PARENTAL RECOGNITION AND THE "MEW CALL" IN BLACK-BILLED GULLS (LARUS BULLERI)

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In both gulls and terns (Laridae) evidence suggests that individual recognition of offspring by parents develops more or less coincident with the onset of brood mobility. Evidence that individual recognition of parents by young also develops at the same time has been obtained for the Crested Tern (Sterna bergii) (Davies and Carrick, 1962), Ring-billed Gull (Larus delawarensis) (Evans, 1966), and Laughing Gull (L. atricilla) (Beer, 1969). As individual recognition is an important means of maintaining family unity (Alley and Boyd, 1950; Ramsay, 1951), particularly after the onset of extended brood mobility in or near a congested colony (Bateson, 1966), such recognition might be expected to be particularly well-developed at an early age in colonial species whose young leave the nest and form flocks soon after hatching. The primary objective of the present study was to test this hypothesis by studying the ontogeny of parental recognition by chicks of the Black-billed Gull (L. bulleri), a highly colonial species (Black, 1955; Beer, 1965), whose relatively precocial young may leave the nesting area, often to intermingle with other broods, within 1 to 2 days after hatching (Beer, 1966). Studies of parental recognition by young Ring-billed Gulls (Evans, 1966) had indicated that chicks were able to recognize the call the parents gave repeatedly when feeding them; in the present study, the parental calls given in this context were therefore selected to test for parental recognition by the young.

In Black-billed Gulls, chick feeding is typically preceded or accompanied by a soft, staccato purring that has been described as a "soft crooning sound" of 1.5 to 2 seconds duration and may be transcribed "Chrrrrooooooo" with a smooth decrease in pitch (Beer, 1966, compare with Figures 1, 2). Comparison with the vocalizations given in similar situations by the Herring Gull (L. argentatus) (Tinbergen, 1953: 105, 135, 225; Moynihan, 1955: 143), the Black-headed Gull (L. ridibundus) (Moynihan, 1955: 45, 95), the Ring-billed Gull (Moynihan, 1958a: 111; 1958b: 121), and various other gull species (Moynihan, 1955, 1962) suggests that this call is similar in function, and possibly homologous to the "mew call" characteristic of other Larus gulls. This call in the Blackbilled Gull differs strikingly to the human ear from the comparable call of the Herring Gull that Tinbergen (1953) named the "mew call." The name "mew call" is adopted here following the usage of Moynihan (1958a: 112) who described it as "the least confusing, if not the most descriptive, of the possible alternatives."

Courtship activities were still in progress when I arrived in the Blackbilled Gull breeding colony on 15 October 1964, hence it was possible to extend the scope of the studies to include observations on the frequency of occurrence and analyses of the physical characteristics of the mew call in contexts other than those associated with feeding of the young, including courtship feeding and copulation, nest relief, and incubation.

The Black-billed Gull study colony was located on the gravel shore of the Taierie River, near Middlemarch in Central Otago province, New Zealand (see Beer, 1966, for description and history of this colony). I watched the birds from a blind placed near the edge of the colony. Chicks used in experimental tests were color-marked with felt marking pencil on the day of hatching, then left with their parents except when removed for experimental purposes. Tape recordings and playbacks were done with a Uher 4000 Report portable tape recorder. Mew calls were recorded with a microphone placed on the territory or beside the nest and connected to a tape recorder in the blind by an extension cord. This technique made it possible to monitor the calling adult by both visual and auditory modalities, thereby ensuring correct identification and accurate determination of context. Placing the microphone near the vocalizing bird also reduced background noise and permitted the elimination of most extraneous colony sounds. Sound spectrograms were produced with a Model 675 Kay Electric Missilyzer.

COURTSHIP AND NESTING ACTIVITIES

Most Black-billed Gulls typically arrive at the breeding colony no more than 1 week prior to the onset of egg laying (Beer, 1966). During this period the mated pairs begin to occupy breeding territories around the periphery of a nucleus formed by the first pair(s) to initiate nesting. More than a single initiation may occur, leading to the formation of distinct subcolonies. At least four such subcolonies were clearly distinguishable in the colony I studied in 1964. Subcolonies may have a degree of functional autonomy, as indicated by repeated independent upflights of subcolonies when sheep moved past the periphery of the colony. Within each subcolony nests are typically close together, distances to the nearest nest averaging only 49 cm (range 27–83 cm) in 1963 (Beer, 1966), and an identical average of 49 cm (range 35–75 cm) for the nests measured in the present study. Clutch size is typically two eggs (Black, 1955; Beer, 1965).

Courtship feeding.—Actual feeding during courtship, with food passing from the male to the female, was noted 39 times. Without exception the offering bird preceded or accompanied such courtship feeding by mew calls (Figure 1C). In 25 instances the mew calls were associated with apparent



Figure 1. Sound spectrograms of Black-billed Gull mew calls. (Missilyzer settings: low impedance input; mark 7-7.5; wide band; flat shape; normal pattern). A, B, during regurgitation intention movements; C, during courtship feeding; D, E, during nest relief; F, G, while feeding chicks, food in bill tip; H, while feeding chicks, no food in bill tip. (Mew calls E and F were given by the same individual, as were calls G and H.)

regurgitation movements, but no food was transferred (Figure 1A, 1B). Moynihan (1955: 95) has described similar behavior in the Black-headed Gull as "regurgitation intention movements."

Courtship feeding and regurgitation intention movements were similar in their relationship to subsequent copulations: 10 of 39 courtship feedings were followed within a few minutes by copulations or attempted copulations, as were 3 out of a total of 25 regurgitation intention movements $(\chi^2 = 1.01, P > 0.3)$. This similarity suggests that in this species the actual passage of food during courtship feeding does not significantly affect the probability that copulation will follow. Nest relief.—During daylight hours nest relief occurs, on the average, about once every 2 hours (Beer, 1965). In 1964 mew calls were associated with nest relief in all but 5 of a total of 84 recorded instances of nest relief (Figure 1D, 1E). Typically (86 per cent of observed instances in which mew calls were given), the bird taking over incubation duties was the only member of the pair to emit mew calls, but in six instances only the sitting bird gave them. Mew calls by both members of the pair also occurred six times. As with mew calls associated with courtship, feeding of one mate by the other occurred during nest relief, but in only nine instances. The newly-arrived bird passed food to the sitting bird in six of these instances, and only three times did the incubating bird feed the other. In addition to feeding during nest relief, the arriving mate deposited nest material at the nest in at least nine instances (14 per cent).

Mew calls associated with feedings occurred at all stages of incubation. Mew calls were also heard at two nests as the adults turned the eggs, and once, during nest relief, at a nest containing pipped eggs. Mew calls directed at the mate were also noted after the hatch was complete and the chicks had been fed one or more times. Once the chicks had hatched the tendency to mew at and feed the mate was largely replaced by similar behavior directed towards the chicks.

Chick feeding and food deprivation.—In at least 31 (21 per cent) of a total of 150 chick feedings the parent did not give a mew call. More typically the parent either preceded or accompanied chick feedings by one or more repetitive series of mew calls. During chick feeding bouts, the parents gave mew calls either with the bill empty (Figure 1H) or with food held in its tip (Figure 1F, 1G).

As the mew call appeared to function to attract the chick toward its source of food, i.e. the parent, I investigated the possibility that food deprivation might increase the tendency of chicks to approach mew calls, as it does the rate at which gull chicks peck when begging food (Weidmann and Weidmann, 1958; Hailman, 1967). The effect of food deprivation on the speed with which chicks approached adult mew calls was tested in 11 chicks from 2-3 days of age.

In the morning of the day the tests were to be conducted, the bill of one chick from a given experimental brood was sealed with a strip of tape covered with a layer of fast-drying glue to prevent its receiving food from the parent. A control chick was left in the nest with bill unsealed. Between 7 and 10 hours later, the bill-taped and control chicks from each nest were removed from the colony and released simultaneously from positions at least 1 m apart and approximately 1 m from a loudspeaker. An adult mew call was then played repeatedly until at least one of the

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chicks approached the speaker. Observations from the blind showed the control chicks were usually fed while the bills of the experimental chicks were sealed, thus creating a differential degree of food deprivation between the members of each test pair.

Food-deprived chicks were the first to approach the speaker in 9 of the 11 test pairs ($\chi^2 = 4.4$; P < 0.05). These results indicate that acute food deprivation may enhance the rate at which colony-reared chicks approach the source of mew calls and hence, presumably, their parents.

DEVELOPMENT OF MOBILITY AND RECOGNITION OF PARENTAL MEW CALLS

According to the interpretation advanced by Beer (1966), Black-billed Gull chicks are relatively precocial in that they develop locomotor powers at an early age and may leave the breeding territory when only 1–2 days old. My observations also indicated that early emigrations from the subcolony unit may occur, especially in chicks that hatched towards the middle or latter part of the breeding season. In the first subcolony to hatch in 1964 the chicks remained in the nest somewhat longer. In 18 early nests under observation, no chicks left their nests during the first 3 days, two broods (17 per cent) left on the 4th day, and nine (50 per cent) on the 5th day after hatching. The primary cause of this delay appeared to be the parents' tendency to brood their young more during the colder weather of the early portion of the breeding season. In addition the absence of older young early in the season may have been less disturbing.

When broods emigrated away from the subcolony, the young from different broods commonly came in contact with one another (see Beer, 1966), but color-marking emigrant broods showed that family units were maintained, suggesting that individual recognition between parent and offspring was developed by the time emigrations occurred. To determine how early chicks developed the ability to recognize parental mew calls, tape-recorded calls were used as described below.

Mew calls were recorded from adults actively feeding their chicks during the first 1–2 days after hatching. After mew calls were recorded, one chick from each of two separate broods were removed from the colony and placed approximately 1 m from a loudspeaker. A mew call from a parent of one of the test chicks was then played over the speaker, and repeated until at least one chick approached the speaker. The minimum number of mew call repetitions required to elicit approach responses in at least one chick for each test was highly variable, ranging from as low as one call to as high as 91. The minimum number of mew calls showed no consistent change with age; average numbers were 28 for chicks at 1 day of age, 19 at 2 days,

	Test age in days			
	1	2	3	4
Number of tests ¹	10	13	12	4
Correct offspring approached first	4	8	10	4
Percentage	40	62	83	100
χ^2	0.40	0.69	5.33	
Р	0.95 > P > 0.50	0.50 > P > 0.30	P < 0.05	

TABLE 1 Recognition of Parental Mew Calls

 1 A test consisted of simultaneously releasing two chicks, each from a different brood, in front of a loudspeaker emitting mew calls recorded from a parent of one of the chicks.

28 at 3 days, and 33 at 4 days of age. Playing of mew calls from the loudspeaker was normally continued beyond the initiation of the first approach response, until at least one chick had reached the speaker. Chicks were then returned to their release points in front of the speaker, and the procedure was repeated using the mew call from a parent of the second chick. I gave a total of 39 tests to 29 chicks at from 1 to 4 days of age. No chick was tested more than once on any day, and none was tested on more than 2 days.

When chicks were released during these tests, they typically crouched silently prior to the playing of mew calls. When the loudspeaker was activated, chicks either remained crouched and silent, or else raised their heads and cheeped, either with or without subsequent approach responses towards the loudspeaker.

The development of parental mew call recognition by the chicks was assessed first by comparing response latencies between the chicks tested with each adult mew call tape. According to the null hypothesis that the chicks exhibited no mew call recognition, chance would dictate that the offspring whose parental call was being played would be the first chick to approach the loudspeaker in approximately 50 per cent of the tests. Significant positive departures from this proportion were therefore taken as evidence for preferential responsiveness to, and hence recognition of, parental calls. As shown in Table 1, the proportion of tests in which the correct offspring approached first increased from randomness at 1 day of age to over 80 per cent at 3 and 4 days of age. Differences were significant by 3 days of age ($\chi^2 = 5.33$; P < 0.05).

At 1 day of age, all but two chicks cheeped indiscriminately to parental and strange mew calls. The proportion of indiscriminate responders dropped for chicks tested at 2 days of age, when 7 of 13 chicks responded



Figure 2. Sound spectrograms of Black-billed Gull mew calls given by parents actively feeding young chicks, illustrating variations between (across) and within (down) individual adults. (See legend of Figure 1 for Missilyzer settings.)

to both the parental and the strange calls, while the other 6 chicks cheeped only in response to parental calls. The proportion of discriminate to indiscriminate responders changed but slightly at 3 days of age, when four of nine chicks for which records were maintained cheeped in response to parental calls, but not to the calls of strange adults. All four chicks tested at 4 days of age cheeped when mew calls of one of their own parents were played, but remained crouched and silent when mew calls of strange adults were played.

The proportion of chicks that vocalized selectively to mew calls of their own parents increased significantly (P < 0.03) between 1 and 4 days of age. These results, as well as those in Table 1, suggest that young chicks in their first day after hatching respond indiscriminately to mew calls either of their parents or of other adults, but with increasing age the parental calls become relatively more effective in eliciting chick vocalizations and approach responses.

Sound spectrograms were made of more than 40 mew calls given by parent Black-billed Gulls feeding their young to determine if the calls of different adults contained differences that could provide a possible basis for individual recognition by the young. Figure 2 presents three of these records selected randomly from each of three representative individuals for which at least six records were available. They show clearly that all the calls of a given adult (columns) tend to be similar, whereas those of different individuals exhibit recognizable differences.

DISCUSSION

The mew calls illustrated in Figure 1E-1H and Figure 2 indicate that the degree of within-individual variability is small compared to the differences present in the calls of different individuals. Recent studies of the fish-call of the Sandwich Tern (Sterna sandvicensis) (Hutchison et al., 1968) show a similar condition in that species. As recognition of parental calls must presumably develop through experience with them (Ramsay, 1951), this high degree of similarity in successive calls of individual adults appears to provide a means for chicks to learn to recognize the call of a particular parent, while the differences between the calls of different adults permit mobile chicks to discriminate between their parents and other adults they may encounter. The repeated utterance of mew calls by Black-billed Gull parents while feeding young chicks doubtless facilitates the early development of parental recognition by the young. The mew calls given during nest relief (compare Figure 1E and 1F), which occurred after the eggs had pipped as well as earlier in the incubation period, suggest the further possibility that the young may learn, or at least begin to learn, their parents' characteristic calls prior to hatching, in a manner similar to that Tschanz (1965) suggests for the Common Murre (Uria aalge). The apparently indiscriminate responsiveness of most of the 1-dayold chicks tested in the present study provides no evidence that these chicks were able to recognize and respond selectively to parental calls. While the results do not rule out the possibility that some characteristics of parental mew calls may be learned prior to hatching in this species, they do suggest that the opportunities for learning afforded by occasional calls given during nest relief over pipped eggs are probably slight compared to those afforded by the repetitive series of calls parents typically utter while feeding the young chicks the first day after hatching. In either event, obviously the frequency of occurrence and the physical characteristics of mew calls are such that parental recognition can develop as early as 2 or 3 days after hatching. The ability to recognize parental mew calls by this age may provide an important mechanism favoring brood unity coincident with or prior to the onset of brood mobility.

When heard at a distance in the colony or when monitored through the

tape recorder, the mew calls of adult Black-billed Gulls sound basically similar, whether given in the context of feeding chicks, courtship feeding, regurgitation intention movements, nest relief, or leading chicks across or away from the territory. Sound spectrogram analyses of frequency and duration of mew calls support the conclusion that these parameters, although subject to considerable individual variation (Figure 2), differ little if any according to context or function (Figure 1). The similarity of mew calls in different contexts is especially well illustrated by Figures 1E and 1F, both made from recordings of the same adult, one during nest relief, the other when the bird was actively feeding a chick. The basic similarities between the spectrograms of mew calls shown in Figure 1 are in accord with the earlier findings of Beer (1966), who noted that the postures (probably low-intensity choking) and calls performed by the male as a prelude to courtship feeding are identical to those exhibited by either parent when attracting chicks for feeding. The present study shows in addition that the same calls are given during nest relief, and also provides evidence that the low-intensity choking call may be the same as the mew call, as Moynihan (1955) suggests for the Black-headed Gull.

The position of the bill while uttering mew calls varies within the Larinae from a wide-open position in the Herring Gull (Tinbergen, 1953: 11; Moynihan, 1955: 139) to a moderately open or almost closed position in the Ring-billed Gull (Moynihan, 1958a). In the Black-billed Gull (Beer, 1966) and the closely related Black-headed Gull (Moynihan, 1955: 95), the bill is held slightly open during mew calls. My observations of the contexts in which mew calls were given by Black-billed Gulls suggested the possibility that these differences in bill position may have a functional basis, the bill being nearly, but not entirely closed in species such as the Black-billed Gull that characteristically give the mew call while simultaneously offering food to mates or offspring. The retention of this bill position for mew calls given when no food is present may also be of functional significance, as a similar degree of bill opening at this time would presumably favor the production of the same individually recognizable calls by a given adult in both contexts. Support for this interpretation is provided in Figures 1F and 1G, which were recorded while the calling parent held food in the bill tip; comparison of these spectrograms with those of calls by the same individual adults with no food in the bill (Figures 1E and 1H) reveals no marked differences in the calls that can be attributed to the presence or absence of material in the bill.

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SUMMARY

The development of recognition of parental mew calls by the young, and other aspects of reproductive behavior associated with the mew call were studied in a colony of Black-billed Gulls at Middlemarch, New Zealand. Adults gave mew calls during courtship feeding, nest relief, and when feeding or leading their chicks. Sound spectrogram analyses showed that although differences exist between individuals, mew calls do not differ within individuals or according to the situation in which they are used.

Food-deprived chicks of from 2-3 days of age approached mew calls emitted by a loudspeaker more rapidly than did parent-fed controls. Colony-reared chicks of the same age also approached mew calls of their own parents more rapidly than did chicks from other broods, and tended to cheep preferentially to parental calls, thereby indicating an early development of parental mew call recognition by the young. The early development of parental recognition apparently constitutes a mechanism favoring brood unity after the onset of mobility of the young.

Mew calls are characteristically given with the bill held partially open. It is suggested that this bill position is associated functionally with a tendency to give the mew call while presenting food to mate or offspring, and that the retention of this bill position when the bill contains no food favors the utterance of the same individually recognizable calls in both contexts.

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