

Imprinting and Mobility in Young Ring-Billed Gulls, *Larus delawarensis*

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I	INTRODUCTION	195
II	DESCRIPTION OF COLONIES AND GENERAL PROCEDURES ..	196
III	DEVELOPMENT OF INDIVIDUAL LOCOMOTOR ABILITY ..	198
IV	MOBILITY OF THE BROOD	198
	Methods of observation	198
	Excursions from the nest site	199
	Permanent movements away from the nest site	202
	Brood movements during sudden disturbances	204
	Movements of chicks in an undisturbed colony	205
V	APPROACH RESPONSES TO FIXED INANIMATE OBJECTS ..	206
VI	APPROACH RESPONSES TO A FAMILIAR REARING AREA ..	208
VII	APPROACH RESPONSES TO ADULTS	210
	Stimulus conditions	210
	Food reinforcement	213
	Approach responses to mew calls of particular individuals	214

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VIII	APPROACH RESPONSES TO CHICKS	219
	Stimulus conditions influencing approach responses	219
	Effect of early social experience	222
	Approach responses to particular individuals	224
IX	APPROACH RESPONSES TO MOVING INANIMATE OBJECTS	227
	Initial responses to strange objects	227
	Selection of familiar objects	229
X	DISCUSSION	233
	Developmental relationships between mobility and approach responses	233
	Imprinting in semi-precocial gulls	236
	Functional significance of imprinting in mixed colonies	239
	Development of responses to predators	241
	The significance of semi-precocial development in gulls	243
XI	SUMMARY	244
	ACKNOWLEDGMENTS	245
	REFERENCES	246

I. INTRODUCTION

Young gulls hatch in a relatively advanced stage of development, fully covered with natal down, and able to execute coordinated movements on the day of hatching. This type of development has been classed as semi-precocial, a condition in which the young, although able to locomote at an early age, remain at or near the nest site where they are fed by their parents (Nice 1962). Several problems in behaviour development and adaptation of young gulls, implicit in this description, have received only limited and incidental attention. These problems constitute the principal subject matter of the present study.

The virtual absence of physical barriers to wandering in young chicks that are highly dependent on parental care and yet able to move about suggests that mobility is controlled by behavioural means. In gulls, the ample opportunity for early social experience at the nest suggests that the early development of gregarious tendencies, involving learned discriminations at the species level as in the 'imprinting' of precocial species (Pattie 1936; Lorenz 1937; Hess 1959a; Sluckin 1965) may play an important role in the control of brood mobility. In addition, the occurrence of a relatively rapid development of learned discriminations, constituting the basis for individual recognition of parents and brood mates, would also contribute to the control of mobility and to the maintenance of family units (Ramsay 1951). As pointed out by Bateson

(1966), such individual recognition by the young should be especially well developed in ground-nesting colonial species such as gulls, where opportunities for brood mixing are often extreme. To be effective in maintaining brood cohesion, the development of such recognition should precede, or at least coincide with, the onset of any major movements away from the vicinity of the localized nest site (Davies & Carrick 1962).

The present study was designed to investigate the progress of brood mobility with age in a semi-precocial, colonial, gull species, and to relate these findings to those obtained from an experimental examination of the early development of approach responses to selected biological and inanimate stimuli. The analyses of approach responses were designed to include tests of the hypotheses: (1) that approach responses of semi-precocial gull chicks follow a developmental sequence similar to that of precocial species, in which the range of effective stimuli is rapidly narrowed on the basis of early experience with them; and (2) that food reinforcement received during periods of social feeding is not necessary to the development of approach responses to generalized and specific stimuli. Ring-billed gulls (*Larus delawarensis*), which nest on the ground in large, dense colonies (Emlen 1956), were selected as the most appropriate available species.

II. DESCRIPTION OF COLONIES AND GENERAL PROCEDURES

Studies of ring-billed gulls were conducted during the breeding seasons of 1962 to 1966 on five colonies, all located within a $\frac{1}{4}$ -mile radius of the base of a peninsula jutting out into Lake Huron at Rogers City, Michigan. The distal portion of the peninsula contained a colony of over 700 pairs of herring gulls (*Larus argentatus*) (1964 census), some of whose territories lay adjacent to the outermost Ring-billed Gull nesting areas. The mainland location of the colonies exposes them to occasional intrusions by mammalian predators, as in 1965 when one colony was severely disrupted in this manner (Emlen et al. 1966); no data were subsequently used from this predated colony.

The number of nests varied considerably from year to year. A complete count of nests apparently in use was conducted in 1964, on 17 and 18 May, approximately one week before the onset of hatching. Numbers of nests, listed according to contents, are shown in Table 1.

Observations on undisturbed birds in the colonies were made from blinds, placed either within or beside the nesting areas. Because gulls at Rogers City are on the mainland and accessible by automobile, they appear to have become partially habituated to human activities, and

were not unduly disturbed by the presence of the blind. Adults normally returned rapidly to their nests after the mild disturbance caused by entering the blind. An attempt was made to leave conditions as normal as possible at these times by moving up to or through the colony slowly.

Ring-billed gull chicks used for laboratory studies were collected from the colonies as piped eggs, and hatched in an incubator set up in the laboratory. Within 12 hr after hatching, chicks were removed from the incubator and placed in rearing pens heated by incandescent light bulbs. All chicks reared in the laboratory were fed by hand three times daily, with fish-flavoured ('Friskies') cat food. Following experimental tests, chicks no longer required were placed with foster parents in the colony, care being taken to place them well away from areas being used for observational or experimental purposes. Experimental chicks that were taken from the colony after hatching and used for field tests were returned to their own nests except where further experiments required that they be left with foster parents.

Tape-recorded vocalizations of adult and young gulls were used in several play-back

Table 1. Census of Ring-Billed Gull Nests in Use at Rogers City, Michigan, 17 to 18 May 1964

Eggs per nest in use	Colony no.				Total nests	
	1	2	3	4	No.	Per cent
1	45	26	114	6	191	5.4
2	148	42	311	7	508	14.2
3	1348	175	1280	27	2830	79.1
4	30	4	8	2	44	1.2
5	0	0	3	0	3	0.1
Total nests	1571	247	1716	42	3576	100

Colony no. 5, used for observation of brood movements, contained an estimated 500 nests in 1962; nests were formed normally in 1963, but there were few if any young fledged due to high mortality of young chicks that year. The colony was subsequently abandoned in 1964.

experiments. Recordings from particular birds were obtained by placing a microphone beside the nest. Identification was established by monitoring the input to the microphone and simultaneously observing, with binoculars, the bill, head and body movements of the vocalizing bird. Tape speed was set to run at $7\frac{1}{2}$ in. per min. Except where indicated otherwise below, recording and play-back were done with a Nagra III portable tape recorder.

Methods used in measuring brood movements and the special procedures employed in the experimental studies are included in the appro-

priate sections below. The various statistical tests employed in these studies were conducted according to the procedures described by Goulden (1952) and Siegel (1956).

For the studies of locomotor ability (Section III, p. 198) and of mobility in the colony (Section IV, p. 198 et seq.), ordinal age designations were used, observations on the day of hatching being referred to the first day, and so on. The ages of experimental chicks used in the subsequent sections are designated by cardinal numbers. Except where otherwise stated, ages are accurate to the nearest day.

III. DEVELOPMENT OF INDIVIDUAL LOCOMOTOR ABILITY

Locomotor ability in ring-billed gull chicks begins, during the first day after hatching, with a slow, shuffling gait. Initially, steps are made in a crouched posture in which each tarsometatarsus is held in contact with the substrate. Older chicks support their entire weight on the feet, thus assuming a more erect posture and increasing the possible stride. As in the franklin's gull (*Larus pipixcan*) (Nice 1962), ring-billed gull chicks are well able to walk by the end of the second day.

From observations of laboratory-reared chicks immediately prior to feedings, it was found that the proportion of chicks standing fully erect, on their feet, in response to my voice and movements increased with chick age, from 8 per cent during the first day to 73 per cent during

Table 2. Changes with Age in the Frequency of Erect, Standing Posture Before Feedings in Response to Human Presence by Laboratory-Reared Ring-billed Gull Chicks

Chick's age (days)	No. of chicks observed	No. of observations per day	Standing responses	
			No.	Percentage
1st	32	80	6	8
2nd	32	96	22	23
3rd	32	96	57	59
4th	32	64	45	70
5th	23	49	36	73

the fifth day (Table 2). These results suggest that the functional development of the locomotor apparatus extends over at least the first 5 days after hatching.

IV. MOBILITY OF THE BROOD

Studies of the herring gull (Strong 1914; Goethe 1937; Tinbergen 1953a) and black-headed gull (*Larus ridibundus*) (Kirkman 1937), have provided general descriptions of brood movements in typical ground-nesting species of colonial gulls. The development of brood mobility with age in such species has also been described in quantitative terms, as illustrated by studies of the common gull (*Larus canus*) and herring gull by Koskimies (1952). From these and other comparable studies it is evident that upon hatching, gull chicks tend to be relatively immobile, most movements being restricted to the nest in its immediate vicinity. Subsequent increases or frequency and extent of mobility, although apparently typical of all ground-nesting gull species, may vary in timing and extent according to habitat conditions, frequency of disruptions, and species (Koskimies 1952).

The typical pattern of increasing mobility with age has been described in general terms for

the ring-billed gull by Bent (1921) and Emlen (1956), but detailed quantitative descriptions are lacking. In the initial phases of the present study, such quantitative measurements of chick movements and related behaviour were recorded and analysed, to extend and elaborate the earlier findings, and thereby to provide a basis for developmental comparisons between mobility and subsequent analyses of approach responses. Particular emphasis was placed on developmental changes over the first week to 10 days after hatching.

Methods of Observation

A moderately-vegetated colony (no. 5) was selected for intensive observational study. All data from this colony were obtained in 1962, when it contained an estimated 500 nests in use. Data were obtained early in the season, before any disturbance had occurred as a result of subsequent large-scale banding operations of chicks.

Prior to the onset of hatching, an observation blind was set up near the centre of the colony. Small wooden pegs were placed 2 m apart in the form of a rectangular grid around the blind. The marked area, which extended 14 m on each side, contained ninety-nine nests, of which forty-three were individually numbered, for purposes of identification. When chicks from these nests hatched they were daubed on the head, sides or back with a coloured dye so that they could be individually recognized from the blind.

Observations from the blind were conducted for 8 successive days, starting 3 days after the first chicks hatched, for an average of approximately 8 (6 to 9) hr per day. At the start, middle and end of each daily observation period the experimental area was inspected by walking through it; at these times, newly-hatched and faded chicks were colour-marked, and the distances from their nests of all resident marked chicks were measured, with a rule, to the nearest 5 cm. The times required for these marked chicks to return to their nests were subsequently recorded whenever possible, from within the blind. Observations recorded from within the blind also included maps drawn to scale of all nest locations and of all movements of colour-marked chicks that were noticed. Records of feedings and brooding activity based on seventy-two 1-hr observation periods of nests with chicks of various ages up to the seventh day of age were also recorded, as were general observations of both chick and parental behaviour.

To control, at least partly, for the frequent disturbance entailed in collecting the above data a second colony (no. 2) was also studied. An area enclosing all of the nesting adults was fitted with markers, placed at 5-m intervals. During the first 4 days of the hatch, 207 newly-hatched chicks were banded with numbered plastic leg bands, and rearranged as necessary in nests to create broods of either one or three. This latter procedure, which occasionally necessitated switching newly-hatched chicks to different parents in the same phase of their breeding cycle,

appeared to have little effect on the normal progression of parental or chick behaviour (compare Table 1 in Emlen & Miller (1969) with Table 3 in this study, p. 200.

When chicks were banded and distributed to their rearing nests, all nest locations were plotted to scale on maps. The colony was then left completely free of human disturbance for one full week, after which a single search for banded chicks was made. The locations of banded chicks, which then ranged in age from their seventh to tenth day, were plotted on maps and were used to obtain measures of the distances between the original nests and the recapture sites. The data from this second, relatively undisturbed colony provided a means of evaluating some of the effects of my daily activity on brood mobility in colony no. 5.

Excursions from the Nest Site

Average measurements of localized brood movements and associated behaviour observed in colony no. 5 are listed in Table 3. The chick age in this table refers to the age of the oldest chick(s) in each brood. Hatching span data recorded for thirty-four nests indicated that all chicks hatched out on the same day in twenty-three nests (68 per cent); there was a spread of 1 day in six nests (18 per cent) and of 2 days in five nests (14 per cent). The late hatching of the second and third chicks in these latter two groups of nests did not cause any corresponding systematic delay in onset of brood mobility. Measurements of brood mobility listed in Table 3 were based upon the locations of the chicks plus the attending adult when one of the latter was present, or upon the location of the chicks alone when no adult was present.

During the first day after hatching, chicks remained in the nest cup, with one or the other parent brooding them except for brief periods when the chicks were fed or when the colony was disturbed. Broods were first observed out of the nest on the second day after hatching. The percentage of broods observed out of the nest subsequently increased with chick age

Table 3. Measurements of Excursions from the Nest Cup and Related Behaviour During the First 9 Days after Hatching in Ring-Billed Gulls

Column	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Oldest chick's age (day)	Percentage of broods out of nest (broods observed)	Percentage time brooding average per hr (brood/hr observed)	Feedings of chicks, average per hr (brood/hr observed)	Percentage of feedings away from nest (feedings seen)	Average no. of stops per excursion (no. of excursions)	Average maximum distance from nest cup (no. of excursions)	Average distance of stops from nest (no. of stops)	Average distance moved per excursion (no. of excursions)	Average time per excursion (no. of excursions)
1st	0 (13)	92 (12)	0.58 (12)	0 (6)	0 m	— (0)	— (0)	— (0)	— (0)
2nd	10 (21)	83 (10)	1.40 (10)	15 (13)	3.0 (2)	0.75 (2)	0.58 (6)	1.50 (2)	13.0 (1)
3rd	38 (32)	83 (10)	1.36 (11)	7 (14)	1.0 (12)	0.58 (12)	0.58 (13)	1.12 (12)	4.3 (9)
4th	66 (32)	62 (11)	0.91 (11)	18 (11)	1.9 (24)	0.89 (22)	1.06 (45)	2.19 (24)	22.2 (16)
5th	87 (30)	48 (9)	0.80 (10)	56 (9)	1.6 (17)	0.86 (18)	0.79 (28)	2.14 (14)	25.7 (12)
6th	100 (30)	37 (10)	0.40 (10)	75 (4)	1.2 (30)	0.77 (30)	0.96 (37)	2.07 (30)	21.9 (24)
7th	92 (26)	13 (10)	0.50 (10)	100 (5)	2.2 (20)	1.16 (19)	1.20 (43)	2.45 (20)	19.0 (20)
8th	100 (22)				1.2 (12)	1.11 (13)	1.00 (17)	2.21 (12)	8.1 (9)
9th	100 (18)				2.1 (8)	1.69 (8)	1.97 (16)	3.81 (8)	10.4 (5)
Average		62 (72)	0.85 (74)		1.6 (125)	0.94 (124)	1.07 (205)	2.19 (122)	18.2 (96)
r	0.95	-0.99	-0.61	0.96	0.01	0.86	0.80	0.86	-0.12
P	<0.01	<0.01	>0.05	<0.01	>0.05	<0.01	<0.05	<0.01	>0.05

Each column shows a pair of numbers. The averages or percentages are based on the amount of observation shown by the figure in parentheses. The penultimate row shows the correlation between the chicks age and the measure in that column, with the significance level of this correlation in the row below.

(Spearman Rank Correlation; $P < 0.01$), reaching a maximum of 100 per cent on the sixth day after hatching (Table 3, column 1). Concurrently, the time spent by the parents brooding the chicks decreased ($P < 0.01$) from a high of 92 per cent on the first day to an average of only 13 per cent by the seventh day (Table 3, column 2).

Feeding frequency (Table 3, column 3) increased over the first 2 or 3 days, and then declined. A similar trend in feeding frequencies for this species was observed in an independent study in a nearby colony (Emlen & Miller, 1969). On the day of hatching, the few feedings that did occur were at the nest. With increasing age, there was an increase ($P < 0.01$) in the proportion of feedings that took place away from the nest (column 4), reaching 100 per cent on the seventh day.

Excursions of broods out from the nest cup sometimes consisted of a single movement away from the nest, a pause at this new location, either with or without feeding, followed by a return directly to the nest. More frequently, however, more than one (average = 1.6) temporary stops occurred per excursion before the brood returned to the nest. The number of stops per excursion showed no systematic increase or decrease with age over the first 9 days (Table 3, column 5).

The maximum distance from the nest to which adults led the chicks on excursions averaged 0.94 m for all ages combined up to the ninth day (Table 3, column 6); these maximum distances increased with age over the same age range ($P < 0.01$). The average distances from the nest for all stops that were observed during excursions (column 7) increased with age ($P < 0.05$) in a manner similar to the maximum excursion distances. Similarly, the total round-trip distances moved per excursion increased with age ($P < 0.01$) from approximately 1½ m on the second to third day up to over 2 or 3 m on the eighth and ninth days (column 8). The average time spent away from the nest (column 9) did not show any consistent age trends;

for all ages combined, the average duration of excursions was approximately 18 min.

The directions taken during excursions away from the nest were more or less stereotyped for any given brood. Two measures of this directional stereotypy were obtained from the mapped data. For the first measure, the farthest point from the nest at which a brood stopped during an excursion was chosen as the indicator of the direction taken. The directions of all such points for all mapped excursions of broods for which more than one excursion (average was 5) was observed were measured, and the maximum angle of divergence between excursions was calculated for each brood. Over half (63 per cent) of the divergence angles obtained for twenty-four broods did not exceed 90°, and only rarely (10 per cent) did these angles exceed 180°.

A second measure of the directional stereotypy was obtained by drawing lines on a map from the nest to each of the stops made on individual excursions, and by measuring the minimum angle enclosing all of the stops. Only those excursions involving two or more stops (average was 5) were used. In 59 per cent of the fifty-four excursions measured, the minimum angle enclosing all of the stops did not exceed 40°, and in only 2 per cent (one excursion) did the angle exceed 140°. The above distributions, taken together, indicate that during individual excursions, broods tended to strike out in a particular direction, and stay in that sector until they returned to the nest.

The excursion direction selected was highly variable between broods, but there was a consistent tendency for excursions to be directed away from nearby nests when these were active. This tendency to avoid nearby nests is reflected in the comparison of excursion distances and distances to the nearest nest. The mean distance to the nearest nest (see Fig. 1) for eighty-one nests was found to be approximately 0.85 m, a distance that is less than the average maximum excursion distance of 0.94 m (Table 3, column 6) for broods located in this same area.

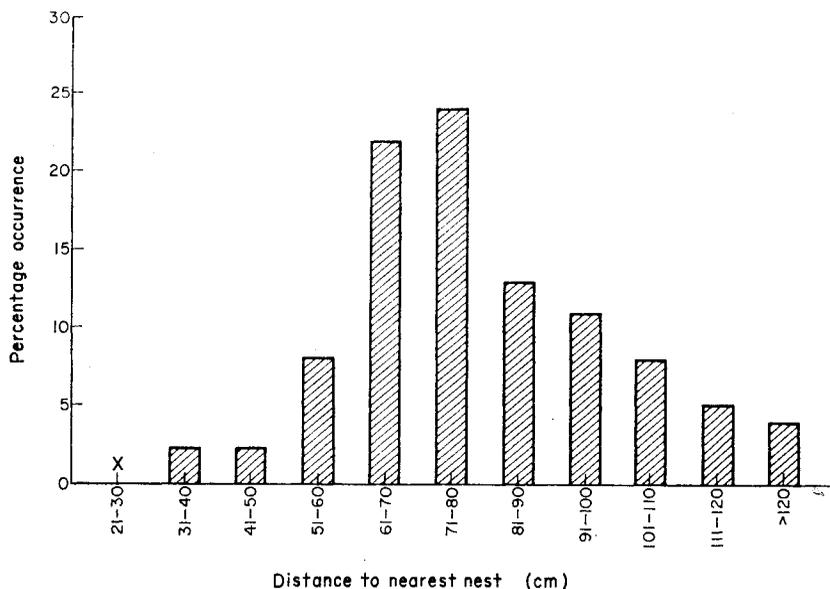


Fig. 1. Distribution of distances from centre to centre of nearest nests in ring-billed gull Colony no. 5, Rogers City, Michigan. $n=83$ nests.

Permanent Movements Away from the Nest Site

In addition to the localized excursions described above, instances occurred in which broods left the original nest and became established at new sites. The distances between the old and new sites were bimodally distributed, broods tending either to move a relatively short distance (from 1 to 5.5 m) and stop at a second site within the nesting area, or else to emigrate beyond the edges of the colonial nesting area, over distances of from 10 to approximately 40 m.

For those broods that remained within the colony, the average distance between original and new sites tended to increase in older broods over the age range of from the fifth to ninth day, from about 1.5 to 5.5 m (Table 4, column 1). Once at a new site, subsequent patterns of brood movements were similar to those of broods that remained at their original sites.

Measurements of excursion distances from new sites within the colony, comparable to those obtained from broods that remained at their original sites, were obtained by using the point on the new site lying nearest to the original

nest as a reference point. The maximum extent of movements from this reference point, as well as the average distance from the reference point of all stops that occurred during excursions, were measured from maps. Over the age range from the fifth to ninth day, the average maximum distances of stops on the new sites were slightly greater than for the broods that did not leave their original nest site (Table 4, column 2); the average distances of all stops observed during excursions (column 3) were sometimes greater, sometimes less, and showed no consistent age trend. Although the number of broods observed on their new sites was small ($n=12$), it seems apparent even from the limited evidence shown in Table 4 that once the new location had been taken up, the extent of localized brood movements did not differ greatly from that of the broods that remained on their original territories.

In contrast to the relatively short distances (average of 2.9 m) moved by broods that stopped at sites within the colony, broods that emigrated out beyond the limits of the nesting

Table 4. Average Distances, in Metres, Moved by Broods to New Sites Within the Colony, and Comparison of Excursion Distances from New and Original Sites

Oldest chick's age (day)	(1)		(2)		(3)	
	Distance between old and new sites (no. of broods)	Average maximum distance of stops during excursions				
		From reference point on new site (no. of excursions)	From nest on original site (no. of excursions)	From reference point on new site (no. of stops)	From nest on original site (no. of stops)	
5th	1.8 (2)	1.75 (2)	0.86 (18)	1.27 (11)	0.78 (28)	
6th	1.4 (4)	1.25 (4)	0.77 (30)	1.08 (6)	0.96 (37)	
7th	3.2 (3)	1.33 (3)	1.16 (19)	1.00 (11)	1.20 (43)	
8th	5.5 (1)	3.50 (1)	1.11 (13)	2.00 (8)	1.00 (17)	
9th	5.5 (2)	1.50 (2)	1.69 (8)	1.00 (4)	1.97 (16)	
Average	2.9 (12)	1.58 (12)	1.01 (88)	1.29 (40)	1.12 (141)	

See note to Table 3.

area travelled an average direct-line distance of approximately 22 m from their original nest before taking up new positions (Table 5, column 1). Such long distance movements first occurred with chicks as young as 3 days of age, but were not common until the fourth and fifth days.

The pattern of movements during emigrations was similar for all age classes involved, and typically consisted of a single series of uni-directional movements alternating with brief stops, one or both parents calling and leading the chicks across the nesting area out to one of

Table 5. Average Distances, in Metres, of Brood Emigrations from the Colony, and Comparison of Rate of Movements of Emigrations and Excursions

Oldest chick's age (day) at time of emigration	(1)	(2)	(3)	(4)	(5)
	Distance from nest moved, approximate* (no. broods)	Average no. of stops en route (no. broods)	Time to emigrate, (minutes) (no. broods)	Rate of emigration approximate* (m per min) (no. broods)	Rate of movements in excursions (m per min) (no. excursions)
3rd	35 (1)	25 (1)	113 (1)	0.31 (1)	0.30 (9)
4th	19 (3)	5 (3)	17 (3)	1.17 (3)	0.34 (19)
5th	20 (3)	8 (3)	41 (3)	0.47 (3)	0.34 (13)
6th	30 (1)	6 (1)	37 (1)	0.80 (1)	0.63 (25)
7th	28 (3)	7 (3)	83 (3)	0.34 (3)	0.55 (21)
8th	16 (2)	7 (2)	33 (2)	0.47 (2)	0.50 (9)
9th	14 (1)	6 (1)	20 (1)	0.70 (1)	1.02 (6)
Average	22 (14)	8 (14)	47 (14)	0.62 (14)	0.51(102)

*During the final portions of their journeys, emigrants moved out beyond the marked area set up for scaled mapping.

See note to Table 3.

the small (2 to 3 m high) cliffs or banks that bordered the colony. The average number of stops during emigrations ranged from five to twenty-five, and showed no systematic age trend over the range of from the third to ninth day (Table 5, column 2). Emigration time ranged from 10 to 113 min (average = 47 min), and also did not vary systematically with chick age.

In columns 4 and 5 of Table 5, the overall rate of movements in metres per minute is compared for emigrations and for the ordinary excursions out from the nest cup. The similarity of the average values between the two groups, even after making allowance for error in the approximation of total emigration distance, suggests that emigrations are brought about by typical rates of movement which are all oriented in the same general direction away from the nest instead of by the alternating movements away from and back to the nest that are characteristic of local excursions.

Systematic records of brood movements subsequent to emigration were not maintained. Occasional records of broods shifting their location from day to day were obtained, however, thus indicating that these emigrant broods

did not always remain localized at a particular site after leaving the nesting area.

Brood Movements During Sudden Disturbances

In the absence of serious disturbances, most major movements of chicks were apparently initiated and guided mainly by parental action. In contrast, when the colony was subject to acute disturbance, as when a human observer walked through it, nearby adults flew up, and the orientation of the rapid, irregular movements of the chicks appeared to be independent of parental direction. Such chick movements typically terminated in a crouch, similar to that noted for the herring gull (Goethe 1937; Tinbergen 1953a) and black-headed gull (Kirkman 1937).

During disturbances caused by my walking through the colony the proportion of chicks found crouched outside of the nest cup increased with age ($P < 0.01$) from nil on the first day to 79 per cent on the fifth and 100 per cent on the sixth day (Table 6, column 1). The average distance moved from the nest also increased ($P < 0.01$) over the same age range (column 2). In all instances, the distances from the nests were small, ranging up to 30 cm for individual

Table 6. Relationship of Age to Frequency and Extent of Chick Dispersal During Acute Disturbance Caused by an Observer Walking Through the Colony

Oldest chick's age (day)	(1)	(2)	(3)	Time (min) for chicks to return to nest		
	Percentage leaving nest (no. chicks)	Average distance moved, for those that left nest (cm)	Maximum distance moved from edge of nest (cm)	(4) Range	(5) Median	(6) Average (no. chicks)
1st	0 (50)	—	—	—	—	— (0)
2nd	12 (76)	6	10	23–35	25	28 (3)
3rd	43 (106)	9	30	4–47	23	22 (20)
4th	67 (66)	10	30	3–36	15	19 (18)
5th	79 (19)	11	30	5–35	13	15 (7)
6th	100 (3)	13	15	5–28	16	16 (5)
<i>r</i>	1.00	1.00				–0.90
<i>P</i>	<0.01	<0.01				<0.05

See note to Table 3.

chicks (Table 6, column 3). Maximum average distances reached only 13 cm, compared to the maximum average distance of 94 cm that these same broods moved during typical excursions with their parents (see Table 3, column 6). It is probable that distances moved during acute disturbances were small in colony no. 5 due to the presence of adequate vegetation near the nests that provided suitable hiding places.

The elapsed time before chicks returned to their nest sites after acute disturbances was highly variable, ranging from 3 to 37 min (Table 6, column 4). Both median (column 5) and average (column 6) times tended to decrease for the older birds.

Movements of Chicks in an Undisturbed Colony

A measure of brood movements under relatively undisturbed conditions was obtained from colony no. 2 that was left undisturbed except for initial banding of freshly-hatched chicks

and a single subsequent search for banded chicks conducted when they had reached their seventh to tenth day of age. The distributions of recapture distances from the original nest site for eighty-eight chicks reared as broods of one and for seventy-four reared as broods of three are shown in Fig. 2. Fourteen chicks (9 per cent) had moved up to or over 10 m, but most (80 per cent) were found within 3 m of their original nest sites. Brood size of one or three had no apparent effect on the distribution.

The range of distances moved by broods in colony no. 2 was similar to that of the intensively studied colony when excursions, movements to new sites, and emigrations from the latter are all taken into account. The occurrence of distances greater than 3 m in Fig. 2 suggests that movements away from the original nest site are characteristic of the species and occur independently of repeated acute disturbances by humans.

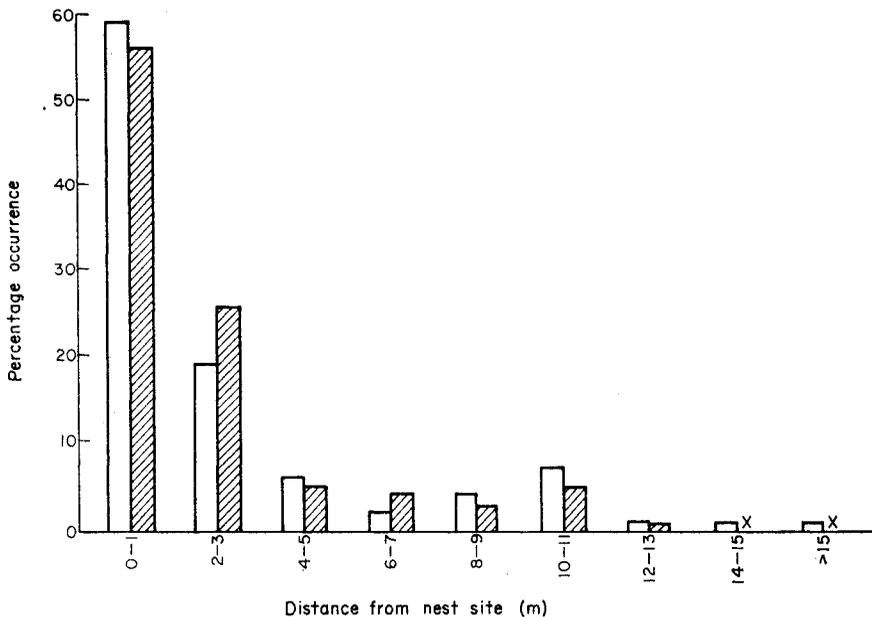


Fig. 2. Distributions of distances between nests and recapture sites of chicks in a relatively undisturbed ring-billed gull colony, no. 2. Chicks were in their seventh to tenth day of age when recaptured. Open columns, reared as broods of one ($n=88$ chicks); hatched columns, reared as broods of three ($n=74$ chicks).

V. APPROACH RESPONSES TO FIXED INANIMATE OBJECTS

Two conditions commonly inducing gull chicks to approach fixed objects in the vicinity of the nest are extremes of weather, such as hot sun, and disturbances of the colony as by a mammalian intruder. The tendency for ring-billed gull chicks to seek shelter from the sun by moving into the shadows cast by fixed objects has been described previously (Emlen 1956), and will not be considered further here.

Hiding and crouch responses, associated with colony disturbances, are typically elicited in chicks of various gull species by adult alarm calls (Strong 1914; Goethe 1937; Tinbergen 1953a; Moynihan 1959). At such times chicks may repeatedly seek out specific hiding places on or near their territory, as described, for example, in the herring gull (Tinbergen 1953a) and black-headed gull (Kirkman 1937). No extensive records of these responses were kept in the present study, but observations were in essential agreement with the published accounts noted above.

Where the number of suitable hiding places is limited, or when a particular hiding place has some definite advantage because of its size, shape, or location, it is possible that the repeated selection of such a hiding place may be due to unlearned preference of a given chick. Alternately, such repeated selection of a particular hiding place may depend primarily on a learned preference associated with a general conditioning to the territory, similar to that suggested for young herring gulls by Tinbergen (1953a). Because of the procedural difficulties inherent in the natural colony situation it is often difficult, if not impossible, to choose between these two alternative, but not mutually exclusive, possibilities.

Implicit in the interpretation that repeated selection of the same hiding place depends on a learned preference, however, is the assumption that young gulls are in fact able to learn the discriminations and motor patterns necessary

to move repeatedly to a specific location. In the present study, this latter possibility was investigated experimentally, for ring-billed gull chicks, as described below.

When colony-reared chicks were placed near the centre of a long rectangular pen, their initial response was to move directly to one or the other side of the pen. This response was used as a standard of comparison to demonstrate learning. The learning problem consisted of training chicks to walk or run directly down the middle of the pen, for progressively greater distances, to a specific hiding place located at the far end of the pen.

The 'pen' used was a flat-bottomed railroad car (=railway waggon) with open top, measuring 9.75 m long by 2.5 m wide, with opaque walls extending up for a distance of 1m. A grass clump was placed at the centre of one end, flanked at distances of 0.5 m and 1 m on either side, by four other distinctively different alternative hiding places consisting of two boxes and two boards. Release sites were marked off down the median longitudinal axis of the car at distances of 1, 2, 3, 4, 6 and 8 m from the grass clump.

Six chicks, two at each of 4, 6 and 8 days of age, were trained individually, starting with releases from the 1-m release site. After each trial, chicks that selected the grass clump were left under it for approximately 30 s, then removed and released from the next more distant site. When a side of the car or one of the alternative hiding places was selected, chicks were picked up immediately, then released at the next closer release point, except that errors made at 1 m were followed by another test from the same distance. Trials were continued until the first correct response was made at the 8-m release point.

The number of trials required to reach the first correct response at successively more distant release points (Table 7) varied widely between individuals for each release point, but total trials for the entire series were not too

different (twenty-six to seventy-two), with an overall average of fifty-six. Despite the variation in number of trials, each chick tested eventually learned to go directly to the grass clump, over

Table 7. Number of Training Trials Required for Young Ring-Billed Gulls to Learn to Move Down a Rectangular Pen Over Successively Greater Distances to a Particular Hiding Place

Chick's age (days)	Cumulative no. of trials to first correct response at successively greater distances					
	1 m	2 m	3 m	4 m	6 m	8 m
4th	9	10	28	29	36	41
4th	1	41	54	55	70	71
6th	8	15	21	24	25	26
6th	1	8	39	54	55	72
8th	33	56	57	60	61	72
8th	13	34	37	44	49	54
Totals	65	164	236	266	296	336
Average	11	27	39	44	49	56
Trials to criteria at successive intervals	11	16	12	5	5	7

the full distance of 8 m. The average increment in number of trials to reach the first correct response at successive release sites ranged from eleven to sixteen for releases made at 1 to 3 m, then dropped to from five to seven trials for the more distant release sites. This decline in trials at the greater distances may be taken as further evidence that learning occurred during the training procedure.

It is worthy of note that the correct solution to the learning problem posed by the above procedure required the chicks to overcome an initial bias leading away from the prescribed hiding place. It is thus considerably more difficult than comparable problems in the colony, where hiding places may be selected initially because of their favourable characteristics.

It is not entirely clear what reinforces the learning of hiding places, either during the above training procedure or when it occurs in the colony. Because selection of such a hiding place is typically followed by a period of quiescence, however, it is probable that some form of 'anxiety' reduction (Mowrer 1939) may be involved in both situations.

VI. APPROACH RESPONSES TO A FAMILIAR REARING AREA

When young ring-billed gull chicks up to 1 week of age were moved by their parents to new locations within the colony, the family units typically remained localized at the new sites (Section IV, p. 202). In no cases were chicks observed to leave the parents and move back to the original nest sites or territories. The behaviour of these young chicks thus provided no evidence for recognition of, or attachment to, the place they were related.

In the domestic fowl, however, it is known that young chicks are able to learn the characteristics of a static rearing environment, and will subsequently select such an environment over one that is strange. For example, chicks exposed to prominently displayed motionless circular or triangular objects for 24 hr during the third, fourth or fifth day of age, showed a significant preference for the familiar object in subsequent choice tests (Gray 1960). Evidence that certain visual characteristics of rearing pens may also be learned has been reported by Bateson (1964a). Domestic chicks at 3 days of age tended to exhibit less avoidance and more rapid approach responses to moving objects that were patterned the same as the walls of their rearing pens, provided that stimulus 'conspicuousness' was not strikingly different between the familiar and strange patterns (Bateson 1964b).

The possibility that preferential approach responses to a familiar rearing environment might occur in young gull chicks was tested in the laboratory as described below. Domestic white leghorn chicks were also tested as a partial check on the adequacy of the procedure.

Rearing pens, measuring $0.56 \times 0.56 \times 0.36$ m high, were used. Each pen was divided by an opaque partition into two equal compartments. The walls of each compartment were covered up to a height of 0.22 m above the floor with stripes 0.32 cm wide, placed at intervals of 2.5 cm, on a plain white background. One compartment of each pen was fitted with green horizontal stripes, the other with red vertical

stripes. Approximately equal numbers of chicks were given rearing experience with each colour pattern.

Chicks of both species were hatched in the laboratory. Domestic chicks were reared as groups of from two to four, gull chicks either singly or in groups of two to five. Rearing pens were equipped with an incandescent light bulb to provide light and heat. Continuous supplies of food and water were provided for the domestic chicks; gull chicks were fed three times daily, either in their rearing pens or in neutral pens consisting of plain cardboard boxes.

Immediately before testing, chicks were placed in neutral holding pens. The central partitions were then removed from the rearing pens, thus exposing the two adjacent and different wall patterns. Chicks were released either singly (isolate-reared) or in pairs (group-reared) at the centre of the pen, and their initial choice of the familiar or strange half of the pen was recorded. A trial was considered complete when the chick(s) had moved entirely into one or the other half of the pen. If no choice was made by 2 min, the test was terminated. Domestic chicks were given repeated tests on the same day; gull chicks received up to three tests on each of two successive days. A total of twenty-six domestic and fifty-two gull chicks were given 146 and 222 tests, respectively.

Domestic chicks at both 4 and 5 days of age selected the half of the pen containing their familiar rearing pattern and colour significantly more ($P < 0.001$) than the alternative, strange half (Table 8). These results may be taken as evidence that the rearing and test procedures were adequate to demonstrate a preferential selection of a familiar rearing environment, at least in this species.

All treatment groups of ring-billed gull chicks selected their rearing pen in more than 50 per cent of the tests (Table 9). This preferential selection approached significance in the 5 day old chicks ($0.10 > P > 0.05$), and was significant

Table 8. Selection of a Familiar Rearing Environment in Group-Reared Domestic Chicks

Test age (days)	No. of chick's tested	No. of tests given	Positive responses		χ^2	<i>P</i>
			No.	Proportion (per cent)		
4	16	100	89	89	60.84	<0.001
5	10	46	38	83	19.56	<0.001
Totals	26	146	127	87		

when tested by χ^2 at 4 days ($P < 0.001$). No significant differences occurred between group-reared and isolate-reared chicks. Chicks fed in neutral pens selected their home environment proportionately more than did chicks fed in their home environment. This latter result is difficult to interpret but does at least suggest that food reinforcement during the rearing period was not necessary for subsequent selection of the home environment.

Although all four treatment groups of gull

chicks selected the familiar environment in over half of the tests at both ages, it is clear from the several low percentage values listed in Table 9 that such preferential responses were not strongly developed. This conclusion is supported by comparison with the higher percentages obtained by the same method for domestic chicks (Table 8). The results do not, of course, rule out the possibility that a tendency to select a familiar rearing environment becomes more strongly developed in gull chicks at a later age.

Table 9. Selection of a Familiar Rearing Environment by Ring-Billed Gull Chicks under Four Rearing Conditions

Rearing condition	No. of tests at each age (no. chicks)		Positive responses				Combined per cent
			4 days old		5 days old		
			No.	Per cent	No.	Per cent	
Isolates fed in rearing pen	30	(10)	20	67	16	53	60
Isolates fed in neutral pen	30	(10)	23	77	19	63	70
Group-reared fed in rearing pen	39	(26)	24	62	20	51	56
Group-reared fed in neutral pen	12	(8)	10	83	10	83	83
Totals	111	(54)	77	69	65	58	64

VII. APPROACH RESPONSES TO ADULTS

The tendency for ring-billed gull chicks to approach or follow their parents is well developed. Such approach responses were especially evident when parents called and led their broods on excursions away from and back to the nest, during feeding bouts, and during emigrations away from the nesting area as described in Section IV (p. 201).

Although establishing the existence and frequency of such approach responses, these observations of broods under essentially natural conditions do not in themselves provide detailed information about the relative effectiveness of the various stimuli that elicit the approach responses. Such observational methods also lack the control and precision needed to provide an adequate basis for determining when, and to what extent, if any, early experience and food reinforcement influence the development of responses to particular stimuli or classes of stimuli. On the other hand, it seems apparent that a purely experimental approach may also prove inadequate for such interpretations because of differences in context between the experimental and natural situations (cf. Tinbergen 1953b).

In the analyses of approach responses described in this and subsequent sections of the present study, an attempt was made to obtain controlled experimental data that would also be applicable to gulls under natural conditions, by using various combinations of the above methods including observations of natural populations, experiments in which both the rearing and testing of chicks were restricted to either the colony or the laboratory, and experiments in which chicks were reared in one situation, either colony or laboratory, and tested in the other. Where alternative choices of these various procedures were available for a given experiment, the more natural context was selected where possible, provided this did not appear to jeopardize the required degree of experimental control.

Stimulus Conditions

Several observations of chicks in the colony suggested that approach responses to adults were enhanced by the combination of individually effective stimuli acting simultaneously on receptors of more than one modality of the chick. For example, approaches to momentarily silent adults appeared less rapid and direct than approaches to adults emitting mew calls. The effectiveness of mew calls in eliciting approach responses was further suggested by repeated observations of adults calling back into the nest very young chicks that had been experimentally displaced distances of up to 0.5 m from the nest cup. As previously described by Moynihan (1958) for ring-billed gulls as well as for other related species, mew calls were also commonly noticed when parents called chicks to them prior to or during feedings at or near the nest.

On the basis of the above observations, both natural occurrences of mew calls, in which the visual characteristics of the calling adult were also present, and tape-recorded play-backs of the same calls, in which the adult bird was absent, were selected for experimental purposes. These stimuli were then presented to normal, deafened and blindfolded chicks in experiments designed to study the relative effectiveness and possible summation effects of visual and auditory input. By selecting experimental chicks from various rearing conditions and age classes, data pertaining to the effect on approach responses of early social experience were also obtained.

A. Effectiveness of Visual Stimuli

The effectiveness of visual stimuli from adults in eliciting and orienting approach responses was tested experimentally with chicks in which the hearing ability was seriously impaired by destruction of the tympanic membranes and columellae. Five chicks hatched in the laboratory and six of the same age taken from the colony were anaesthetized with

Nembutal, and operated* on during the latter part of their first day after hatching. Following the operations, chicks were reared and fed in the laboratory until the third day, during which time they appeared to recover fully from the operation. Six of the operated chicks exhibited no responses to various noises or adult calls. The other five sometimes cheeped in response to taped mew calls, when these were played at a high volume, but did not orient towards or approach the sound source. Since these birds were not getting directional cues from sound, it was considered valid to include them with the other six for the experiments.

Ten of the experimental and ten unoperated control chicks, half of which were hatched in the laboratory and half in the colony, were tested in the colony during their third day. Adults having 1- to 2-day-old chicks were selected as test stimuli. Offspring of the stimulus adults were removed, and pairs of test chicks, consisting of one experimental and one control, were placed approximately 1 m outside of the nest, and their responses to the mewing adults observed. Following these tests, all chicks were left with foster parents to determine if chicks with impaired hearing would survive in the natural environment.

With one exception, control chicks were the first to approach the adults (Table 10), thus providing evidence for a summation effect of visual and auditory stimuli. Equivalent results have been obtained for precocial species (Smith & Bird 1963). All of the operated chicks that had been taken from the colony after at least a part of a day in the nest approached adults during a 10-min observation period, whereas only one of the operated chicks that were hatched in the laboratory did so, a difference that departs significantly from random ($P < 0.05$; Fisher exact probability test, 2-tailed). These data indicate that visual stimuli alone were sufficient to produce rapid oriented approach responses to adults

*Operations were performed by Dr Masakazu Konishi in our temporary field laboratory established at Rogers City, Michigan, in 1966.

but, with one exception, only in those chicks that had prior experience with adults. The conclusion that auditory stimuli were not necessary to elicit approach responses in chicks having early experience with adults was confirmed in two additional chicks that were totally deafened by removal of the cochlea and returned to their parents before the end of their first day. These chicks remained with their parents for at least four more days, and were observed to approach, follow and be fed by their parents.

Table 10. Effect of Impaired Hearing, on Initial Approach Responses to Adults, when Tested at $2\frac{1}{2}(\pm\frac{1}{4})$ Days of Age, and Subsequent Short-term Survival when Left in the Colony with Foster Parents

	Hatched and reared in the laboratory until tested		Reared in colony for first 12 to 24 hr, then in laboratory until tested	
	Impaired hearing	Controls	Impaired hearing	Controls
No. tested	5	5	5	5
First of pair to approach	0	5	1	4
Approached within 10 min	1	5	5	5
Attended by adult within 10 min	4	5	5	5
Survived first night with foster parents	4	2	2	2
Survived for 3 days with foster parent	4	1	2	2

Mortality over the first night was high for both control chicks and those with impaired hearing (Table 10). Thereafter, all operated chicks and all but one control survived for the succeeding 3 days, at which time observations were terminated. The data in Table 10 thus provide no evidence for reduced survival in the chicks with impaired hearing. The fact that the operated chicks that were hatched in the laboratory survived at least as well as or better than

Table 11. Effect of Blindfolding on Orientation and Approach Responses to Mew Calls from a Loud-speaker (Colony-Reared Ring-Billed Gull Chicks, 2 to 3 days old)

	No. tested	No. and per cent approaching speaker	Approach latency average (min)	No. and per cent that turned towards speaker
Before blindfolding	15	14 (93%)	0.50	14 (93%)
Blindfolded	15	5 (33%)	1.50	12 (80%)
After removal of blindfold	15	13 (87%)	0.65	13 (87%)

any other group suggests that their initial reluctance to approach adults may have been overcome after subsequent exposure to their foster parents.

B. Effectiveness of Auditory Stimuli

The effectiveness of auditory stimuli in eliciting approach responses was further tested by releasing chicks individually, midway between two loud-speakers that were placed 2 m apart. A mew call was played at a constant volume once every 4 s from one of the speakers until the chick approached the speaker, or for a period of 2 min if no approach response occurred. Sound production was alternated from one side to the other for tests with successive chicks to eliminate possible direction bias.

Sixteen chicks that were hatched in the laboratory were tested by the above procedure at $\frac{3}{4}$ ($\pm \frac{1}{4}$) day after hatching. All approached the active speaker within 2 min, the average latency being 1.39 min. These results demonstrate that mew calls are effective in eliciting approach responses by as early as the first day, even in the absence of prior post-hatching experience with such calls.

The effect of mew calls under conditions of restricted vision was examined in fifteen chicks taken from the colony at 2 to 3 days of age and tested as described above. Control tests before vision was impaired were given immediately after chicks were taken from the colony. Each chick was then fitted with a blindfold consisting of small, shallow, opaque cones, measuring approximately 2 cm across the base, which were

glued over each eye with 'Duco' cement. Chicks were then tested while blindfolded and again after the blindfolds were removed.

All but three of the fifteen blindfolded chicks turned both head and body towards the speaker that was emitting the mew calls (Table 11). Only five (33 per cent) actually approached the speaker, however, thus indicating a significant reduction in approach responses compared to their performance before blindfolding ($\chi^2=9.19$; $P<0.01$) and after the blindfolds were removed ($\chi^2=6.80$; $P<0.01$). These results indicate that mew calls alone are usually sufficient to orient chicks, but in the total absence of visual cues, the frequency of actual approaches is small.

C. Intensity of Auditory Stimulation

When adult mew calls were monitored with a microphone placed beside the chicks at the nest, the calls of the parents at the nest were decidedly louder than those of neighbouring adults. This result, coupled with the observation that chicks as young as 1 day of age typically responded to the calls of their parents and not to the multitude of similar calls produced by other adults located farther away in space, suggest that loudness of adult mew calls may be an important variable in eliciting approach responses.

The influence of intensity of auditory stimulation was tested experimentally by varying the distance between a constant sound source and the point at which chicks were released. Thirty chicks of from 1 to 2 days of age were removed from the colony and placed on level ground,

midway between two loud-speakers. A mew call from a strange adult, spliced into an otherwise blank continuous loop of tape, was played repeatedly, once every 4 s, at a constant volume, from one speaker. Half of the chicks were tested at a distance of 2 m from each speaker, the other half at 6 m. Response latencies were measured from the time the mew call first sounded on a given test until the test chick moved 0.5 m towards the active speaker.

Table 12. Effect of Distance on the Rate of Approach Responses to Mew Calls from a Loud-Speaker (Colony-reared Ring-Billed Gull chicks, 2 to 3 days old)

	Distance from loud-speaker	
	2 m	6 m
Average latency	15.5 sec	26.2 sec
Median latency	11 sec	18 sec
Range	4-41 sec	4-120 sec

Median latency and average latency were both less at the shorter distance (Table 12). The difference in latencies was significant when analysed by an unpaired *t*-test ($t=2.44$; $P<0.05$). Since it may be assumed that mew call loudness was greater at the 2 m release point, the shorter latencies at this distance indicate a positive effect of intensity on the tendency to approach. In view of Schneirla's (1965) suggestion that high intensity stimuli tend to evoke withdrawal responses whereas low intensity stimuli tend to evoke approach, it can be noted that the intensities of sound used in these experiments were undoubtedly within the intensity range typical of the colony, and hence may have been below the critical level, if such exists, that would have resulted in increased latencies or actual withdrawal responses at the higher intensity.

Food Reinforcement

Since gull chicks are fed by their parents and, further, since mew calls commonly occur in association with such feedings, it would not be unreasonable to assume that approach re-

sponses to adults or to mew calls per se are influenced by food. Hailman (1964, cited in Klopfer & Hailman 1965; Hailman 1967) has found that food reinforcement may enhance the pecking response of herring gull chicks, thus indicating the possible importance of such reinforcement in the development of social responses in these chicks.

The possibility that food reinforcement is necessary for the maintenance of approach responses to parents was tested by preventing the delivery of food between parents and chicks or between siblings at the nest. The bills of freshly-hatched chicks (two were taken directly from the shell) were sealed with narrow strips of plastic-coated 'Mystik' tape over which was applied a coating of 'Duco' cement. Five broods were set up with one bill-taped chick and one normal control, and five were set up with one bill-taped and two control chicks. Experimental chicks were removed from the colony three times daily and hand fed, in isolation. After each feeding, bills were resealed before returning the chicks to their nests. Chicks were examined before and after each feeding to establish that the bills were completely sealed. Mortality was high over the first 3 to 4 days, but did not differ appreciably between the experimental (50 per cent) and the control (33 per cent) chicks ($P=0.463$; Fisher exact probability test, 2-tailed).

Observations at the experimental nests indicated that the bill-taped chicks socialized normally with their parents and siblings; they remained close to home, and showed no increased tendency to disband or move away. Bill-taped chicks as old as 3 and 4 days were observed to approach their parents and to follow them across the territory, both in broods having controls and those in which controls were no longer present. On three occasions, parents were seen to go through attempted feeding sequences with the bill-taped chicks. These sequences included parental mew calls, approach of the chick to the adult, pecks at the parent's bill by the chick, and regurgitation of food by

the parent followed by additional pecks at the bill or food. After each of these incidents the chicks' bills were examined, and found to be completely sealed, hence there could have been no passage of food between parent and chick.

From the above observations, it can be concluded that food reinforcement from parental or sibling feeding is not a necessary condition for the maintenance of normal approach responses to adult gulls, at least during the first few days after hatching.

Approach Responses to Mew Calls of Particular Individuals

Individual recognition of parents by their young has been demonstrated in several species of ground-nesting colonial sea birds, including the adie penguin (*Pygoscelis adeliae*) (Sladen 1958; Penney 1963), the common murre (*Uria aalge*) (Tschanz 1965), and the herring gull (Goethe 1937). In the herring gull Goethe (1937, pp. 84–86) cited observations indicating that preferential responses to parents occur in chicks from 2 to 3 weeks old and he also presented evidence that these chicks are able to recognize their parents' calls. More recently it has been found that recognition of parental calls develops by at least 6 days of age in the laughing gull (*Larus atricilla*) (Beer 1969), while in the relatively precocial black-billed gull (*L. bulleri*) recognition of parental mew calls develops as early as 2 to 3 days after hatching (Evans 1970). In the present study, experiments were performed to test for both the occurrence and the chronological development of preferential approach responses to mew calls of the parents.

An initial test for responses to calls of a particular parent was done by recording the mew calls of a parent actively feeding its 10- to 12-day-old chicks, then later the same day, repeatedly playing one of these calls back to the chicks in the absence of the parents. A Wallensak T 1700 portable tape recorder with extension speaker was used for this experiment.

The speaker was first placed 5 m away from

the chicks, with two other broods being located between the speaker and the experimental brood. When the mew call was sounded, all three experimental chicks began to approach the speaker, moving around the chicks from the intervening broods, none of which showed any response to the speaker even though they were initially closer to it than were the experimental chicks. This procedure was repeated, with essentially the same result, with the speaker placed 10 m from the experimental chicks.

Two chicks from the above experimental brood and two chicks of similar age from a different brood were then removed from the colony and placed in a patch of weeds, first 10 m, then 20 m from the speaker. In both instances, the experimental chicks responded vocally immediately to their parent's mew call, and eventually came over to the speaker; the other chicks moved away in the opposite direction.

The above observations indicate that 10- to 12-day-old ring-billed gull chicks can recognize the mew calls of their own parent and respond by approaching the source of such calls. To obtain information on the age at which such preferential approach responses develop, two additional experimental procedures were followed, one (latency test) based on comparisons of response latencies between chicks from different broods when approaching a single stimulus source, the other (choice test) based on preferential responses of individual chicks to one of two rapidly alternating stimuli.

(1) **Latency test.** This test was similar to that used to demonstrate individual recognition parental mew calls in young black-billed gulls (Evans 1970). For ring-billed gulls the latency test was conducted by taking two chicks, each one from a separate brood, and placing them 1 m apart and approximately 2 m from a loud-speaker which was set up on level ground well away from the colony. A tape-recorded mew call, previously obtained in the colony from a parent of one of the test chicks, was then played back

over the loud-speaker approximately once every 2 s, until at least one chick approached the speaker. Both chicks were then handled and replaced at their original release points, and the procedure was repeated, this time using a mew call previously recorded from a parent of the other chick.

Under the conditions employed in these tests, half of the chicks were exposed successively to a familiar, then to a strange call, and half were exposed to these same calls but the first being familiar, the second strange. Recognition of parental calls would presumably be demonstrated by the occurrence of a significant number of tests in which the offspring of the parent whose call was being played approached the loud-speaker more rapidly than did the other chick. Records were accordingly kept of the identity of the chick, from each test pair, that was the first to approach the speaker when a particular mew call was played.

Seventy-two ring-billed gull chicks reared as broods of three were tested once each, at ages ranging from 3 to 5 days. All age classes showed a slight tendency to respond more rapidly to the familiar, parental mew calls, but the number of instances in which differential response rates occurred were not statistically significant for any single age class (Table 13).

In contrast to the positive results obtained by the latency test for the black-billed gulls (Evans

Table 13. Differential Rate of Approach Responses to the Recorded Mew Calls of Parents by Offspring Compared to Non-Offspring (Recordings and Play-Back Done with a Uher Model 4000 Report Portable Tape Recorder)

	Age (days)		
	3	4	5
No. of tests	24	24	24
Offspring approached first	14	14	14
Percentage	58	58	58
χ^2	0.67	0.67	0.67
P	0.50 < P < 0.30	0.50 > P > 0.30	0.50 > P > 0.30

1970), the results listed in Table 13 provide no evidence that 3- to 5-day-old ring-billed gulls recognize and respond more rapidly to mew calls of their own parents. Observations of the young gulls during these tests indicated that these differences probably represent real species differences, the poorer performance of the ring-billed gulls being associated with a less rapid development of the tendency to inhibit responses to the strange calls. Although it is clear from Table 13 that individual recognition was not demonstrated for young ring-billed gulls by the latency method, it is also evident that the results do not rule out the possibility that such recognition does develop at an early age in this species, or that preferential approach responses to familiar parental calls could occur under more sensitive test conditions.

(2) **Choice test.** The possibility that preferential responses to familiar parental mew calls might occur when chicks were permitted to choose between strange and familiar calls that were presented together was tested in a manner similar to that used for murrets by Tschanz (1965). Single chicks were released by hand, 2 m from each of two loud-speakers which were placed such that they subtended an angle of 90° from the chick. Using a continuous loop of tape and a switch that activated the two speakers alternately, a mew call of the test chick's parent was played from one speaker, alternating every 2 s with a mew call of another adult from the other speaker. Biases due to speaker, speaker location, or intensity of calls of particular adults were controlled by first testing a chick 'A' against the mews of adults 'A' and 'B', then testing chick 'B' against the same calls from the same speakers. Sixty chicks (not those used for the above latency tests) were tested once each at from 2 to 4 days after hatching. Twenty-four of those tested at 2 or 3 days were selected, without reference to their initial performance, and tested a second time, at 5 days.

Under the conditions of this choice test, an increasing preferential approach response to

Table 14. Preferential Approach Responses to Recordings of Parental as Compared with Non-Parental Mew Calls by Ring-Billed Gull Chicks (Recordings and Play-Back Done with Nagra III Portable Tape Recorder)

	Age (days)			
	2	3	4	5
No. of tests	12	24	24	24
No. approaching parental mew	7	16	17	19
Percentage approaching parental mew	58	67	71	79
χ^2	0.33	2.67	4.17	8.17
<i>P</i>	0.95 > <i>P</i> > 0.50	0.20 > <i>P</i> > 0.10	<i>P</i> < 0.05	<i>P</i> < 0.01

parental mew calls was demonstrated with increasing age (Table 14). At 2 days of age, seven of twelve chicks (58 per cent) selected the speaker emitting mew calls of their own parents. This proportion does not differ significantly from random ($0.95 > P > 0.50$). Proportionately more chicks approached the calls of their own parents at 3 days (67 per cent) and at 4 days (71 per cent), the 4-day chicks significantly so ($P < 0.05$). By 5 days, nineteen of twenty-four chicks (79 per cent) approached the mew calls of their own parents ($P < 0.01$).

The above demonstrations of preferential approach responses by chicks to recordings of mew calls of their own parents implies the existence of discriminable differences between the calls of different adults. Also, since such discriminations were presumably based upon prior experience with the familiar calls, it is apparent that mew calls of a given individual must have some element(s) of similarity between them. That these considerations do in fact apply to mew calls was indicated by inspection of sound spectrograms made from sixty-six calls of seven adult ring-billed gulls. Examples of these records, selected randomly from three representative individuals for which at least six records were available, are illustrated in Fig. 3. It is evident from these illustrations that differences between calls of particular individuals are less than the differences between calls of separate individuals, and thus could provide a

basis for the recognition of specific individuals by the chicks.

(3) **Discussion.** Although quite different results were obtained by the latency (Table 13) and choice (Table 14) methods, there seems no reason to assume that one or the other test method is invalid, or that the results merely reflect chance differences. On the contrary, it seems apparent that the methods provide two quite different measures of the behaviour involved, the first assessing differences in *rate* of response, the second assessing the *orientation* of the response. Whereas significant differences obtained by either method would be sufficient to demonstrate recognition of the parental mew calls, it is probable that the choice method, which requires an essentially simultaneous discrimination, is a more sensitive test than the latency method which requires successive discriminations between strange and familiar stimuli presented one at a time. When considered thus, the different results obtained by the above methods are in general agreement with theoretical predictions from learning theory and with several, although not all, empirical findings derived from comparing the effects of successive and simultaneous stimulus presentations during discrimination training (see Kimble 1961, pp. 361–76 for further discussion of these methods and related theory; also Franck 1966; Hailman 1967).

Comparison of the above latency and choice

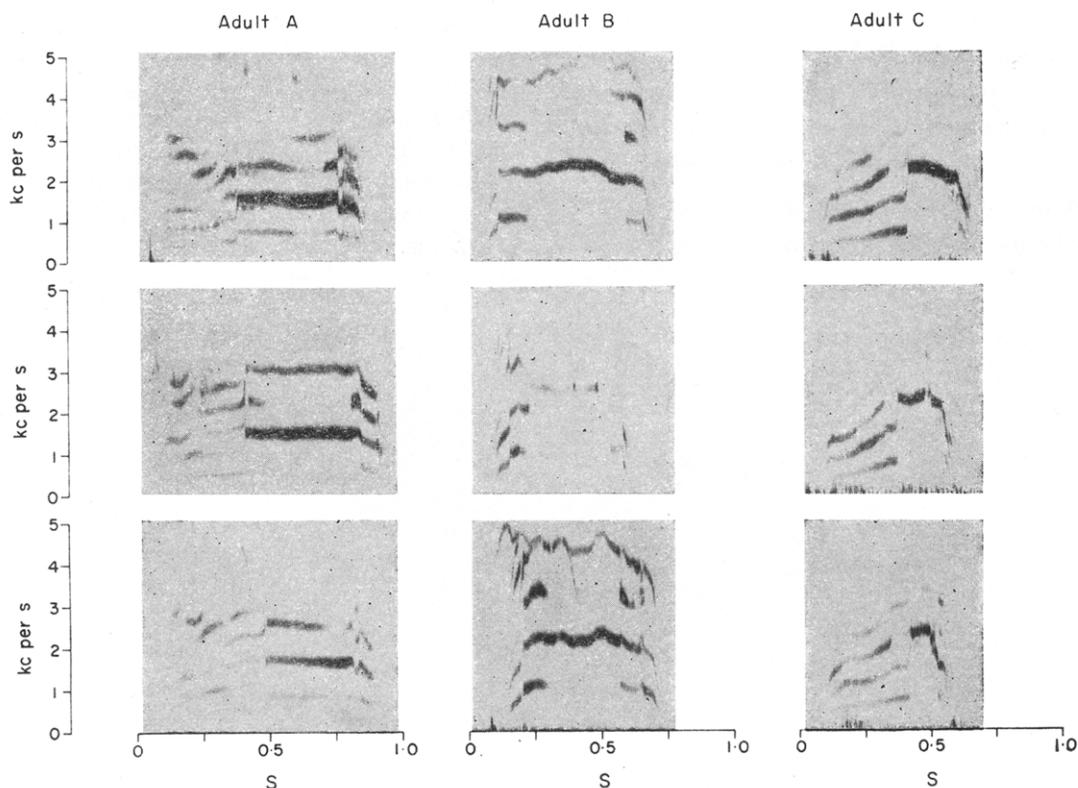


Fig. 3. Sound spectrograms of ring-billed gull mew calls, illustrating variations between (across) and within (down) individual birds. (Calls recorded on Uher Model 4000 Report; spectrograms made with a Kay Electric 'Missilyzer' Model 675. Settings: Low impedance input, AGC 30, Mark 7.5. wide band, flatshape, normal pattern.)

methods with situations present within the colony suggests further that a functional significance may be attributed to the observed differences in results. As long as at least one parent remains with the brood, simultaneous discriminations between the familiar parent and other adults are possible, and would presumably constitute an effective mechanism favouring selection of the parent by the chick. Should a chick become lost or stray from the family unit, however, a more or less indiscriminate responsiveness to other adults would presumably tend to favour the initiation of adoptions with foster parents until the time, if ever, that the biological parent was again available. Essentially indiscriminate responsiveness to individual adults,

in the absence of the parents, coupled with a high degree of selective responsiveness to one of the familiar parents when that choice situation exists, would thus seem potentially adaptive to the young of ground-nesting colonial species.

Indiscriminate adoption of stray chicks by adults would appear to be less favourable, in an evolutionary sense, to the foster parents, especially if an addition to their brood reduced the likelihood of survival or reproduction in their own offspring due to insufficient care or food (Lack 1954, 1966; but see also Vermeer 1963; Harris 1964; Harris & Plumb 1965). The well-documented tendency of adult gulls to attack and injure, often critically, strange young that trespass on their territories (e.g. Ward 1906;

Herrick 1912; Strong 1914; Kirkman 1937; Tinbergen 1953a; Emlen 1956), however, presumably functions to reduce the likelihood of such indiscriminate adoptions. These conflicting tendencies, of displaced chicks seeking adoption and the active repulsion of strange chicks by potential foster parents, may there-

fore provide at least a partial explanation for the maintenance of a relatively high degree of infanticide within colonies of ground-nesting gulls. If so, there would appear to be no compelling reason to invoke 'group-selection' (Wynne-Edwards 1962, pp. 484-5 and 530-41) as a necessary mechanism to account for the evolution and maintenance of this phenomenon.

VIII. APPROACH RESPONSES TO CHICKS

Of the various social stimuli received by young ring-billed gulls within the colony, it is probable that the most significant are those from the parents, which are the providers of food, shelter and protection, and which make possible the orderly development of the chick's integration with adult members of the species. The biological significance of stimuli from other chicks within the brood is less obvious. The almost constant proximity of siblings, however, indicates that whatever their function, such stimuli do at least form a major portion of the total input from social companions.

The following section describes observations and experiments that were designed to examine some of the stimuli and types of experience associated with approach responses to other chicks. Methods similar to those described in the previous section for responses to adults were used. Because chicks were used both as test subjects and as stimulus objects in the present section, experimental control of both test chicks and stimuli was more readily obtained than in the previously described experiments in which adults were used as test stimuli. For this reason, it was possible to study the effects of varying the amounts and timing of rearing experience with social companions more extensively in the present than in the previous section.

Stimulus Conditions Influencing Approach Responses

Approach responses to chicks were frequently observed in the apparent absence of vocalizations from the stimulus chick. These observations suggest that visual stimuli alone are sufficient to elicit approach responses between chicks, but do not rule out the further possibility that vocalizations from other chicks also elicit or facilitate such approaches. The relative effectiveness of visual and auditory stimuli from other chicks, and the effects of summation between these stimuli, were tested experimentally

by reducing the perceptual capacities of the chicks and by varying the external stimulus situation.

A. Effectiveness of Visual Stimuli

The hypothesis that visual stimuli are sufficient to elicit approach responses to other chicks was tested experimentally with ten chicks in which the hearing ability was seriously impaired (see Section VII, p. 211). Tests were conducted on the third day after hatching.

When released two at a time, 1 m apart on a smooth surface, all of the operated chicks aggregated, thus verifying that visual stimuli alone are sufficient to elicit approach responses to other chicks.

The further possibility that vocalizations may facilitate the rate of approach responses under normal conditions of visual input was tested by comparing approach latencies between the ten chicks with impaired hearing ability and fifteen, non-operated controls of the same age and rearing history. Pairs of chicks from each group were given a total of twelve tests per group, pairs being selected such that no two chicks were tested together more than once. Average approach latencies were 58 s for the chicks with impaired hearing, compared to only 27 s for the controls, a significant difference when tested by an unpaired *t*-test ($t=2.35$; $P<0.05$). The longer approach latencies between pairs of chicks having impaired hearing suggest that although visual stimuli are sufficient to elicit approach responses, they are less effective than visual and auditory stimuli combined.

B. Effectiveness of Auditory Stimuli

The effectiveness of chick distress calls (Moynihan 1959) in eliciting and orienting approach responses between chicks was tested under three conditions of visual input.

(1) **Vision unimpaired, stimulus chicks visible.** A rectangular earthen trough approximately 1 m

long was constructed and separated into three compartments by inserting fully transparent wire screens near each end. A stimulus chick was placed in each end compartment, and a test chick at the middle of the centre compartment. The presence or absence of vocalizations by the stimulus chicks were noted. Nine colony-reared chicks, ranging from $\frac{1}{2}$ to $4\frac{1}{2}$ days of age, were given a total of ninety-one tests.

Of the ninety-one tests given, neither stimulus chick vocalized in thirty-six tests (40 per cent), and both vocalized in ten tests (11 per cent). During the remaining forty-five tests, one of the stimulus chicks vocalized, the other did not. For these latter forty-five tests, test chicks approached the vocalizing chicks thirty-four times (76 per cent), a value significantly greater than that expected by chance ($\chi^2=11.76$, $P<0.001$). These results suggest that when chicks are visible, approach responses may be oriented by chick vocalizations.

(2) Vision unimpaired, no stimulus chick visible.

Two loud-speakers of similar visual and acoustical properties were placed approximately 2 m apart on flat ground, and chicks were placed singly at the midpoint between them. Vocalizations of a strange chick were played over one speaker for 2-min test periods, alternate speakers being used on successive tests. Twenty-seven colony-reared chicks, ranging in age from 2 to 3 days, were given a total of fifty-one tests in which one speaker was active, and thirty-nine control tests in which both speakers were silent.

Results of the above tests (Table 15) indicate no significant difference ($\chi^2=0.0018$; $P>0.95$) in the proportions of chicks that moved from the release point when chick vocalizations were emitted from one of the speakers (39 per cent) compared to when both speakers were silent (41 per cent). For the twenty chicks that did move when one speaker was active, eighteen (90 per cent) approached one or the other of the speakers, fourteen going towards the speaker emitting the chick vocalizations and four to the silent speaker.

Table 15. Effect of Chick Vocalizations in Eliciting and Orienting Approach Responses to a Loud-Speaker (Colony Reared Ring-Billed Gull Chicks at 2 to 3 days of age)

	Vocalizations from one of two speakers	Both speakers silent
No. of chicks that failed to move for 2 min	31	23
Chicks approaching active speaker	14	0
Chicks approaching silent speaker	4	7
Chicks leave release point but approach neither speaker	2	9
Total no. of chicks that leave release point	20	16
Total no. of tests	51	39

The results suggest that in the absence of visual stimuli from another chick, vocalizations had little effect in initiating locomotor responses, but did exert a slight influence on the orientation of the active chicks. Comparison with the results obtained when chicks were tested by this procedure but with adult mew calls (Table 11, not blindfolded) indicate that the adult calls were more effective in initiating approach responses than were the chick vocalizations (distress calls) used in the present section.

(3) Test chicks blindfolded. Chick vocalizations were played from one of two loud-speakers placed approximately 2 m apart as described in the above section. Fifteen blindfolded chicks (see Section VII, p. 212) were placed singly, midway between the two speakers and observed for the following 2 min. Fourteen (93 per cent) remained inactive, at the release point, for the duration of the 2-min test period; the single active chick approached the speaker that was emitting the chick vocalizations.

It is evident from the results that vocalizations were not usually sufficient, in themselves, to elicit approach responses in blindfolded chicks. As in (2) above, these results indicate

that chick vocalizations are less effective than adult mew calls (cf. Table II, blindfolded) in initiating oriented approach responses.

C. Variations in Stimulation

Observations of temporarily isolated chicks joining others in large aggregations that formed during extended periods of disturbance in the colonies late in the season suggested that approach tendencies were increased by stimulation from several chicks assembled together. This effect appeared to be less pronounced in densely-vegetated colonies where stimulus input was necessarily reduced by the cover between chicks. These hypotheses were tested experimentally by varying cover density and by comparing rates of approach between single and paired chicks.

In an area away from the nesting colony four test situations, each containing one of four different levels of vegetative density, were used to test the effect of reduced visual input on approach responses between colony-reared chicks. Fourteen chicks, ranging from 2 to 8 days of age, were released four at a time at points representing the corners of a square 10 m on a side marked out within each of the test areas. The number of chicks aggregating in a 5-min period following each release was recorded.

The proportions of chicks aggregating were greater in the more open situations (Table 16).

The large drop in aggregative responses due to the presence of only four clumps of vegetation demonstrates the effectiveness of even a small amount of cover in reducing aggregation. In this particular instance, it is probable that the reduced aggregative tendencies are attributable both to the reduction of visual input from other chicks and to the provision of hiding places. Reduction in stimulus input assumes more importance in explaining reductions in aggregations between the medium and dense cover areas, both of which contained an excess of potential hiding places.

The effect of enhanced stimulus input was examined by releasing a single chick at a point 1 m from where two others were simultaneously released, together. Records were kept of the times and identities of the chick(s) that first crossed a line drawn midway between the two release points. Thirty chicks of from 1 to 2 days of age were given thirty tests, each chick being tested once as a single and twice as a member of a different pair.

All three chicks remained at the release points until the end of the 2-min test period in one of the thirty tests. Single chicks were the first to cross the midline in twenty-three (77 per cent) of the tests, compared to six (20 per cent) first crossings by the pairs (Table 17), a result that differs significantly from random ($\chi^2=8.53$; $P<0.01$). The more rapid rate of approaches by single

Table 16. Measures of Ring-Billed Gull Aggregative Behaviour Under Different Degrees of Cover Density

	Cover condition			
	(1) Open limestone flat	(2) Four vegetation clumps, each 1 m from each release point	(3) Medium vegetative cover	(4) Dense vegetative cover
No. of tests in which all four chicks aggregated (no. tests given)	15 (17)	3 (12)	1 (14)	0 (10)
Proportion of groups aggregating (per cent)	88	25	7	0
No. of chicks aggregating with one or more others (no. chicks tested)	65 (68)	36 (48)	32 (56)	6 (40)
Proportion of chicks aggregating (per cent)	96	75	57	15

chicks is further indicated by the shorter average, median and lower range of times (Table 17) for those tests in which single chicks were first to cross the midline compared to those in which the pairs crossed first.

Table 17. Comparison of Approach Response Rates Between Pairs and Single Ring-Billed Gull Chicks Reared in the Colony as Broods of Three

	Single chick first to cross midline	Pair first to cross midline
No. of occasions	23	6
Average time (s)	28	45
Median time (s)	25	44
Range in time (s)	8-80	18-81

*Does not include one of the thirty tests, in which all of the chicks remained at the release sites for the duration of the 2-min test period.

Under the conditions of the above test it seems reasonable to assume that the pair would provide more visual stimuli than would the single chick. In addition, each member of the pair would presumably receive a greater range and intensity of stimuli from the other member of the pair than from the more distant single chick. If so, then the more rapid rate of approach by the single chicks may be taken as evidence that an increase in the number or intensity of stimuli from other chicks increases approach tendencies.

Effect of Early Social Experience

It is known from studies of aggregative behaviour in domestic chickens that approach responses in this species may be influenced by the extent of early exposure to other individuals (Pattie 1936; Guiton 1959; Baron & Kish 1960; additional examples reviewed in Sluckin 1965). The hypothesis that group-rearing experience is necessary for the normal maintenance of generalized approach responses to other chicks in ring-billed gulls was tested by varying the timing and extent of social exposure. The possibility that food reinforcement is necessary for the maintenance of these responses was tested by repeating essentially the same experi-

ment but with controlled feeding conditions in the laboratory.

A. Rearing Experience with Brood Mates in the Colony

As discussed by Lorenz (1965), it is not necessarily correct to assume that the development of behaviour in isolate-reared young ('Kaspar Hausers') is equivalent to that of individuals of the same age and species that develop under more natural conditions. As mentioned previously, in the present study an attempt was made wherever possible to avoid this type of distortion by using colony-reared chicks as experimental subjects in place of, or in addition to, chicks reared under controlled but necessarily artificial laboratory conditions. This procedure was considered especially applicable in experiments assessing the influence of early experience on approach responses to chicks.

The large number of nests present in the ring-billed gull colonies at Rogers City made it possible to rear a large experimental population consisting of many broods of one, thereby producing chicks that had the benefit of essentially normal social interactions with their parents, but which lacked intimate social experience with other chicks. The responses of these 'pseudo-isolate' chicks to other chicks were then compared with normal group-reared controls taken from broods of four. Because the presence of the parents in both the experimental and control broods ruled out the possibility of severe abnormalities arising due to a total lack of social interaction with conspecifics, it seems reasonable to assume that any differences found in the responses of the group-reared and 'isolate'-reared populations are attributable to differences in the extent or timing of their rearing experience with other chicks.

The occurrence of approach responses to other chicks was tested in colony-reared chicks having three different degrees of social experience with other chicks: (1) group-reared, as broods of four, (2) group-reared for one day before testing, otherwise reared as broods of one, and (3) 'pseudo-isolate', reared as broods

of one.

Experimental broods were set up as follows: On the day of hatching, 224 nests were set up with only one chick, the surplus eggs or chicks being removed to other nearby nests in the same stage of the breeding cycle. One hundred and eighty-eight chicks were placed in forty-seven other nests as broods of four. All broods were then left to be reared by the parents or foster parents until testing. After isolate-reared chicks were tested, they were set up as broods of from two to four, and then tested the following day. Social experience with other chicks was ensured for these latter groups by confining them around each nest by a wire fence.

For testing, chicks of a given age and treatment group were removed from the colony two at a time and released 1 m apart on an open flat area. After each release, records were kept of the number of chicks that aggregated during the subsequent 2 min. Since this measure of aggregation does not distinguish between differential responsiveness on the part of the two chicks tested, test pairs, rather than individuals, were used as the unit of comparison for statistical analyses. Sixty-six pairs from broods of four and fifty-nine from broods of one were tested at from 1 to 6 days of age.

The proportions of chicks approaching during the 2-min test periods are plotted against age, for each of the three experimental groups, in Fig. 4. At one day of age, group-reared chicks and 'pseudo-isolates' were essentially the same, indicating no effect attributable to rearing experience over the first day. On subsequent days, group-reared chicks consistently showed greater tendencies to aggregate. For all ages combined, group-reared chicks aggregated significantly more ($\chi^2=10.03$; $P<0.01$) than did those reared singly.

The middle curve in Fig. 4 illustrates the effect of one day of group-rearing experience preceding the test period for chicks that were previously reared singly. Up to 4 days of age the performance of these chicks was little different from group-reared chicks, and at 3

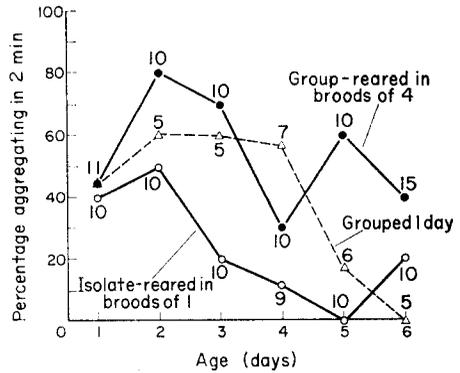


Fig. 4. Aggregative responses during the first 6 days of age in ring-billed gull chicks reared in nests in the colony under three different conditions of exposure to other chicks; 125 pairs given 153 tests. Figures=numbers of pairs tested.

and 4 days they showed a stronger tendency to approach than did isolates of the same age. This tendency was reversed at 5 and 6 days of age, when they responded at levels more like those of isolates than those of group-reared chicks.

Taken together, the data in Fig. 4 suggest that aggregative tendencies between chicks were present up to 1 or 2 days after hatching whether or not they had received prior intimate social experience with brood mates in the colony. On subsequent days, aggregative tendencies persisted in the group-reared chicks, but declined to low levels by 4 or 5 days of age in isolate-reared chicks. In addition, it can be tentatively concluded that group-rearing experience for one day resulted in the normal development of aggregative tendencies if such experience occurred prior to about 4 days of age, but had little if any measurable effect at later ages.

B. Group Rearing Independent of Social Feeding

In the experiments described above, all chicks were reared and hence fed by parents. It is thus possible that approach responses by group-reared chicks were maintained not because of social experience per se, but rather as a result of positive reinforcement obtained during feeding bouts, at which time chicks may peck small bits of food from the bills of brood mates

(Hailman 1961). The possibility that such food reinforcement was necessary to the maintenance of approach responses was tested by feeding both isolate and group-reared chicks singly, in the laboratory.

Pipped eggs were collected from the colony and hatched in the laboratory. Chicks were removed from the incubator within 12 hr after hatching and placed either singly or in groups of four in brooder boxes having opaque walls. An incandescent light was placed in each brooder box to provide light and heat. Starting at approximately 1 day after hatching, chicks were removed from the brooder boxes three times daily, placed individually in plain cardboard boxes and hand fed. As with the colony-reared chicks described in the preceding section, a portion of those initially reared in isolation were subsequently reared as groups of four for 1 day. A total of 127 different chicks were given 167 tests at ages ranging from 1 to 7 days. No chick was tested more than once on any one day.

The proportion of pairs that aggregated over a distance of 1 m during 2-min test periods are shown in Fig. 5. Group-reared chicks (top curve) showed a high level of aggregative tendencies from the first day; 95 per cent of these chicks aggregated for all tests combined. In contrast, chicks that were reared as singles reached a peak of 47 per cent on the second day, then declined rapidly thereafter. For all tests combined, they aggregated significantly less often than did the group-reared chicks ($\chi^2=61.25$; $P<0.001$). These results indicate the importance of social rearing experience in maintaining early approach responses between chicks and show, in addition, that reinforcement of these responses by food received during periods of social feeding, as when parents feed their brood in the colony, is unnecessary.

The middle curve in Fig. 5 provides further evidence that aggregative tendencies are enhanced by one day of social experience on the day prior to testing when this experience is received during the first 3 to 4 days after hatch-

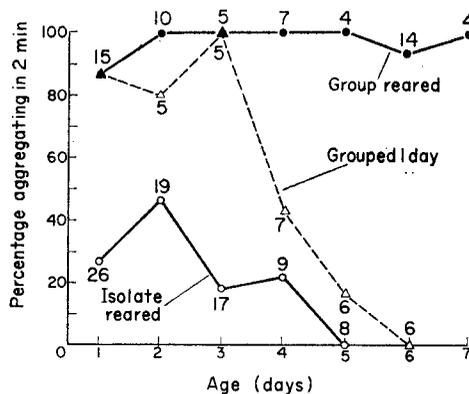


Fig. 5. Aggregative responses during the first week in ring-billed gull chicks reared in the laboratory under three different conditions of social exposure to other chicks, but fed in isolation; 127 chicks given 167 tests. Figures=numbers of pairs tested.

ing. Chicks that were group-reared up to one day of age aggregated significantly more than those reared singly ($\chi^2=11.30$; $P<0.001$). For those chicks that received 1 day of group-rearing experience before testing at 5 and 6 days, in contrast, aggregation dropped to 17 per cent and 0, respectively; at the end point (day 6) the proportion aggregating was significantly lower than for group-reared chicks ($P<0.001$, Fisher exact probability test, 2-tailed). The greater effect of 1 day of social experience when given before 3 to 4 days of age, along with the equivalent data obtained from chicks reared in the colony (Fig. 4), suggest the existence of an early critical period for the effect of social experience on the development of aggregative tendencies.

Approach Responses to Particular Individuals

Provided that early experience with other chicks occurs, as it normally does under natural conditions, it is possible that a further development of learned discriminations could lead to individual recognition of brood mates and hence to a greater degree of cohesion within the family unit. The demonstrated ability of chicks to recognize the mew calls of their own parents by 4 and 5 days of age (Section VII, p. 216) suggests further that individual recognition of brood mates, if present, may develop at a

relatively early age. This possibility was tested in three sets of experiments, two involving brood mates in the colony, and one involving rearing companions in the laboratory.

A. Preferential Responses to Brood Mates

One hundred and eighteen chicks reared in the colony as broods of four and tested for aggregative tendencies (Fig. 4, group reared) were tested for preferential approach responses to brood mates at from 1 to 6 days of age by placing two chicks from each of two different broods of the same age at four points representing the corners of a square 1 m on a side. Chicks were placed such that each chick had a brood mate at one adjacent point and a chick from a different brood at the other adjacent point. Records were kept of the identities of aggregating chicks. In those instances in which the brood mate and one of the strange chicks were approached at approximately the same time, so as to make a time distinction questionable, the responses were tabulated as a tie.

Of the 118 chicks tested, nineteen did not approach others, and could not be used as evidence for or against preferential responses to brood mates. For the remaining ninety-nine chicks, approaches to others usually occurred within the first minute after release. As suggested by the large number of chicks falling into the tie category (Table 18), the typical response, especially for the younger chicks, was to move towards the centre of the square, thus contacting a strange and familiar chick at approximately the same time. Excluding these ties, significantly more chicks first approached a familiar than a strange chick ($\chi^2=6.25$; $P<0.02$).

Additional tests in which responses were restricted to a choice between a strange and a familiar chick were conducted in the field, using the earthen trough, separated with a netting into three compartments, described previously. Two stimulus chicks, one from each of two different broods, were placed in the small end compartments. A test chick from one of the same broods was placed at the centre of the

Table 18. Frequency of Approach Responses to Brood Mates and Non-Brood Mates in Colony-Reared Ring-Billed Gull Chicks During the First 6 Days After Hatching

Chick age (days)	No. approaching (no. tested)	First approach made to:		
		Familiar chick	Unfamiliar chick	Tie
1	17 (20)	2	1	14
2	19 (20)	0	0	19
3	20 (20)	0	0	20
4	14 (19)	2	0	12
5	14 (19)	2	2	10
6	15 (20)	7	0	8
Totals	99 (118)	13	3	83

middle section, and records made of the stimulus chick it first approached. The end containing the brood mate was alternated between tests to rule out any place habit. Six chicks from four broods were given a total of forty-two tests at 3 and 4 days of age.

Table 19. Preferential Approach Responses to Brood Mates in Ring-Billed Gull Chicks

Age at test (days)	No. of tests	Approached familiar chick	Approached unfamiliar chick	<i>P</i>
3th	22	10	12	>0.50
4th	20	15	5	<0.05
Totals	42	25	17	

Results (Table 19) indicate that chicks at 3 days of age chose randomly but by 4 days the same chicks chose the brood mate significantly more than the strange chick ($\chi^2=5.0$; $P<0.05$).

B. Preferential Responses Independent of Social Feeding

Tests designed to rule out the possible effects of food reinforcement, received during periods of social feeding, were conducted in the laboratory. Thirty chicks, hatched in the laboratory, were reared as pairs in plywood cages measuring $0.61 \times 0.38 \times 0.30$ m high, and tested at $4\frac{1}{2}$ ($\pm\frac{1}{2}$) days of age. Chicks were fed singly, in plain

cardboard boxes, three times daily. During such feedings, members of each foster pair were separated by another feeding box containing a strange chick to reduce the likelihood of auditory conditioning to the rearing companion at that time.

Tests were conducted in automatically recording tip-floor cages constructed from plywood according to the general plan described (Gray 1960). Cage dimensions were $1.22 + 0.38 \times 0.30$ high. Compartments 0.30 m in length were separated off with wire screen at each end of the cage and provided with separate, firmly secured floors. The centre compartment was fitted with a floor, balanced in the middle such that it would tip down when weight was applied on either side; microswitches were installed and set to close an electrical circuit when the floor was tipped down on one end and to break the circuit when the floor was tipped down on the other end. Each microswitch was then wired to an individual channel of an Esterline Angus recorder. The recorder was set to run at 3 in. per min, thus providing a continuous record, accurate to the nearest second, showing which half of the cage was being occupied during a given test period.

Immediately before each test, two stimulus chicks, one from each of two pairs, were placed singly in opposite end compartments of the test cage. One of the remaining chicks (the test chick) from one of the same two pairs was placed under a beaker, approximately 5 cm from the centre of the central compartment, towards the strange chick. The lights were turned off, the beaker removed, then the lights and recording instrument were turned on simultaneously and allowed to run for 2 hr.

Placement of the test chick in the half of the pen away from its familiar rearing companion may have produced a slight bias towards negative results; this procedure was nevertheless followed because it removed the possibility of the opposite bias that could have resulted if inactive chicks

were inadvertently released towards the other side, thus producing a spurious positive record. This procedure also provided a latency measure of the time taken by each test chick to make its first crossing into the half of the pen containing the familiar chick.

Possible biases due to direction were reduced by leaving the stimulus chicks unchanged while the alternative test chick was tested. Positive responses thus required the test chick in the second test to approach the opposite chick to that of the chick in the first test. Stimulus chicks were not subsequently used as test chicks, hence each two pairs provided data for only two test chicks.

Table 20. Preference for Approaching Foster Sibling rather than Stranger by Laboratory-Reared Ring-Billed Gull Chicks Tested at $4\frac{1}{2}$ Days of Age (N =fifteen chicks)

	Minutes	Per cent
Average response latency	4.6	
Average time on side nearest familiar sib*		
First hour	37.5	63
Second hour	50.2	83
Combined	87.7	73
Range		1-99

*A significant proportion (13/15) of the chicks spent over half of the test period on the side nearest their familiar foster sibling ($\chi^2=8.07$; $P<0.01$).

The average time spent on the half of the pen containing the foster brother was 73 per cent for all fifteen test chicks combined (Table 20). Thirteen of the fifteen test chicks spent over half of the 2-hr test periods on the side of the cage containing the foster brother (Table 20). This proportion, which differs significantly from random ($\chi^2=8.07$; $P<0.01$) indicates the presence of a preferential tendency for these $4\frac{1}{2}$ -day-old chicks to approach and remain near their familiar rearing companions, even in the absence of prior food reinforcement received during social feeding.

IX. APPROACH RESPONSES TO MOVING INANIMATE OBJECTS

The demonstration of a critical period for the development of aggregative tendencies, coupled with the virtual independence of this development from food reinforcement (see Section VIII, p. 223), suggests fundamental similarities to 'imprinting' as it occurs in precocial species of galliform and anseriform birds (Lorenz 1935, 1937; Sluckin 1965; Bateson 1966). Two additional characteristics of approach responses commonly associated with imprinting were examined: (1) initial approach responses to strange objects and subsequent withdrawal from strange objects as the chicks grow older (see Hess 1959b), and (2) the development of discriminations such that when given a choice, chicks approach an object that has become familiar through experience with it in preference to a strange object (see Klopfer & Hailman 1964).

Initial Responses to Strange Objects

In the black-headed gull, Kirkman (1937) reported that a young colony-reared chick 'struggled across the nest to my clapping hands' and that another 'moved out three times towards an active notebook . . .' (p. 174) (see also Impekoven 1969). Although Kirkman interpreted these responses as hunger reactions, they are suggestive of the approach responses to strange objects that are typical of young precocial chicks. When 12 to 24 hr old, black-headed gull chicks began to show 'incipient escape or flight reactions' (Kirkman 1937) to the hand or other strange objects, and by the fourth to seventh day withdrawal and fleeing responses were well developed (1937, p. 178).

While handling young ring-billed gull chicks during the first few days after hatching, I have observed approach and withdrawal responses to my hand similar to those described above for black-headed gull chicks. To obtain more systematic data on these responses, young chicks up to 3 days of age were removed from the colony, placed on a flat surface, and their

responses to my hand, when moved to and fro directly in front of them, were recorded. Fifteen chicks were given a total of sixty-three tests. The proportion of chicks that approached declined rapidly with increasing age from a high of 92 per cent during the first day of age to 9 per cent on the third day.

The above observations suggest that young gull chicks tend to approach strange objects and that this tendency declines rapidly after the first day. This tentative conclusion was tested further by presenting a strange inanimate stimulus object to an additional population of colony-reared chicks at ages ranging up to 6 days.

Two hundred and twenty-seven chicks reared in the colony as broods of one or four were taken from the population of 250 colony-reared chicks that was used in the previously described aggregation experiments (Fig. 4 and Table 18). The effect of the prior testing were assessed by testing half of the chicks for aggregative responses and then with the inanimate stimulus used in the present experiment; half were tested in reverse order. Response frequencies analysed according to test order showed no significant effects on either aggregation or on response to the strange inanimate object that could be attributed to prior testing.

The stimulus object consisted of a metal square 12.7 cm on a side, painted in a checkered pattern with black and white squares 2.5 cm on a side. Chicks of known age were removed from the vicinity of the colony and placed on the ground directly in front of the stimulus object which was held stationary, in a vertical position, with the aid of a handle attached to its back side. The object was then slowly moved away from the chicks, and tipped from side to side to provide additional movement. The stimulus object was moved over a distance of approximately $\frac{1}{2}$ m alternately away from and towards the chick until the chick either ap-

proached or withdrew. Tests were terminated and the chick classed as a non-responder if no approach or withdrawal responses were elicited within two minutes. The presence or absence of chick vocalizations during the test period was also recorded.

Response frequencies did not differ significantly between chicks reared as broods of four and those reared as broods of one, hence the data from both rearing conditions were pooled for analysis of effects due to test age. The proportions of non-responding chicks and the proportions responding with either approach or withdrawal responses are plotted in Fig. 6. Non-responders made up approximately 20 to 30 per cent of the chicks at 1 and 2 days of age, but only 2 and 6 per cent at 3 and 4 days, respectively; all chicks responded by 5 and 6 days of age. The proportions showing approach responses exhibited the same general trend as that seen in the experiments with the hand, going from a high of 78 per cent approaching at 1 day of age to only 8 per cent at 4 days and nil at 5 days of age. The withdrawal responses showed the opposite trend, going from a low of 5 per cent at 1 day up to 100 per cent by 5 and 6 days of age.

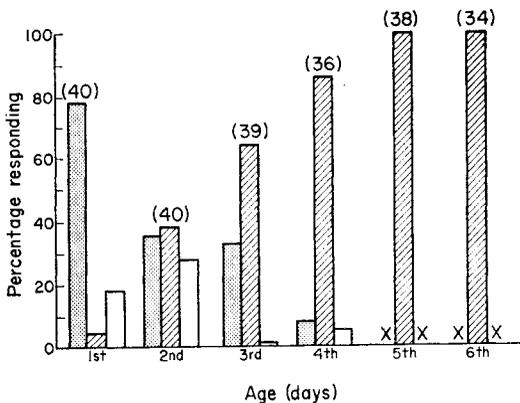


Fig. 6. Proportions of colony-reared ring-billed gull chicks approaching (stippled columns) or withdrawing (hatched columns) from a strange inanimate stimulus object over the first 6 days of age. Open columns=no approach or withdrawal. Figures=numbers of chicks tested at each age.

Chick vocalizations when in the presence of the strange inanimate stimulus were frequent at 1 day of age (70 per cent), but declined thereafter, reaching nil or almost negligible levels by 5 days (Fig. 7). Vocalization frequencies were greatest for the chicks reared as broods of four, at least up until 4 days of age, but these differences due to rearing conditions were not significant ($\chi^2=1.51$; $0.30 > P > 0.20$).

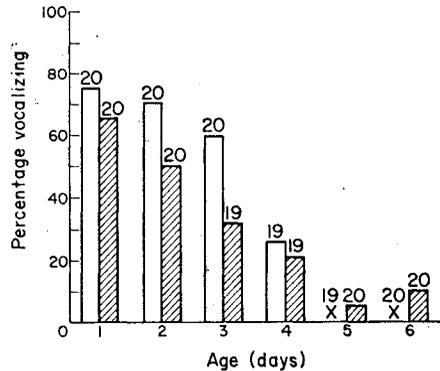


Fig. 7. Percentage of ring-billed gull chicks emitting vocalizations in the presence of a strange inanimate stimulus object. Chicks were reared in the colony as broods of 1 (open columns) or 4 (hatched columns), and tested once each, away from the colony, at ages ranging from 1 to 6 days. Figures=number of chicks tested.

Comparison between Figs 6 and 7 indicate a close, but inverse, correlation between the frequencies of withdrawal responses and vocalizations over the age range tested. This inverse relationship between withdrawal responses and vocalizations is apparently opposite in sign to that obtained for some precocial species tested in the laboratory (Hess 1959a; Hess & Schaefer 1959; Schaller & Emlen 1962; Collias 1962). It is possible that this difference may reflect a true divergence between these species, but it seems equally probable that they may be in part a result of differences in the social or other experience received in the natural, as opposed to the laboratory, rearing situations. It would seem unlikely, for example, that young Galliformes reared by their parents in nature would respond to a strange stimulus, e.g. a predator, by emitting vocalizations. This latter inter-

pretation is consistent with observations that when a human 'predator' approaches natural broods of young sharp-tailed grouse (*Pedioecetes phasianellus*), for example, the chicks typically flee, and remain silent for at least several minutes. When the disturbing stimulus is no longer present, vocalizations may be emitted by the chicks, as well as by the mother, as the brood reassembles (personal observations).

Selection of Familiar Objects

The development of preferential responses by young ring-billed gulls to familiar inanimate objects was studied in the laboratory. Domestic white leghorn chicks were also tested to provide comparable data for a precocial species (cf. also McBride et al. 1969).

Rearing and testing of experimental chicks were done in the automatically recording tip-floor plywood cages, described in Section VIII (p. 226) modified by fitting each cage with a single floor, hinged at the middle, and extending over the entire 1.22 m length of the cage. During the rearing period, cages were divided into two equal compartments with temporary opaque screens.

Stimulus objects used to test for discrimination were constructed from cylinders (tin cans) of two different sizes, painted with one of two different patterns and colours (Table 21). Each object was suspended on a flexible shaft from a support placed across the width of the top of the cage, 0.30 m in from either end (see note to Fig. 8). The top of each flexible shaft was attached by a system of levers to an eccentric

shaft that revolved once each 2 s, causing the stimulus objects to rotate, alternately clockwise then counter-clockwise, through an angle of approximately 30°. It was assumed that with this alternating circular motion, the patterns on the cylindrical stimulus objects would provide a stimulus situation capable of producing essentially continuous visual flicker, a stimulus property known to be effective in inducing initial approach and subsequent discriminatory responses (James 1959; Smith 1960; Smith & Hoyes 1961).

Four cages, each equipped with two stimulus objects that differed in size, pattern and colour, were arranged according to the floor plan shown in Fig. 8. To provide continuous light and heat, incandescent light bulbs were placed midway between the shafts containing the stimulus objects and the cage ends. The temperature at floor level under the lights was held at approximately 35°C for domestic chicks and 32°C for gull chicks.

Fourteen ring-billed gull chicks and twenty domestic chicks were hatched in the laboratory, removed from the incubator within 12 hr after hatching, and placed singly in the rearing cages. Domestic chicks were reared without food or water; gull chicks were removed three times daily, for periods of approximately 5 min each, and fed singly in plain brown cardboard boxes. Except for these periods of feeding, all chicks were allowed continuous access to their moving stimulus objects throughout the rearing period, which extended until the chicks were tested at

Table 21. Specifications of Cylindrical Stimulus Objects (Painted Tin Cans) used in Chick Discrimination Tests

Description	Size		Patterns	Colours
	Height	Diameter		
Large cylinders	10.8 cm	11.1 cm	0.3 cm diagonal stripes, 2.54 cm apart	Eberhard Faber felt markers, 680 blue or 680 green over white paper
Small cylinders	9.8 cm	5.4 cm	0.6 × 1.6 cm vertical rectangles, vertical separation 0.6 cm, horizontal separation 1.9 cm	'Testor's' no. 11 blue or no. 24 green, over white enamel base

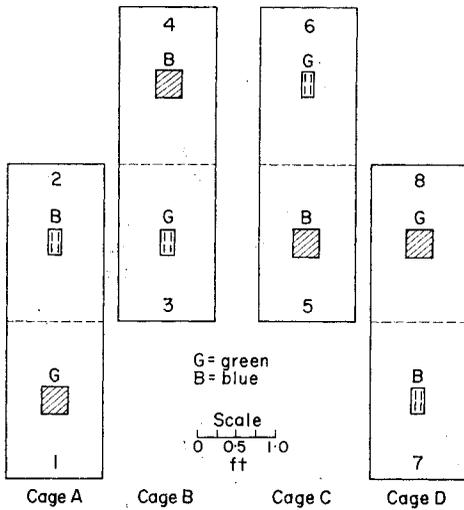


Fig. 8. Floor plan arrangement of cages and stimulus objects used to test discrimination responses in domestic and ring-billed gull chicks. The stimulus cylinders were suspended with their axes vertical, 0.3 m from a side wall and with their bases about 1 cm above the cage floor.

3½ (±¼) days of age.

Prior to each set of tests, the motion in the stimulus objects was stopped, and the chicks from each cage were removed and held singly, in temporary holding pens. At this time, the opaque screens were removed from the centre of the cages, and a 100-W incandescent bulb

was placed at the centre of each cage to provide additional illumination. Wire netting screens with 0.65 cm mesh were inserted approximately 2.5 cm in from each stimulus object, thus producing a central test chamber approximately 0.6 m long from which the test chicks could see and approach, but not reach, the stimulus objects.

Four chicks, one from each of the four rearing conditions, were selected for each test run. To reduce the probability that chicks might respond to directional cues in the room, chicks were tested in different cages from those in which they were reared. For example, the chick reared in compartment A1 (Fig. 8) was tested in cage D, which was equipped with stimulus objects having the same colours, sizes and patterns as cage A, but oriented in the opposite direction. Test chicks were released from under a glass beaker as described above in Section VIII except that after removal of the beakers the stimulus objects were set moving before the lights and recorder were turned on.

Results of the discrimination tests, tabulated according to the proportion of times spent on the half of the test cage containing the familiar stimulus objects, are listed in Tables 22 and 23

Table 22. Approach Responses to Familiar Rearing Objects in 3½-Day-Old Domestic Chicks

Rearing stimulus	No. tested	Selected familiar object	Latency average (min)	Min in half of pen nearest familiar object				
				1st hour	2nd hour	Sum 2 hr	Per cent	Range (per cent)
Large green	5	4	2.52	36.48	44.33	80.81	68	49-88
Large blue	5	4	1.87	41.68	41.23	82.91	69	15-98
Small green	5	5	1.18	52.36	50.61	102.97	86	72-99
Small blue	5	5	2.37	50.53	49.52	100.05	83	63-97
Totals	20*	18*						
Average			1.98	45.26	46.42	91.68		
				75%	77%		77	15-99
Overall per cent of time spent in half of pen nearer these objects:			Large familiar objects	= 68%			Small familiar objects	= 85%
			Blue familiar objects	= 76%			Green familiar objects	= 77%

*18/20 selected the familiar object for over 50 per cent of the total 2-hr test period ($\chi^2 = 12.8$; $P < 0.001$).

Table 23. Approach Responses to Familiar Rearing Objects in 3½-Day-Old Ring-Billed Gull Chicks

Rearing stimulus	No. tested	Selected familiar object	Latency average (min)	Min in half of pen nearest familiar object				
				1st hour	2nd hour	Sum 2 hr	Per cent	Range (per cent)
Large green	3	3	3.75	45.27	53.58	98.85	82	71-99
Large blue	4	4	1.80	45.72	58.70	104.42	87	80-98
Small green	4	3	6.43	44.45	58.25	102.70	86	49-98
Small blue	3	3	7.97	51.68	59.92	111.60	93	83-98
Totals	14*	13*						
Average			4.99	46.78	57.61	104.39		
				78%	97%		87	49-99
Overall per cent of time spent in half of pen nearer these objects:			Large familiar objects = 85%	Small familiar objects = 89%				
			Blue familiar objects = 90%	Green familiar objects = 84%				

*13/14 selected the familiar object for over 50 per cent of the total 2-hr test period ($\chi^2 = 10.29$; $P < 0.01$).

for each of the four types of stimuli used. For domestic chicks (Table 22), the half of the cage containing the familiar stimulus object was selected 77 per cent of the time for all chicks combined, and for over half of the 2-hr test periods by eighteen of the twenty chicks. The high proportion of chicks selecting their familiar stimulus object for over 50 per cent of the time differs significantly from random ($\chi^2 = 12.8$; $P < 0.001$). These results may be taken as evidence, first, that the test procedure was adequate to demonstrate discrimination between the familiar and strange stimulus objects and second, that these chicks exhibited a preferential tendency to approach and remain closer to the familiar objects.

Differences between the first and second test hours were not significant for domestic chicks, nor were there any systematic differences between chicks reared with blue and those with green objects. Small objects were selected 85 per cent of the time by chicks reared with them, whereas the corresponding selection of large familiar objects was only 68 per cent (Table 22). The differences due to large compared to small objects were further analysed by making comparisons for each test hour be-

tween pairs of chicks from the same test run that were reared with objects of the same colour but of different sizes. In sixteen of the twenty paired comparisons, more time was spent before the familiar objects by chicks reared with small, as opposed to those reared with large, stimulus objects ($\chi^2 = 7.2$; $P < 0.01$).

In ring-billed gulls (Table 23), thirteen of the fourteen chicks tested spent over half of the test period on the side of the cage containing their familiar stimulus object; the remaining chick spent 49 per cent of the time next to the familiar object. As in domestic chicks, the number of gull chicks selecting the familiar objects differed significantly from random ($\chi^2 = 10.29$; $P < 0.01$). In contrast to domestic chicks, all but one of the gulls showed an increase in the time spent near the familiar object in the second, as opposed to the first, test hour. Gull chicks exhibited no systematic differences due to size or colour pattern of the stimulus objects.

Comparisons between Tables 22 and 23 show that the latencies for initial approaches to familiar objects were longer in gulls than in domestic chicks. Despite the longer latencies, however, gull chicks spent more time (87 per cent) than

did domestic chicks (77 per cent) on the half of the cage containing their familiar stimulus objects. The high proportion of ring-billed gull chicks that selected their familiar object, coupled with the high proportion of time spent close to that object, demonstrate fairly conclusively that the young of this species are

similar to the young of typical precocial species in that they are able to learn the discriminations necessary to select familiar visual stimuli at an early age and are able to do this in the absence of prior feeding bouts associated with the stimulus object.

X. DISCUSSION

Developmental Relationships Between Mobility and Approach Responses

The mobility of young ring-billed gulls and the approach responses and discriminations associated with such mobility were found to undergo a progressive and interrelated development over the first week of age. These relationships are summarized below, first in the form of a chronological integration of the various experimental and observational data obtained in the present study, followed by a more detailed consideration of developmental stages in the ontogeny of mobility and associated behaviour in ring-billed gulls.

A. Chronological Summary

On the day of hatching no excursions or feedings away from the nest were observed (Table 3), and chicks did not move away from their nests even during periods of acute disturbance (Table 6). A strong tendency to approach indiscriminately a wide range of stimuli, including adult gulls, recorded mew calls (Section VII), gull chicks (Section VIII), or moving inanimate objects (Section IX) was also in evidence during the first day. The initial restriction of chicks to the nest despite the early development of generalized approach tendencies appeared to be due primarily to the almost continuous presence of the parents at the nest (Table 3), coupled with the relatively undeveloped locomotor ability of the chicks at this time (Table 2).

On the second day of age, excursions from the nest in response to the calling and leading of the parents were observed in a small proportion (10 per cent) of the broods. Over the next 4 days, excursions became more frequent, and the distances moved from the nest progressively greater. Concurrently, brooding by the adults declined (Table 3) and locomotor ability of the chicks increased.

Coinciding with this stage of increased brood mobility, there was a narrowing in the range

of stimuli that elicited approach responses to those particular classes, whether adults, chicks, or inanimate objects, with which the chicks had received prior rearing experience (Sections VII, VIII and IX). In the absence of experience with these objects, approach responses to them declined steadily over the first 3 to 4 days after hatching. This age range during which a young bird approaches strange moving objects has been called the 'sensitive period' in precocial species (e.g. Fabricius 1951, 1964). When early rearing experience with adults and chicks was provided, approach responses to these objects were maintained (Table 10; Figs 4 and 5) even in the absence of reinforcement derived from feeding. Preferential responses to familiar as opposed to strange inanimate objects also occurred (Table 23). Aggregative responses in chicks that experienced only 1 day of group-rearing experience immediately prior to testing declined when this experience was received after 4 or 5 days of age (Figs 4 and 5), suggesting that there is an early critical period for the effectiveness of such experience.

The early restriction in the range of effective stimuli to classes of familiar objects such as adults or chicks apparently ensures the normal development and maintenance of approach responses to social companions of the species. During excursions of broods within a congested gull colony (Fig. 1), however, chicks after the first day of age are exposed to stimuli from many neighbouring birds, yet rarely approach them under normal undisturbed conditions. Several results obtained with experimental chicks (Sections VII and VIII) suggest that the tendency to restrict approach responses to parents and brood mates at this early stage is related to the intensity of stimulation received from them. Reduced stimulation due to impairment of hearing (Table 10) or to various degrees of visual restriction (Tables 11 and 15) decreased approach responses. Similarly, the presence of cover, a condition common within the colony, reduced

approach tendencies to other chicks (Table 16), while the enhanced stimulation produced by two stimulus chicks, compared to one, increased approach tendencies (Table 17). The effect of intensity of a stimulus was also indicated by the more rapid rate of approach responses to closer and hence louder mew calls (Table 12). These results, coupled with an attenuation of adult calls with distance (Section VII), suggest that the early restriction of approach responses to parents and brood mates is due primarily to their proximity. The effectiveness of such proximity during temporary excursions away from the nest is presumably enhanced by the tendency of parents to avoid their nearest neighbours at that time.

During periods of acute disturbance, the alarm flights of the adults and the movements of older chicks to hiding places (Section V) cause abrupt disruption of the family units. The relatively short distances moved by young chicks under these conditions (Table 6) and their demonstrated ability to learn to go to specific hiding places (Table 7), however, protect against the occurrence of uncontrolled dispersal. The reunion of broods after an acute disturbance may at times be facilitated by a tendency of chicks to return to their familiar nest or rearing area (Goethe 1937, pp. 76–8). The limited experimental evidence that was obtained for preference for a familiar area in the present study (Table 9), however, and the observation that apparently normal patterns of chick movements were maintained when broods moved to new areas within the colony (Table 4), suggest that such selection plays only a minor role in brood localization and cohesion, at least during the first 4 to 5 days after hatching.

By 4 and 5 days of age, the beginnings of individual recognition of parents and brood mates provides an important new mechanism for uniting broods after disturbance and for maintaining family units during movements in and from the colony. For adult responses in several species of Laridae, Davies & Carrick (1962) have noted that the time at which parents

recognize their own chicks is more or less coincident with the age at which extensive brood movements begin. In the present study, the development of preferential responses to parental as opposed to non-parental mew calls (Table 14, Fig. 3) and to siblings as opposed to other chicks (Tables 19 and 20) coincided with an increase of extended mobility in the form of emigrations from the nesting area (Table 5), indicating that for ring-billed gulls, there is a correlation between extended brood mobility and the ability to individually recognize other chicks as well as the parents. A similar recognition of and preferential responses to parents and siblings thus develop sufficiently early in these species to be of importance in controlling approach responses and maintaining the brood as a unit after the onset of extended movements away from the nest site.

B. Developmental Stages

The preceding chronological summary serves to point out the close temporal relationships that were found between the extent of brood mobility and the degree of differential responsiveness to various stimuli. For each of these developmental sequences it is possible to delineate at least three functionally relevant stages, each of which is closely correlated in time of onset and duration with the equivalent stage of the other sequence.

Although not widely used as an aid to classification and description of behaviour, developmental stages have been advanced previously for both mammals (Williams & Scott 1953) and birds (Nice 1943, p. 57) including precocial species (Nice 1962), and require no particular justification provided they are interpreted with caution, without typological rigidity (cf. Mayr 1968), and in full awareness 'that there is nothing rigid about these stages; the change from one to the next is often gradual. . .' (Nice 1962, p. 34).

When developmental stages are used as categories of classification defined by behavioural criteria, it is apparent that they do not

necessarily reflect equivalent stages in the physiological or casual mechanisms mediating the measured stimuli and responses. There thus would appear to be no a priori reasons to assume that the timing of the developmental stages of mobility and of differential responsiveness to different stimuli should necessarily be correlated with each other, or that they should be identical in species having widely different developmental rates or in those adapted to different ecological situations. For this reason, and to avoid any implications of a necessary temporal correlation, the three stages listed below are defined only in terms of mobility, leaving open the delineation and comparison of the associated developmental stages in approach responses and discriminations. Although the three stages could be equally well defined within either sequence, mobility was selected on the grounds of functional priority, i.e. it seems reasonable to expect that if any significant degree of mobility is present in ground-nesting species, survival of young chicks would be greatly enhanced by, or perhaps dependent upon, an ability to discriminate and respond differentially to predators and parents, sibs and parents, perhaps parents and other adults, and so on (cf. Bateson 1966).

The three successive stages in the development of mobility in ring-billed gulls can be characterized as follows:

I. Incipient mobility. Starting at the time of hatching and extending on through the first day, grading into Stage II on the second, third and fourth days. Characterized by chicks remaining in or on the edge of the nest. Feeding occurs at the nest, and chicks crouch without running from the nest when alarmed.

II. Restricted mobility. Starting on the second day and extending through the third day, grading into Stage III by the fourth and fifth day. Characterized by the onset of excursions, away from and back to the nest. Mobility restricted to the vicinity of the nest site. Parents may lead chicks away from the nest temporarily

for feeding, and chicks typically flee from the nest and crouch or hide nearby when alarmed.

III. Extended mobility. Starting on the fourth day, and increasing thereafter. Termination was not clearly defined by the present study, but tentatively may be set at the time of fledging. Characterized by the onset of permanent emigrations away from the vicinity of the nest site to other areas within or close to the colony. Emigrating broods are typically led away by their parents, and chicks may flee from the territory or colony when alarmed.

Except for differences in defining criteria, the above stages of mobility are in close agreement with the mobility aspects of the developmental stages recognized by Nice (1962). Her first three stages are characterized as 'a period of immobility' (Nice 1962, p. 32), the equivalent of the single stage of incipient mobility described above. Similarly, Stages IV and V of Nice, which are characterized, respectively as 'a period of relative mobility' and a period of 'full activity' would appear to be equivalent to the stages of restricted mobility and extended mobility of the present study. The similarity is further illustrated by the statement that 'semi-precocial birds pass (the stage of relative mobility) largely in or near the nest.' (Nice 1962, pp. 33-4; compare with Stage II, above). Similarities between the perceptual aspects of the developmental stages proposed by Nice and those observed in the present study are considered below.

As discussed by Hinde (1966, pp. 363-4), the early development of approach responses and discriminations in precocial birds is typically characterized by a progressive narrowing in the range of effective eliciting stimuli. For species in which imprinting occurs, there is typically a rather wide, but not entirely unrestricted, range of visual and auditory stimuli that are effective when presented for the first time and at an early age (Hinde 1966; Thorpe 1963, p. 130). With increasing age and experience, responses become more restricted or oriented preferentially,

first to familiar classes of stimuli, whether adults, other chicks, or inanimate objects, to which the chick has become imprinted (Hinde 1966) and eventually to particular members of the species (Bateson 1966).

Results obtained in the present study indicate that a similar progressive restriction in the effectiveness of eliciting stimuli develops over the first 4 to 5 days of age in ring-billed gull chicks. As in precocial species, this developmental progression in young gulls falls into three operationally distinct levels, starting with a more or less general responsiveness to a wide range of stimuli, followed by what may be called 'species recognition' (Lorenz 1937; Dilger & Johnsgard 1959) and, lastly, 'individual recognition' (Ramsay 1951; Collias 1952; Bateson 1966). The times at which these three levels emerge in the development of young ring-billed gulls are closely correlated with the previously described stages of mobility. These developmental correlations are listed in Table 24.

It is evident from an examination of Table 24 that the developmental sequence associated with the progressive narrowing in the range of effective stimuli can be described in different ways, and that consistency between stages is not always in evidence. For example although 'species recognition' and 'individual recognition' provide consistent descriptive terms for Stages II and III respectively, there is apparently no commonly used equivalent for Stage I, which is unsatisfactorily referred to in Table 24, as 'innate propensity' to respond to a wide range

of stimuli (cf. Thorpe's discussion of imprinting, 1963, pp. 128-31). Usage of the second series of descriptions listed in Table 24, which are described in terms of preferential approach responses to the various stimuli or classes of stimuli (after Hinde 1966, pp. 359-74) seems to provide a more adequate conceptual base.

According to Nice (1962, p. 165), discriminations at the species level develop in most altricial bird species at about the same behavioural stage as in precocial species, i.e. at the end of her Stage III (Nice 1943, 1962). The perceptual aspects of the stages I through III proposed by Nice therefore appear to be equivalent to Stage I of the present study (Table 24). Although less clear, it is probable that the perceptual aspects of development are also similar for the later stages. The major criterion separating Stages IV and V of Nice (1962, p. 34) is the onset of aggression, which was often first directed at strangers (Nice 1962, pp. 124 and 138). The importance of recognizing strange conspecific individuals as such in aggressive acts has been implied for a wide variety of animal species including birds (Lorenz 1964), hence the criterion utilized by Nice is not inconsistent with the criterion of 'individual recognition' used to differentiate between Stages II and III in Table 24 above.

Imprinting in Semi-Precocial Gulls

Several results obtained in the present study suggest close similarities between the development of stimulus-specific approach responses in young gulls and the phenomenon of imprint-

Table 24. Temporal Relationships Between Developmental Stages of Mobility and the Progressive Restriction in Range of Stimuli Effective in Eliciting Approach Responses in Young Ring-Billed Gulls

Developmental stage	Stimulus-response correlates of developmental stages	
	Recognition	Approach-responses
Stage I: incipient mobility	'Innate propensity' to respond to a wide range of stimuli	To a wide range of initially effective stimuli
Stage II: restricted mobility	Species recognition	To particular classes of familiar stimuli
Stage III: extended mobility	Individual recognition	To stimuli associated with particular familiar individuals

ing in precocial species. A progressive narrowing in the range of stimuli effective in eliciting approach responses, as discussed in the preceding section for ring-billed gulls, suggests one such similarity (cf. Sluckin 1965; Hinde 1966; Bateson 1966). As discussed below, a reduced role of conventional reinforcers, coupled with the occurrence of sensitive and critical periods in the development of ring-billed gulls, are indicative of further similarities.

A. Reinforcement

Food. The experimental studies of approach responses (Sections VII, VIII and IX) suggest that many discriminations, including those equivalent to recognition at the species level as well as those sufficiently exact to permit individual recognition, can develop at an early age and in the absence of food reinforcement. These results confirm similar findings with typical precocial species in which the parents do not feed their young (Sluckin 1965; Bateson 1966) and also with those species such as the coot (*Fulica atra*) (Alley & Boyd 1950; Hinde, Thorpe & Vince 1956) which resemble the Laridae in that the young are fed by their parents (Nice 1962).

Many of the experiments that led to the conclusion that reinforcement received during feeding bouts is not essential to the development of discrimination in young ring-billed gulls do not rule out possible effects of food received incidentally, as from the feathers or the base of the bill of brood mates, or from regurgitations (cf. Hailman 1967). Instances in which food was obtained in this manner in the laboratory were rarely observed, but cannot be ruled out. The experiments with bill-taped chicks reared by their parents in the colony thus assume particular significance, as they provide the required degree of control in that the bills of the chicks were sealed at all times except for the brief periods when the chicks were fed by hand in a box away from the colony.

Although food reinforcement was found to be unnecessary for the early development of

discriminations and preferential responses in young ring-billed gulls, the results obtained do not rule out the possibility that food reinforcement, when present, may enhance the development of such discriminations. Of particular relevance are the recent studies of Hailman (1967) in which it was found that the pecking rate of herring gull chicks at models of herring gulls and laughing gulls was increased when chicks received prior training in which pecking at the models was followed by food reinforcement. Controls, which had no previous food reinforced training with the models, pecked at a significantly lower rate when presented with the same models in the test situation. Comparison, between the two trained groups showed, further that a greater number of pecks were delivered at the familiar, reinforced model than at the other, even for herring gull chicks trained with laughing gull models. It therefore seems probable that when present, food reinforcement may be an important, but not necessary, factor in the development of preferential responses.

Heat and contact. Two possible reinforcers, in addition to food, that have been studied in relation to imprinting in precocial species are heat and contact. Heat provided by other individuals was necessarily present in all social rearing situations used in the present study, and hence could conceivably have acted as a reinforcer. However, evidence that heat reinforcement was not necessary for the development of preferential approach responses was provided by those chicks that were reared with and subsequently selected inanimate and non-heated stimulus objects (Fig. 8, Tables 21 and 23). Klopfer & Hailman (1964) also found no effect of temperature treatments provided to young peking ducklings (*Anas platyrhynchos*) immediately after exposure to the imprinting object.

The possible effects of contact as a reinforcer for precocial species in imprinting situations have been suggested by Collias (1952), and have been reviewed by Salzen (1967). Positive evidence

that contact may be important is provided by experiments in which domestic chicks showed different degrees of attachment to familiar visual stimuli of different textures (Taylor & Taylor 1964; Sluckin, Taylor & Taylor 1966). In the present study, all ring-billed gull chicks except 'isolates' were reared in contact either with parents, other young, or models, hence reinforcement arising from contact with these objects could have acted to reinforce the learning of discrimination. Critical evidence, however, is lacking.

The findings reported in Sluckin et al. (1966) and Taylor et al. (1967) suggest that contact may also influence responses to fixed objects in situations other than those typically associated with imprinting to social companions. In the gull colony, chicks commonly contact various fixed objects such as vegetation, hence it is possible that they receive reinforcement by tactile means at these times. Rearing procedures in which chicks occasionally contacted cage walls (Section VI) would provide similar opportunities, as would the procedure in which chicks were trained to run down a long rectangular pen to reach an arbitrarily selected hiding place (Section V). The possibility that contact may have reinforced the learning exhibited in these latter chicks is not necessarily contrary to the previous suggestion (Section V) that anxiety reduction may have been important, since presumably contact could function merely as a sensory channel to provide the requisite information for such emotional effects (cf. also Moltz 1960).

In conclusion, it is probable that reinforcement associated with the early development of discrimination and preferential approach responses or attachments in young ring-billed gulls does not differ appreciably from that associated with imprinting in the more thoroughly studied precocial species. The available data indicate that although conventional reinforcers may have an effect in both groups, they do not appear to be essential in either. By elimination, this conclusion leads to the sug-

gestion that early discriminations and social responses in young gulls may be strongly influenced by simple 'exposure' or 'perceptual' learning, as suggested for precocial species (Sluckin & Salzen 1961).

B. Sensitive and Critical Periods

Methodology and terminology. The concept of the 'sensitive period', introduced by Fabricius (1951), may be defined as 'the period during which a young bird will follow a moving object it has not encountered before' (Fabricius 1964, pp. 331-332). Fabricius has also outlined important differences between the 'sensitive period' thus defined and an age span designated as the 'critical period' for imprinting (Ramsay & Hess 1954), which has typically been assessed by varying the age of exposure to a stimulus, then either testing for the presence or absence of a response to the same stimulus, or testing for preferential responses to the familiar over a strange stimulus (see Klopfer & Hailman 1964). This 'critical period' for imprinting has been variously described as 'the period for maximum imprinting' (Ramsay & Hess 1954, p. 199), or 'the period of maximum imprintability' (Fabricius 1964, p. 331). As such, it is essentially equivalent to the 'sensitive period' as used by Hinde (1966, p. 366), and particularly as used by Bateson (1966), who describes it as the 'optimum period of imprinting' (Bateson 1966, p. 178). Since two operationally distinct concepts are evidently involved, the distinction (Fabricius 1964) between 'sensitive' and 'critical' periods is adhered to in the present study.

To measure the critical period, or even to establish the existence of learned preferences for familiar stimuli in the context of imprinting, the importance of using tests requiring a choice between two (or more) stimuli, rather than those requiring only the presence or absence of a response to a single stimulus, has been stressed by Sluckin (1965) and by Klopfer & Hailman (1964). It can be noted, however, that operationally, the choice method is basically similar to a combination of two successive tests in which

a familiar and a strange stimulus are presented independently, except that the choice method calls for simultaneous, rather than successive, discriminations. In the present study, where colony-reared siblings, rather than the more conventionally used inanimate objects (Sluckin 1965; Bateson 1966) were initially used as stimuli to assess the existence and duration of the critical period, it was found most practicable to utilize successive discrimination tests, in which approach responses to familiar stimuli (Fig. 4) occurred in chicks that also exhibited withdrawal responses to strange stimuli (Fig. 6).

Temporal relationships. Many studies of imprinting in precocial species have investigated the temporal relationships between the *sensitive period* for initial approach responses to strange stimuli and the *critical period* for imprinting (reviewed in Fabricius 1964; Sluckin 1965; Bateson 1966). From these studies has emerged the general conclusion that both typically occur at more or less the same time and at an early age. Exceptions to such a temporal correlation are common however, and include instances where the sensitive period, especially to auditory stimuli, is prolonged (Hinde et al. 1956; Boyd & Fabricius 1965; Bjärvall 1967; other examples cited in Fabricius 1964), and instances where prolonged exposure to social companions can result in the development of apparently normal species-specific responses in birds that are several days or even weeks old (Wood-Gush 1958; Baron & Kish 1960; Baron, Kish & Antonitis 1962; Waller & Waller 1963; Kruijt 1964).

In the present study, a measure of the sensitive period in ring-billed gulls was obtained by measuring aggregative tendencies of isolate and 'pseudo-isolate' chicks reared in the laboratory and colony respectively, and tested against other chicks (Figs 4 and 5). For both groups, aggregative responses fell to levels below 50 per cent of maximum values by 3 days of age. A comparable measure of the critical period was obtained for both colony-reared and laboratory-

reared chicks by assessing the effects of social rearing with other chicks for one day immediately preceding testing of aggregative responses. In these tests, aggregative tendencies declined sharply to levels below 50 per cent of the maximum values at from 4 to 5 days (Figs 4 and 5). These results indicate that the critical period terminated approximately 1 to 2 days after the termination of the sensitive period. Because the measure obtained for the duration of the critical period may be influenced by the duration of exposure, as discussed in the preceding paragraph, it is probable that had the critical period been established on the basis of social exposure extending over a period of only a few minutes or hours, as has been commonly done in studies of precocial species (Ramsey & Hess 1954; Jaynes 1956; Hess 1959a, b; Klopfer & Gottlieb 1962; Waller & Waller 1963; Klopfer and Hailman 1964), the duration of the critical period would have been shorter, possibly coincident with or even shorter in duration than the sensitive period, thus making it equivalent to what has been suggested as the typical situation in precocial species (Fabricius 1964, p. 332).

Functional Significance of Imprinting in Mixed Colonies

One of the major conclusions derived from studies of imprinting in precocial birds has been that early termination of the sensitive and critical periods ensures that chicks restrict their approach responses and subsequent social behaviour to members of their own species (Lorenz 1937; Bateson 1966). In mono-specific gull colonies where the dispersion of the chicks is typically limited to the vicinity of the colony at least until fledging, it is less obvious that an *early* termination of these periods is necessary to prevent dysgenic attachments to other species. In mixed colonies, however, where breeding adults of more than one species may have adjacent nests, the development of preferential approach responses to the parental species at an early age, prior to the onset of even limited

mobility in Stage II, would appear to be potentially important in ensuring the development of species-specific social bonds.

A reliable estimate of the proportion of gull colonies that contain members of more than one species is difficult to establish, but evidence suggests that such events are far from uncommon. As mentioned in Section II (p. 196) both ring-billed and herring gulls nested at the Rogers City colonies where the present studies were conducted. Although the main nesting concentrations of the two species did tend to remain discreet in these colonies, there were several points of contact, and occasional overlapping of the two species where their major concentrations came together. The caspian tern (*Hydroprogne caspia*) has also been recorded nesting with the ring-billed gulls at Rogers City (Tordoff & Southern 1959). Recent observations that I made of ring-billed gull colonies in Manitoba, Canada, suggest that such contact between this and other Larid species is widespread. Of four ring-billed gull colonies examined in 1967, all contained other Laridae nesting in proximity, including one with herring gulls and three with common terns (*Sterna hirundo*). An association between nests of ring-billed gulls and both common and caspian terns on a small island in Lake Winnipegosis has been described elsewhere (Evans, Krindle & Mattson 1970).

That mixed colonies may be the rule for ring-billed gulls is suggested by descriptions of seven colonies by Bent (1921). Six of these colonies had nests of other Larid species, including herring gulls, california gulls (*Larus californicus*) and common terns; the seventh had double-crested cormorants (*Phalacrocorax auritus*) nesting on the same island. Several of the colonies also had an assortment of ducks present, a condition also prevalent within the colonies of various species of Laridae nesting on islands or in marshes in Manitoba (personal observation). As at the Rogers City colonies, Bent (1921) also found some intermingling of the nests of the various species, as indicated by the descrip-

tion of one colony in which ring-billed gulls were 'mingled with (california gulls) to some extent' Bent 1921, p. 133), and in another where 'the nests of the (ring-billed) gulls and (common) terns were closely intermingled' (Bent 1921, p. 134).

The apparently widespread occurrence of gull colonies containing more than one species is further illustrated by examples such as that described by Moynihan (1956) for the ring-billed, california and herring gulls in Manitoba; by Black (1955) and Gurr (1967) for the red-billed gull (*Larus novaehollandiae*) and Black-billed gull (*Larus bulleri*) in New Zealand; by Brown (1967) for the herring gull and lesser black-backed gull (*Larus fuscus*) in England; by Smith (1966a) for several species of the large *Larus* gulls in the arctic; by Vermeer (1968) for ring-billed and california gulls in Alberta; by McLeod & Bondar (1953) for various associations of gulls, terns, white pelicans (*Pelecanus erythrorhynchos*) and double-crested cormorants on Lake Winnipegosis; and by Belopol'skii (1957) for Laridae and many other colonial sea birds nesting on islands in the Barents Sea. These examples are illustrative rather than exhaustive. Contrary to the conclusions reached by Orians & Willson (1964) that, although they may be adjacent, 'colonies of gulls . . . and . . . terns are species-specific' (p. 741), the above examples serve to document a rather high incidence of mixed-species breeding associations amongst gulls and terns and between these and other less closely related species (see Bent 1921, for other examples).

From my observations at Rogers City and in Manitoba, it was apparent that where two or more gull or tern species nested together, the nests were not spaced so that those of different species abutted against each other, but rather were spaced out, presumably by means of inter-specific territorial behaviour on the parts of the adults involved. This conclusion is in agreement with the observations of mixed colonies of ring-billed, california and herring gulls described by Moynihan (1956), and with descriptions of

mixed colonies of large *Larus* gulls in England (Brown 1967) and in the arctic (Williamson & Peyton 1963; Smith 1966a). That different species of ground-nesting Laridae breeding in similar and structurally simple habitats should exhibit marked inter-specific territorial behaviour is entirely consistent with the generalized conclusions derived by Orians & Willson (1964) from an examination of data from various other taxa.

In gull colonies where more than one species nest in adjacent territories, it seems evident that the formation of social bonds with adults or chicks other than those of the parental species is a distinct possibility. Because of this possibility, it is particularly significant that in the experiments designed to test the effect of early sibling experience on approach responses to other chicks (Section VIII), it was found that chicks reared in the colony as broods of one ('pseudo-isolates') showed a significant reduction in subsequent aggregative responses to other chicks after 3 to 4 days of age. The general similarity between the data for the colony-reared chicks (Fig. 4) and for those reared in complete visual isolation from other chicks in the laboratory (Fig. 5) suggests that whatever experience the colony-reared pseudo-isolate chicks may have had with other chicks from adjacent nests, it was not sufficient to foster the development of social attachments to other chicks, even though the pseudo-isolates did appear to socialize normally with their parents. It would thus seem highly probable that in mixed colonies, young chicks would imprint to their own parents and siblings with which they had intimate rearing experience but not to members of the other species even if the nests of the latter were located at a distance no greater than that typical of inter-nest distances in a monospecific colony. As implied earlier, the degree of species-specificity derived would no doubt be dependent upon the development of attachments to parents and siblings prior to the onset of a degree of mobility that would be sufficient to bring young chicks in close and ex-

tended contact with another species or, in extreme cases, that might lead to inter-specific brood mixings and adoptions. Where this latter possibility exists, the early termination of the sensitive period, approximately coincident with the onset of brood mobility in Stage II as found in the present study, would thus seem advantageous to ensure the normal development of species-specific attachments.

In his study of isolating mechanisms in certain *Larus* gulls, Smith (1966a) has experimentally demonstrated the importance of subtle species-specific cues, such as eye-ring colour, in the development and maintenance of normal intra-specific pairing (cf. also Brown 1967). Smith (1966a) has further suggested the possibility (p. 73) that the development of species-specific selection of and attachments between mates may be dependent upon some form of 'fixation' by the chick on the characteristics of its parents. The well-developed capacities of young gull chicks to establish detailed discriminations, as demonstrated in the present study, is consistent with such an hypothesis, but does not rule out the possibility that mate preferences in gulls could be established at a later time (cf. Schutz 1965). In either event, however, the early establishment of species-specific relationships as a result of an early termination of the sensitive period would no doubt contribute to the orderly development of conspecific mate preferences in closely related species nesting in mixed colonies.

Harris (1970) has recently shown that the choice of mate of *Larus fuscus* and *L. argentatus* could be altered by cross-fostering between the two species.

Development of Responses to Predators

Several investigators (e.g. Paludan 1951, p. 98; Tinbergen 1953a, pp. 180-181; Kruuk 1964, p. 92) have drawn attention to the fleeing and hiding responses of young gulls as an anti-predator mechanism. The utility of this mechanism, which is especially well developed in ground-nesting species, is dependent upon the chick being able to move sufficiently to flee or hide, and on the chick being able to respond

appropriately to the relevant stimuli, including adult alarm calls and predators or their equivalent (Kruuk 1964; Smith 1966b; Sections IV and VIII of this study). If these latter, direct responses to predators are to be effective in young chicks, the discriminations and mobility required for fleeing should both develop at an early age, and should be more or less correlated in time. Such an interpretation is consistent with the close correlation actually found between the termination of the sensitive period and the onset of mobility in young ring-billed gulls.

Where exposure to predators or potential predators is extensive, as for example when Herring Gulls from adjacent colonies repeatedly prey on ring-billed gull chicks (Emlen 1956), fleeing responses of the chicks to these predators may conceivably become attenuated as a result of habituation (cf. Thorpe 1963, pp. 336-344; Hinde 1966, pp. 363-365). Habituation to visual stimuli is common in young birds, and has been documented for several precocial species (Schaller & Emlen 1962; Bateson 1964a, 1964c; Evans 1968). In domestic chickens, however, it has been found that withdrawal and other agonistic responses to initially strange visual stimuli habituate less rapidly on successive days after hatching (Evans 1968). Although critical evidence is lacking for gulls, similar considerations presumably would apply. If so, the likelihood of non-adaptive habituation to predators would become reduced at or soon after the termination of the sensitive period and concomitant onset of mobility.

Studies of precocial species (Fabricius 1964; Boyd & Fabricius 1965; Bjärvall 1967) have shown that the sensitive period for approach responses to auditory stimuli may be delayed well beyond the onset of mobility and the termination of the sensitive period to visual stimuli. Consideration of the natural context in which these modalities function suggests the simple hypothesis that any selection pressures exerted by essentially silent predators on the sensitive period for approach responses to visual stimuli would not similarly apply to the auditory

modality. In the absence of such predator effects, a prolongation of the auditory sensitive period, to assure following in late imprinters (Boyd & Fabricius 1965; Bjärvall 1967), would be favoured. Considered together, different sensitive periods for visual and auditory modalities would thus seem to provide an optimum advantage to mobile young: a prolonged auditory sensitivity would assure following of vocalizing parents without raising the possibility of non-adaptive approaches or lack of fleeing to silent predators which would be avoided as a result of an early termination of the visual sensitive period.

In gulls, responses of chicks to predators and human intruders are further characterized by the early development of hiding and crouch responses, in or near the nest, elicited by the alarm calls of the adults (Tinbergen 1953a; Smith 1966b; Kruuk 1967; Section IV of this study). Reduction in movement resulting from crouch responses, acting in conjunction with the chicks' cryptic colouration presumably functions as anti-predator mechanisms (Tinbergen 1952). In addition, it is evident that such crouch responses also function to counteract dispersal due to the fleeing responses discussed above, thereby keeping the brood together and reducing the likelihood of attacks that may occur when chicks wander onto the territory of neighbouring adults (see Ward 1906; Strong 1914; Kirkman 1937; Emlen 1956).

Several observations made during this study suggest that the movements of chicks during periods of disturbance by predators are also influenced by variables, including chick density, cover, and magnitude or duration of the alarm. Observations made throughout the study indicated, for example, that where vegetation or other small objects like stones, logs, etc. were scarce or lacking in the colony, chicks typically ran to other chicks and stood or crouched beside them during periods of alarm. Where, in addition, chick densities were high and disruptions prolonged, such approach responses between chicks commonly resulted in extensive

aggregations (Section VIII), especially when the chicks were older and more mobile. These observations are in agreement with the experimental findings (Section VIII) that when chicks were released in areas having different degrees of cover, aggregative tendencies dropped off rapidly with increasing density of vegetation. In a well-vegetated colony, restriction of visual contact with other chicks (habitat 'cutoff'; cf. Chance 1962; Melchior 1965) would presumably reduce extensive aggregations and simultaneously favour a more limited and adaptive dispersal to the hiding places provided by the same vegetation. The small effectiveness of chick vocalizations in eliciting approach responses (Section VIII) coupled with the rapid decline with age in calling by chicks under disturbed conditions (Section IX) reduces even further the chance of chicks aggregating and increases the likelihood of dispersal to nearby hiding places which is possibly more adaptive.

The Significance of Semi-Precocial Development in Gulls

The interpretations discussed above suggest that the close temporal correlations between the progressive development of mobility and development of discriminations involved in species and individual recognition adapt the young to their natal environment. The data obtained in the present study suggest, in addition, that the functional interpretations of these relationships in semi-precocial gulls do not differ appreciably from those applicable to more typical precocial species, except that the developmental rates of the semi-precocial species are less rapid.

In ground-nesting species, the importance of at least some brood mobility as a dispersal mechanism to permit chicks to reach shelter from weather (Emlen 1956), and predators (Tinbergen 1953a; Kruuk 1964), would appear to create selection pressures favouring a relatively early onset of mobility and its correlated perceptual processes. In colonial species, however, brood localization at some place is also favoured, so that chicks

of a given brood may easily be located and fed by their parents (Nice 1962).

The trend towards localization, although apparently present in all semi-precocial gull species, would appear to be maximal in those that nest where ground predation is slight and where extended mobility could be lethal, as in typical cliff-nesting species such as the kittiwake (Cullen 1957) and swallow-tailed gull (*Creagrus furcatus*) (Hailman 1965; Snow & Snow 1967) and in some other more generalized species such as the large *Larus* gulls where local populations may sometimes make use of tree (Dutcher & Bailey 1903) or cliff nest sites (Emlen 1964; Smith 1966b). In contrast, where ground predation is greater, as in ground-nesting herring gulls (Tinbergen 1952), or where chicks remaining in the nest are subject to possible destruction by floods as in the black-billed gull of New Zealand (Beer 1966), a greater tendency towards dispersal is evident. The ring-billed gull, which nests on the ground in dense colonies that are typically located on islands where ground predators are few (Bent 1921), appears to fall between these extremes, exhibiting an initial localization within a restricted territory that facilitates brood care in densely packed island colonies, followed by a progressive but limited dispersal away from the congested nest area.

The delicate balance ultimately maintained between localization and dispersal tendencies in semi-precocial gulls is apparently shifted in the various species, in some favouring localization, in others dispersal, according to the type of nest site to which the species is primarily adapted. By allowing for brood cohesion and parental care in all situations, while at the same time making possible a relatively broad range of adaptive variations in brood mobility, semi-precocial development would appear to be an important adaptation that has permitted the utilization of available nest sites by various gull species in a wide range of oceanic and inland habitats throughout the world.

XI. SUMMARY

Studies of imprinting and the development and control of brood mobility in young ring-billed gull chicks (*Larus delawarensis*) were conducted during five breeding seasons at five colonies located near Rogers City, Michigan. Observations of brood movements, recorded to scale on maps, were obtained from a blind. Experimental studies of approach responses to social and non-social stimuli were conducted by varying the stimulus situation and early experience of both colony-reared and laboratory-reared chicks.

Ring-billed gull chicks are able to move in a partially crouched position during the first day after hatching. Excursions away from and back to the nest began on the second day, and were observed in all broods by the sixth day. Total distance moved on excursions and the average maximum distance of excursions increased with age. Permanent emigrations from the nest occurred by the third day and were observed more frequently thereafter. Measurements of chick movements in a colony that was left undisturbed indicated that brood emigrations are characteristic of the species and not due merely to the intrusion of an investigator.

Young gulls initially approached a wide range of stimuli. As early as the first day, incubator-hatched chicks approached adult mew calls, chicks and inanimate models. Blind-folded chicks oriented towards adult vocalizations, but approached less frequently than controls. Partially-deafened chicks approached both adults and other chicks, but did so less rapidly than unoperated controls. The combination of auditory and visual cues thus appears to be more effective than either alone.

Chicks reared by gulls as broods of four aggregated significantly more during experimental tests than did chicks reared singly as 'only children'. Chicks reared as singles except for one day of experience in a group immediately prior to testing aggregated like typical group-reared chicks up to 4 or 5 days of age, then

declined to the low levels characteristic of chicks reared singly, suggesting the presence of an early critical period for the aggregative effects of group-rearing experience. Approach responses to moving inanimate objects were similarly influenced by early experience. Training experiments indicated that chicks were also able to learn to go to a specific hiding place, and select a familiar rather than a strange rearing site. Experiments with chicks that were hand-fed and otherwise reared either by their parents or in the laboratory provided evidence that reinforcement in the form of feeding was not necessary for the maintenance of apparently normal approach responses to adults, to chicks, or to inanimate objects.

Observations within the colony indicated that approach responses were selective to parents and brood mates. Experiments showing that approach responses to chicks were reduced in the presence of cover, that single chicks approached pairs significantly more than the converse, and that the rate of approach responses increased with mew call loudness, all suggest that the selectivity of approach responses was in part a result of the greater intensity, and hence effectiveness, of stimuli from members of the family unit because of their proximity. Experimental evidence indicated that by 4 to 5 days of age, the development of individual recognition of parents and brood mates provided an additional and more stable selective mechanism that could function in the maintenance of family units and in the control of brood movements.

The development of mobility in young ring-billed gulls may be conveniently referred to three successive but overlapping stages: I, *Incipient Mobility*, extending from hatching through the third or fourth day, characterized by chicks remaining in or on the edge of the nest; II, *Restricted Mobility*, from the second to fourth or fifth day, characterized by temporary excursions away from the nest, and III, *Extended Mobility*, from the fourth day on through

fledging, characterized by permanent emigrations away from the territory or nesting area. These same stages of mobility correlate closely with a corresponding progression of perceptual development, characterized by response to a wide range of initially effective stimuli in Stage I, recognition of particular classes of familiar stimuli, or 'species recognition' in Stage II, followed by the subsequent development of recognition of particular individuals in Stage III.

The experimental data indicate a close similarity between the development of preferential approach responses in young ring-billed gulls and the phenomenon of imprinting in more typical precocial species. Methodological and terminological problems associated with the concepts of the sensitive and critical periods are discussed. It is suggested that when delineating the biologically meaningful critical period for a particular species, the use of criteria based upon natural conditions are preferable.

Semi-precocial development in gulls appears to favour brood localization coupled with controlled dispersal, thereby facilitating both localized parental care and adaptive dispersal responses to predators. It is suggested that semi-precocial development thereby constitutes an important adaptation in gulls that has enabled the group to exploit a wide range of nesting habitats throughout the world.

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