughing gull (*L. atricilla*), Impekoven & Gold (1973) found that exposure of pipped eggs to one of two different series of long calls resulted in a significant elevation of vocal responses to the familiar series relative to an unfamiliar series when tests were conducted before hatching.

After hatching, however, the young failed to show any preference for the familiar call with respect to orientation or position (Impekoven & Gold 1973, p. 347 and Tables IV, V. See Evans 1973 for similar results in herring gulls, *L. argentatus*). Evidently other mechanisms are required to augment or maintain the effects of embryonic exposure.

After hatching, young gulls are frequently exposed to both auditory and visual stimuli from their parents. This natural situation suggests two additional mechanisms for the development of individual recognition. (1) The simultaneous presence of visual and auditory stimuli from the parent means that the pairing of a parent's call with a visual imprinting stimulus could lead to a selective reinforcement of the familiar call and hence to individual call recognition. Evidence in support of this hypothesis was recently obtained for young ring-bills (Evans 1977b). (2) Since parents commonly emit calls while feeding the young (Tinbergen 1953; Evans 1970a), it is possible that feeding in the presence of a parental call constitutes another mechanism whereby young gulls can learn to recognize and respond selectively to individually distinctive parental calls. An experimental test of this hypothesis for laboratory-reared young ring-billed gulls constituted the primary objective of the present study. Changes in responsiveness to the test calls between day 1 (before training) and day 7 (after training) were also measured, to determine the main developmental pattern (maintenance, facilitation, or induction, cf. Gottlieb 1976) present

during the ontogeny of individual call recognition in this species.

### Methods

#### Subjects

Eggs were obtained from a breeding colony in Manitoba within two weeks of laying, and incubated in a darkened, forced-air incubator held at  $37.5 \pm 0.5$  C. Young were removed from the incubator within 12 h of hatching, provided with a small plastic leg band for individual identification, and reared in groups in pens equipped with a 15-W incandescent light to provide warmth. Beginning late in the first day, young were fed four times daily with fresh frozen fish fillets supplemented with liver.

#### Stimuli

In the ring-billed gull, feeding of the young brood at or near the nest is commonly associated with the emission of mew calls by the parent (Evans 1970a; terminology as in Tinbergen 1953). Two mew calls, recorded at active nests from adults belonging to two different pairs, were used as training and test stimuli. Sound spectrographs of mew calls of ring-billed gulls have been published elsewhere (Evans 1970a) and show that calls from different individuals are distinctively different. Each call was spliced into an otherwise blank loop of tape and played back at a rate of approximately once every 2 s at a peak intensity of approximately 70 dB (B scale, fast; General Radio Corp. sound level meter, as measured from the centre of the training and test pens, 56 cm from the loudspeaker).

#### Apparatus

Training with food and all tests were conducted in plywood tip-floor pens described and illustrated previously (Evans 1972). Each pen was separated with wire screen into three compartments: two end compartments, each with a loudspeaker, and a central compartment for the gull. The floor of the central compartment was hinged at the middle so that it would tip down at either end when a gull moved away from the centre of the pen. A microswitch under the tip-floor controlled the output of the loudspeakers such that only the speaker at the end of the pen opposite to that occupied by the gull was active at any one time. During testing, another microswitch under the floor recorded on an event recorder the number of times the young gull moved from one end of the pen to the other (number of approach responses). High-intensity

vocalizations emitted during tests by one-day-old young were recorded on an event recorder by means of a sound-operated relay that was set to close a switch when the young uttered a chitter call (equals high intensity distress call of Moynihan 1959), but not as a result of the less intense adult mew calls used as test stimuli. In tests with older young (seven days), another call type, the peer (Hailman 1967) also became common. To permit differentiation of the peer and chitter calls, all tests with seven-day-old young were recorded on videotape, and the calls emitted by the young were subsequently counted manually from the combined audio and visual output of a television monitor.

#### Procedure

When one day old, each of 30 young was given an initial test consisting of two successive 2.5-min presentations of the two mew calls and a period of silence in an *abcabc* order, for a total test time of 15 min per bird. Order of presentation of the two mew calls and the period of silence was balanced between individuals. Tests were not begun until at least 1 (usually 2) h after feeding.

After completion of the above test, 10 young were randomly assigned to each of three experimental or control groups: (1) fed for three meals each day in the presence of one or the other mew call, half with each call, (2) as group 1 except that food was withheld until at least 5 min after the completion of exposure to the mew calls (exposed but not food-conditioned controls), and (3) fed in the training pens but never exposed to mew calls (untrained controls).

For training with food, young from group 1 were individually placed near one end of the training pen, and a recording of the appropriate mew call was played through the loudspeaker located at the opposite end of the pen. Immediately after the onset of the call, I offered to the gull a piece of fish fillet held in tweezers in my gloved hand, on the side of the pen closest to the active loudspeaker. If the gull approached, it was fed, the call automatically switched to the speaker at the other end of the pen, and the procedure was repeated with another piece of food. If the chick did not immediately approach the food, I moved my hand closer to the chick, and attempted to lure it toward the loudspeaker. Prior to satiation, such luring was not normally required after the first few meals in the training pen. A meal ended when the chick would no longer take food offered to it. Meal duration

ranged from 25 s to 1.5 min; modal duration was 40 s.

When handling chicks before and after food training, and while offering them food in the training pen, I always wore a dark, long-sleeved smock and dark brown gloves. At all other times, I wore light clothing and used bare hands to handle and feed the young. It was hoped that this procedure would minimize the likelihood that the young would treat me as a familiar visual imprinting object during food training.

Group 2 controls were treated in exactly the same way as the food-trained birds, except that my gloved hand contained no food during training. Group 3 controls were simply placed in the silent training pens, one at a time, and fed by hand until satiated.

At seven days of age, each of the 30 birds was given a test identical to the one it received before the onset of food training at one day of age. Tests were begun approximately 1 to 2 (mean = 1.6) h after feeding.

Except where otherwise indicated, statistical comparisons within groups were based on Wilcoxon matched-pairs signed-ranks tests (two-tailed); comparisons between groups were based on Mann-Whitney *U* tests (two-tailed).

## Results

### Tests at One Day

Mean approach and chitter responses of all 30 birds to the two test stimuli are listed in Table I. Neither response measure differed significantly between the two test calls in these call-naïve birds. Responses to both test calls were significantly greater than to periods of silence (Table I).

### Tests at Seven Days

After food training, approach responses in group 1 birds were significantly greater ( $P < 0.05$ ) to the mew call previously associated with feeding ( $S^+$  call) than to the other mew call ( $S^-$  call) (Table II). In addition, approaches

to the  $S^+$  call were greater for the food-trained (group 1) birds than for either of the controls (groups 2, 3) (Table II). This difference reached statistical significance ( $P < 0.05$ , one-tailed test) between groups 1 and 3. The two control groups did not differ between themselves, and in neither control group was there a significant difference in approaches to the  $S^+$  and  $S^-$  test calls (Table II).

The effect of food training on peer and chitter responses was in general similar to the effect on approaches, but vocal responses were more variable. Examination of the raw data for vocal responses indicated that some food-trained birds responded to the  $S^+$  call mainly with peers, while others gave mainly chitters. As a consequence, neither vocal response, by itself, was significantly greater to the  $S^+$  than to the  $S^-$  call in the group 1 food-trained birds (Table II). When all vocalizations (peers plus chitters) for each bird in group 1 were combined, however, a significantly greater number ( $P < 0.02$ ) were given to the  $S^+$  than to the  $S^-$  test stimulus (Table II, total calls). In addition, total calls given to the  $S^+$  stimulus were significantly greater for the food-trained birds than for either the group 2 controls ( $P = 0.05$ ) or the group 3 controls ( $P < 0.001$ ). As in the case of approaches, vocal responses did not differ significantly between the two control groups, and neither control group vocalized more to the  $S^+$  than to the  $S^-$  test calls (Table II).

In all three experimental and control groups, there was a tendency for approach responses to be greater to the  $S^+$  and  $S^-$  test calls than during periods of silence. As shown in Table II (last two columns), this difference reached statistical significance for both test calls in the food-trained group 1 birds, but was significant for only one comparison (group 3,  $S^- > \text{Sil}$ ) in the controls. The more consistent elevation of approaches to calls relative to silence in the food-trained birds may be taken as a further indication of the

Table I. Mean Responses to Each of Three Different Stimulus Conditions in One-Day-Old Parentally Naïve Ring-billed Gulls ( $N = 30$ )

Response	Stimulus condition			Statistical comparisons		
	Mew-1	Mew-2	Silence	1 > 2	1 > Sil	2 > Sil
Approaches	7.8	7.0	1.1	NS	0.01	0.01
Chitters	104.3	92.7	70.3	NS	0.01	0.02

Sil = Silence, ns = Not significant ( $P > 0.05$ ). Wilcoxon matched-pairs signed-ranks tests, two-tailed.

**Table II. Mean Approach and Vocal Responses of Seven-Day-Old Ring-billed Gulls during Tests with Each of Three Stimulus Conditions ( $N = 10$  for each group)**

Response	Group*	Test stimulus†			Statistical comparison‡		
		S+	S-	Sil	S+ vs. S-	S+ vs. Sil	S- vs. Sil
Approach	1	11.9	5.5	2.8	0.05	0.02	0.05
	2	4.5	3.0	1.3	NS	NS	NS
	3	2.0	2.9	0.8	NS	NS	0.05
Chitter	1	116.3	81.3	20.9	NS	0.01	0.01
	2	62.0	56.2	10.6	NS	0.05	NS
	3	44.4	36.9	5.2	NS	0.02	0.02
Peer	1	67.3	46.0	95.7	NS	NS	0.05
	2	49.3	33.9	43.9	NS	NS	NS
	3	34.1	40.7	70.5	NS	NS	0.05
Total calls	1	183.6	127.3	116.6	0.02	0.05	NS
	2	111.3	90.1	54.5	NS	0.05	NS
	3	78.5	77.6	75.7	NS	NS	NS

\*Group 1 = food trained with the S+ call between one and seven days.

Group 2 = exposed to the S+ call but not fed at that time (controls).

Group 3 = not exposed to either call during training (controls).

†S+ = mew call used in training for groups 1 and 2, and arbitrarily assigned for group 3 controls. S- = the other mew call. Sil = Silence.

‡Wilcoxon matched-pairs signed-ranks tests, two-tailed. NS = Not significant ( $P > 0.05$ ).

positive effects resulting from exposure to the calls during feeding.

Chitters, like approaches, were greater in the presence of test calls than during periods of silence (Table II). This effect reached statistical significance in all comparisons except one (S- versus Sil in group 2 controls). In contrast, peer calls were usually fewer in the presence of the test calls than during silent periods. Mew calls thus tended to elevate chitters and depress peers. There is some suggestion that this effect was greatest for the food-trained, group 1 birds (3 of 4 comparisons significant; see Table II, last two columns), but similar trends are also evident in the control groups.

#### Comparison Between Days 1 and 7

To facilitate comparisons between days, the number of responses of each gull to the S+, S- and silent test periods on day 1 were subtracted from the number of responses to the same stimuli on day 7. Average net changes between days 1 and 7 for chitters and approaches are illustrated in Fig. 1. In Fig. 1, positive values indicate an increase in response rate from day 1 to 7; negative values indicate a decrease. Significance levels for changes between days are indicated below the appropriate bars.

The results for chitters (Fig. 1, top) indicate that in the absence of any training with the mew calls (group 3 controls), response levels decreased

significantly with increased age for all three test stimulus conditions. Chitters given during silent periods also decreased significantly for the other two groups. Of particular interest are the changes that occurred to the S+ and S- test calls in group 1 and 2 birds. In the group 1, food-trained birds, chitters given to the S+ call at day 7 were maintained at essentially the same level as at day 1, while responses to the S- call dropped significantly with age. This differential effect of training on the S+ and S- calls is presumably responsible for the significant discrimination that developed by seven days (Table II). Chitters to the S+ call were also similar between 1 and 7 days in group 2 controls. The failure of this control group to show a significant discrimination between the S+ and S- test calls was apparently a reflection of their failure to inhibit chitter responses to the S- call to a degree comparable to that of the group 1 birds.

Approach responses to the S+ and S- test stimuli changed with age in a manner similar to chitters (compare top and bottom parts of Fig. 1), although only one of the age changes reached statistical significance for approaches. Approach responses also resembled chitters in that responses to the familiar S+ call were maintained between days 1 and 7; the discrimination learned by group 1 birds was due primarily to a large drop in responses to the S- stimulus,

while failure to inhibit responses to  $S^-$  by group 2 controls contributed to their failure to learn the discrimination between  $S^+$  and  $S^-$  test calls. Approach responses rarely occurred during silent periods at either age (compare Tables I and II), and so did not change appreciably between days 1 and 7 for any of the three groups tested.

### Discussion

The results of the tests at seven days of age indicate that food received during the presentation of an adult mew call can lead to the development of a selectively greater response to that call relative to a mew call from a different adult. Untrained controls, and controls that were exposed to the call and to the food delivery mechanism (my gloved hand) but were not fed in association with the call, failed to develop a significant preference for either call. Since the latter control group and the food-trained group differed only in the presence of food during exposure to the call, it can be concluded that

food constituted the relevant variable mediating the development of selective responsiveness in the food-trained birds. This mechanism, along with reinforcement from visual imprinting stimuli (Evans 1977b) and perhaps embryonic exposure to calls (Impekoven & Gold 1973), provides a complex of potentially effective ways in which young gulls can develop an ability to respond selectively to vocalizations of their own parents. It remains to be proven that these developmental mechanisms are in fact effective in young reared naturally by their own parents within the colony. However, as discussed previously (Evans 1977b), the fact that parents do call to their young while fully visible to them during feeding bouts suggests that the laboratory results have direct relevance to the natural situation.

It should be noted that group 2 controls failed to exhibit a learned discrimination between the  $S^+$  and  $S^-$  test calls, even though the  $S^+$  call was presented in training along with an active visual stimulus, a procedure that was found to produce a significant degree of discrimination learning in this species in an earlier study (Evans 1977b). Several procedural differences probably account for the different results. In particular, birds in this study were trained for only about 3 min per day for 6 days, for a total of about 18 min training, whereas training occurred for a total of 2 h in the earlier study. Also, in the present study care was taken to ensure that the visual stimulus used in training was not one that the young could have been strongly imprinted to prior to training (see Procedure), while in the earlier study extensive imprinting exposure to the visual stimulus was given prior to training. In domestic chicks, it has been found (Evans 1972) that prior imprinting to the visual training stimulus was essential if it was to bring about auditory discriminations when auditory training was carried out at 3 or 4 days of age. In view of the brevity of training and the degree of novelty in the visual stimulus used in the present study, it is perhaps less surprising that group 2 birds failed to learn the discrimination than that they showed as great an effect of training as they did, their responses to both  $S^+$  and  $S^-$  calls being appreciably greater than in the group 3 untrained controls (Fig. 1).

The finding (Table II) that the playing of mew calls tended to increase chitters and decrease peers during testing at seven days was not predicted, but may nevertheless have important implications for parent–young communication

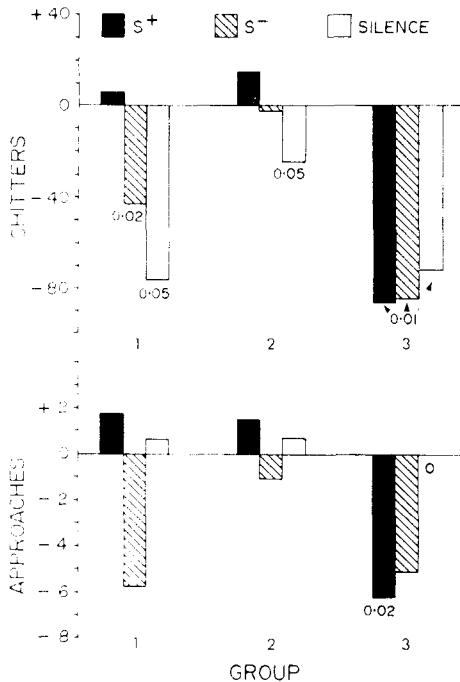


Fig. 1. Mean change in chitter and approach responses between day 1 (before food training) and day 7 (after training). Positive values indicate an increase in responses, negative values indicate a decrease. See footnotes under Table II for meaning of symbols.

in gulls. A similar differential effect of test stimuli on these two call types has also been found in young herring gulls (Evans MS). In both species, an increase in the relatively louder chitter calls in response to a mewling parent could provide a communication link between parent and offspring whenever they become separated by distance and vegetation within the colony.

### Developmental Pattern

According to interpretations of parent–young interactions in gulls based on field observations (e.g. Evans 1970a; Beer 1970), it is functionally important that young gulls not only distinguish between parents and other adults, but that they respond appropriately, approaching parents for feedings or other forms of parental care and protection and either avoiding, or at least not approaching, strange adults. To the extent that chitters by the young tend to facilitate family maintenance or reunion by attracting or stimulating adults to call, it is functionally important that chitters are also elicited selectively by a chick's own parent. Considered developmentally, it is pertinent to ask what developmental pattern young gulls follow in achieving these functionally relevant ends.

At least two quite different developmental patterns would appear adequate to produce a selective responsiveness to a parent's call in young gulls: (1) to begin, soon after hatching, with a strong response to all mew calls, then maintain (cf. Gottlieb 1976) a high level of responding to a parent's call, while responding progressively less to the calls of other adults should these happen to be encountered; or (2) to begin with a weak response to all mew calls of the species, then selectively increase (facilitate, cf. Gottlieb 1976) responses only to the reinforced calls of the parents. From a purely developmental perspective, there seems no compelling reason to expect one of these patterns over the other, or over some intermediate pattern. Inspection of the data in Fig. 1 suggests that the pattern actually present in young ring-billed gulls tends to lie between the two theoretical extremes, but more closely resembles the first alternative, in which responses are initially high to both calls and subsequently are maintained to the reinforced call while declining to the other.

The occurrence of a developmental pattern characterized by maintenance of an initially high response rate to a familiar or reinforced stimulus

is common in young precocial birds that hatch in an advanced state of development (Bateson 1966; Dawkins 1968; Graves 1973; Cowan & Evans 1974; Gottlieb 1976). It appears to be a highly adaptive pattern for behaviours such as approaching social companions or pecking for food, which must be present and functional at or soon after hatching. In ring-billed gulls, approaches and vocal responses by the young to mew-calling parents facilitate feeding of the young and other forms of parental care from an early age (Evans 1970a). An initially strong response to mew calls followed by selective maintenance of responses to the familiar, reinforced calls of the parent thus appears to be a highly adaptive developmental strategy for this species.

It should be emphasized that the pattern of development found here for young ring-billed gulls responding to mew calls of their own species is not necessarily to be expected in all other gull species, or even for other call types within the same species. For example, young laughing gulls (*L. atricilla*) apparently increase, rather than maintain, responses to the long call of their own parents during the first several days of life (Beer 1970). A similar pattern seems likely for responses to the long call in young ring-billed gulls (personal observation). It is tempting to speculate that such differences are an adaptive result of the greater distance-increasing, or threat, function of gull long calls (Tinbergen 1959; Moynihan 1958a).

Another possible adaptive variation in developmental pattern is suggested by recent findings for the herring gull (*L. argentatus*). In this species, parentally naive young exhibit a strikingly weak initial tendency to approach and vocalize to the mew calls of their own species (Evans 1973, 1975), but responses are facilitated significantly by training in the presence of food (Evans MS). Young herring gulls run a significant risk of being attacked and killed or eaten by adults of their own species (Ward 1906; Paludan 1951), especially if they trespass on the territory of a neighbour (Deusing 1939; Parsons 1971; cf. also Hunt & Hunt 1976). Hence it seems highly adaptive that herring gulls should have a developmental pattern characterized by an initially low level of response to adult mew calls, followed by a selective increase in responsiveness to the familiar, reinforced calls of their own parents. As described by Tinbergen (1953), herring gulls are strongly territorial, the adults defending relatively large

areas to which the young become attached. In contrast, ring-billed gull broods often leave their small breeding territories and take up a more nomadic existence within or near the colony (Evans 1970a). These differences in brood mobility may also be relevant to the different levels of responsiveness to mew calls exhibited by the young of these species (cf. Evans 1973, 1975). It is hoped that further comparative studies (McKinney 1978) will provide additional insights into the adaptive significance of these and other variations in developmental patterns, both within and between species.

### Development of Communication

As discussed by Smith (1977), the response made by an animal to a communicated signal provides an operationally usable means of inferring the meaning of the signal to the recipient. According to this usage, it is evident that feeding constitutes an effective means of influencing the development of auditory signal meaning in gulls. Feeding has also been shown to influence the meaning of visual signals in gulls (Hailman 1967; Nystrom 1970). In combination with the direct and indirect effects of visual imprinting stimuli (Evans 1970a, 1977b), food reward appears to constitute a potentially important contingency mediating the development of signal meaning in birds such as gulls in which parents normally feed their young. Although this conclusion may seem obvious in view of the large literature on effects of conditioning with food, the probable role of food reward in the ontogeny of avian communication has received surprisingly little attention (Beer 1970; Marler 1975; Burghardt 1977; Smith 1977).

The positive effect of feeding on chick vocalizations and approach responses suggests that in simplest terms, it tends to facilitate close association between parent and chick. If this meaning is retained into adulthood, one would expect that mew calls would tend to be relatively more common in situations involving close association between adults than would other calls that had been less closely associated with parental feeding of the young. The extensive use of mew calls during courtship and pairing, and immediately before copulation in gulls (Tinbergen 1953, 1959; Moynihan 1958b; Evans 1970b), is consistent with this expectation.

Significantly, feeding of the female by a mew-calling male (courtship feeding) is also an integral

part of pre-copulatory courtship in gulls (Tinbergen 1953, 1959; Moynihan 1958b; Evans 1970b). The results of the present study suggest that such feeding during courtship could act to enhance the close-association meaning of the male's mew call to his mate at this time, thereby facilitating the formation of a stable pair bond and the development of individual recognition of the male by his mate. Courtship feeding may also function as a means whereby a male can contribute food energy to the reproductive process (Royama 1966). If so, then feeding would appear to function similarly in both courtship and in parent-young interactions in gulls, performing the joint functions of providing energy and of influencing the development of signal meaning in both contexts.

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