EGG RECOGNITION BY THE LAUGHING GULL

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SEABIRDS, such as gulls, terns and plovers, differ remarkably from one another in their ability to recognize their eggs. Tinbergen (1936) concluded that terns on returning to the nest orient themselves by cues derived from the eggs to a much greater degree than does either the Herring Gull (*Larus argentatus*) or the Ringed Plover (*Charadrius hiaticula*). While studying the social behavior of the Laughing Gull (*Larus atricilla*) we had the opportunity to test experimentally the cues utilized by this species in satisfying its incubation drive.

Considerable work on the adequate stimulus for incubation had been done previously on the Herring Gull, *Larus argentatus* (Goethe, 1937; Tinbergen, 1934, 1936; Booy and Tinbergen, 1937; Steinbacher, 1937) and European Black-headed Gull, *Larus ridibundus* (Skrebitzky and Bibikova, 1936[1]; Kirkman, 1937) and it was expected that *Larus atricilla* would be found to agree with the latter species, which it resembles to a considerable degree. Our experiments revealed, however, that the adequate stimulus for incubation is not the same in *L. atricilla* as in other species of the genus. The present paper embodies an account of our experiments which brought to light these differences.

It should be stated at the outset that since we were dealing with wild birds it has been impossible to determine how much of the incubation responses are learned and how much innate. This same deficiency is found, however, in all previous work with wild birds. Only when birds breeding for the first time have their eggs removed at the moment of laying will a situation be available for adequately testing innate behavior. Nevertheless, while fully realizing the limitations of this study, it is of interest to determine the adequate stimulus for brooding behavior in a gull not previously investigated because we gain information as to the kinds of sensory data that are significant in the brooding life of this species. Objects in the *Umwelt* of a bird have different valence, in the sense of Russell (1938), and a bird's point of view in regard to what may be significant is often very different from our own. This study shows that the constellation of significant sensory data varies from species to species within the genus *Larus*.

THE COLONY

Our observations and experiments were made in a colony of over 500 Laughing Gulls at Stone Harbor, New Jersey, during May and June, 1938.

[1] We are indebted to Professor K. S. Lashley for the loan of a reprint of this paper which we credit here to the investigators instead of to Borovski, the director, as Lashley (1938) has done.

Two rectangular blinds were covered with heavy duck and placed in two different parts of the colony. Although the authors worked separately in the two blinds they frequently conferred and in this way carried out a planned series of experiments. Mr. R. P. Allen and Mr. J. K. Potter were of assistance in locating the colony and Mr. L. Walsh in preparing the blinds. Assistance in the preparation of these materials was furnished by the personnel of Works Progress Administration Official Project No. 465-97-3-67. The eggs which served as models for our artificial eggs were borrowed from the Department of Ornithology of the American Museum.

RELATIVE ATTRACTIVENESS OF THE INCENTIVES INVOLVED

Previous workers have recognized that the adequate stimulus for incubation may emanate from (a) the nesting site, (b) the nest, (c) the eggs, or (d) from some combination of these elements. We have attempted to determine the relative importance of these different factors by introducing them singly or in different combinations opposed to other single or combined factors. For example, if we place an empty nest on one side of the old nest site and a clutch of eggs on the other side and the bird when returning to the nest area settles at once upon the eggs, we may assume that the eggs are a more effective source of attraction than either a nest or a nest site.

We have performed a series of experiments which are indicated diagrammatically in Text-figure 1. The opposing incentives are indicated along the top and the left-hand side of the figure. By following down and across any pair of incentives on the chart the result obtained with this combination is indicated by the arrow. That is, the bird selected the incentive toward which the arrow points. The number of arrows in any square indicates the number of times the experiment was performed on different birds. Dotted arrows indicate inferred results, as these combinations were not tested. Cross-hatched squares indicate impossible combinations. In every case the arrow indicates merely the first response to the experimental situation. This is presumably a response to visual cues for the results of the whole series are consistent even when two sets of eggs or two nests were used in various combinations, thus balancing the odor of the nest or eggs. After the bird has made a selection, tactile cues may modify the response. These later adjustments are not indicated on the chart.

The chart (Text-figure 1) fails also to give the distances between the two incentives. Since this is a very important factor, the data given in the chart may be repeated in table form and the distances involved, together with some supplementary remarks, added.

Experiment 1 (Square 1)

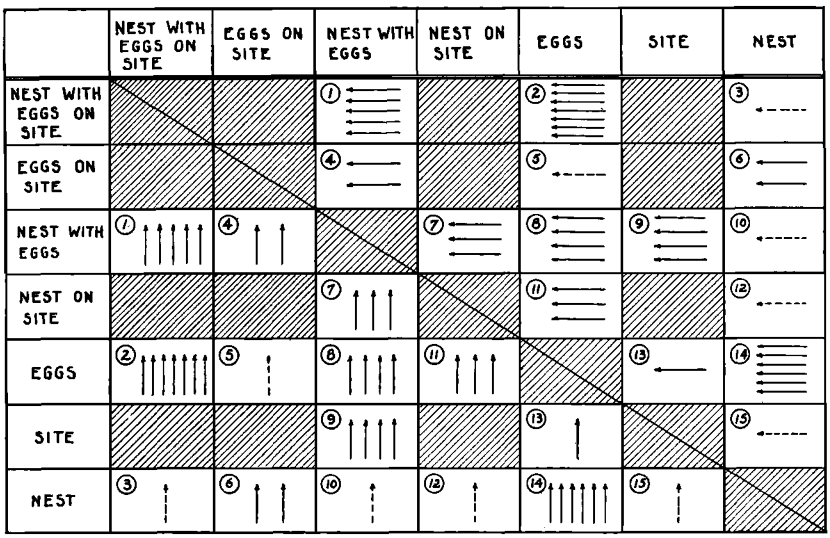
Conditions: Nest and eggs on site vs. nest with eggs.

Distance: 12 inches in four cases; 18 inches in one case.

Result: Bird sits on nest with eggs on site. The experiment was varied once by placing the original eggs in the extra nest, and the foreign eggs in the original nest; and once, by placing the extra nest with eggs on the site, and the original nest with eggs 12 inches away.

Experiment 2 (Square 2)

Conditions: Nest and eggs on site vs. eggs.
Distance: 1 and 12 inches, respectively.



ARROW INDICATES DIRECTION OF RESPONSE

TEXT-FIG. 1.—Diagrammatic representation of the Laughing Gull's response to elements in the nest situation.

Result: Bird sits on nest and eggs on site. Number of eggs outside nest varies. (Described in detail in Experiment 13.)

Experiment 3 (Square 4)

Conditions: Eggs on site vs. nest with eggs.
Distance: 12 inches.
Result: Bird sits on eggs on site. In both cases, the bird hesitated over an hour before settling.

Experiment 4 (Square 6)

Conditions: Eggs on site vs. nest.
Distance: 12 inches.

Result: Bird sits on eggs on site; hollows out crude nest around eggs when it incubates.

Experiment 5 (Square 7)

Conditions: Nest with eggs vs. nest on site.

Distance: Once, 12 inches; once, 18 inches; once, 20 inches.

Result: Bird sits on nest with eggs. In one case, hesitation was considerable; the bird, after having chosen the nest with eggs, went over to and sat on nest on site, twice, for a few seconds each time, but soon appeared uncomfortable and returned to the nest with eggs.

Experiment 6 (Square 8)

Conditions: Nest with eggs on one side of site, eggs on other.

Distance: 18 inches in one case, 24 inches in three cases, from nest with eggs to eggs.

Result: Bird sits on nest with eggs. Choice made after considerable hesitation, but apparently without the bird's attention being directed toward the site.

Experiment 7 (Square 9)

Conditions: Nest with eggs vs. site.

Distance: 12 and 18 inches, respectively.

Result: Bird sits on nest with eggs.

Experiment 8 (Square 11)

Conditions: Nest on site vs. eggs.

Distance: 12 inches in two cases; 32 inches in another.

Result: When the eggs were 12 inches away, they were rolled into the nest within a few hours. When they were 32 inches away, the bird, after sitting uneasily on the nest for twenty minutes, went to the eggs and sat, but still appeared uneasy.

Experiment 9 (Square 13)

Conditions: Eggs vs. site.

Distance: 12 inches.

Result: Bird hesitates, sitting on site twice for a few seconds each time; finally settles on eggs.

Experiment 10 (Square 14)

Conditions: Eggs on one side of site, nest on other.

Distance: 14 and 36 inches, respectively.

Result: Bird sits on eggs. Amount of hesitation varies considerably. Reversing positions caused parent to incubate eggs in new position.

A study of the above data will reveal that the various incentives involved in the incubation response have been arranged in a descending order of attractiveness in the left-hand column of Text-figure 1. Only the site in this table is not adequately evaluated in regard to its attractiveness. This is because we cannot move the site. When we move the eggs farther from the site, the attractiveness of the site as compared with the eggs increases. The relative strength of nest and eggs, on the other hand, can be accurately compared because we can place *nest* and *eggs* at equal distances on either side of the site. But the relative strength of nest and site varies with the distance they are separated. Hence, the relative attractiveness stated in Text-figure 1 holds only for the distances employed in these tests.

Lashley (1915) and Goethe (1937) have shown that birds orient themselves by means of prominent physical features of their environment. Hence the relative distinctness of the site would vary in strength according to the relative conspicuousness of these objects. It is possible that in Experiment 9 the attractiveness at the site was at its extreme. At least the bird sat down twice on the site before directing its attention to the eggs. The first reaction may have been toward site but we have indicated it as eggs because the only persistent reaction was toward the eggs. We have not been able to consider persistent reaction as the criterion throughout this table because secondary tactile cues in many cases entered into the response to modify the primary reaction.

FURTHER ANALYSIS OF THE INCENTIVES INVOLVED

The above experiments shed little light on the essential qualities of the incentives for inducing the incubation response. Further experiments were therefore devised to reveal these qualities.

a) *Nest.*—As shown in Text-figure 1, the nest appears to be the least attractive of the three incentives involved in the incubation response. The fact that a nest with eggs is selected in preference to eggs alone indicates that the nest is, nevertheless, an incentive of some significance. The essential feature of a nest appears to be its hollow. For example, in Experiment 6 we found that when an original nest with eggs is placed on one side of a site and a set of eggs is placed on a flat platform of nesting material on the other side the bird selected the nest. Two experiments made this preference for a deeper nest clearer.

Experiment 11 a

Original, deep nest placed at one side of site; artificial, shallow one, at the other. Identical sets of eggs in the two.

Result: The bird returns, sits on the shallow nest, appears unsettled; finally after ten minutes, moves across to the deeper one. The positions of the nests were then reversed. The bird returned, sat on the shallow nest (on the spot where the deep nest had been on the previous trial) but, after about ten seconds, moved to the deep one. This test was repeated three times. On each trial the bird did the same thing; it sat on the shallow nest on the spot where the deep one had been on the previous trial, then, after a few seconds, it moved to the deep nest.

The deeper nest, therefore, is more attractive to the bird than the shallow one. The bird did not learn to tell the nests apart at sight, but could do so, apparently, by touch. An interesting point is the quick learning of a nest position, which will be discussed later.

Experiment 11 b

Four Clapper Rail eggs in new, deep nest, 12 inches from site. Two gull eggs on original nest, *flattened out,* 12 inches on other side of site.

Result: Bird went directly to gull eggs, and brooded; then stood up, turned and walked to rail eggs (in deep nest) and sat down; remained three minutes, then stood up and went to the gull eggs, and settled down.

Here the gull seemed disturbed by the shallow nest, but on the other hand when it had tried the deeper nest found the small Clapper Rail eggs also inadequate.

b) *The Eggs.*—In the normal course of events there are two ways in which the gulls react to the eggs: by incubating those in the nest, and by rolling in those that have been dislodged from the nest. These two responses may be considered separately.

The reaction to normal eggs in the nest is incubation. This need not be considered further, except to mention that additions or subtractions of eggs had no effect on the incubating reaction so long as the nest was not emptied. In striking contrast the rolling reaction may be affected by several factors: the number of eggs outside the nest, their distance from the nest and whether or not the nest is empty. The importance of these factors in the case of the Laughing Gull was shown by a series of experiments.

Experiment 12

All eggs removed from the nest. Normal eggs placed outside the nest.

Outside Nest	*Result*
a. 3 eggs, 2 inches from rim	2 eggs rolled in
b. Full clutch, 12 inches from rim—See Experiment 8	Eggs rolled in
c. Full clutch, 32 inches from rim—See Experiment 8	See Experiment 8

Experiment 13

Eggs placed outside a nest with eggs in it.

In Nest	*Outside Nest*	*Result*
a. 3 eggs	3 eggs, at 12 inches, 2 inches, and 1 inch from rim	None rolled during observation
b. 1 egg	1 egg, 1 inch from rim	None rolled during observation
c. 1 egg	3 eggs, at 2 inches, 2 at 6 inches, and 2 at 10 inches	None rolled during observation
d. 1 egg	3 eggs just outside rim	2 rolled during observation
e. 2 eggs	6 eggs just outside rim	3 rolled during observation
f. 2 eggs	5 eggs, 2 inches from rim	1 rolled during observation
g. 1 egg	3 eggs, 1 inch from rim	2 rolled during observation

These experiments are too few to give clear-cut results. Nevertheless, they indicate certain tendencies. First, if there are no eggs in the nest the tendency to roll back displaced eggs is much greater than if eggs are present. Second, the tendency is greater the nearer the eggs are to the nest. Third, the greater the number of eggs available the stronger will be the reaction. The distance of the eggs from the nest modifies the result. If the nest is empty, eggs will usually be rolled from at least 12 inches away. If there are already eggs in the nest, eggs will not be rolled in from distances more than two or three inches from the edge of the nest. Lastly, there must be at least three eggs available for rolling (unless the eggs are actually on the rim of the nest). These conclusions apply only for periods of two hours following the disturbance. It is possible that with long periods eggs ignored at first would be later rolled back to the nest.

Eggs may be attractive to gulls because of their color, form, hardness, odor, or a combination of qualities. Following the lead of previous workers with other species of gulls we have attempted to determine the adequate stimuli for eggs to be incubated.

First, the original nest was removed and two identical artificial nests placed in juxtaposition, half on and half off the original site. A clutch of typical eggs is then placed in one nest and a clutch of artificially colored eggs in the other. If the bird chooses the normal eggs consistently, it is concluded that it can distinguish between them and that the normal color is more attractive than the artificially colored ones. In each experiment the position of the clutch is reversed after the choice and the bird given another chance to choose. This eliminates any position habits. Each experiment thus represents two trials.

Experiment 14

Double nest; normal clutch in one, artificially colored eggs in the other.

Various controls were employed in the experiments. In some trials, eggs laid by birds other than the owners of the nest were utilized, thus eliminating the possibility that the bird's selection was based on the recognition of its own eggs. In other trials, the two clutches were made up half from each nest, thus balancing a recognition of individual eggs.

	Total Number of Tests	*Alternative to Gull Eggs*	*Choice*
a.	6	Artificial eggs closely resembling original eggs in color and pattern	Normal eggs
b.	2	Yellow-spotted gull eggs	Normal eggs
c.	6	Blue-spotted gull eggs	Normal eggs
d.	4	Red-spotted gull eggs	Normal eggs
e.	2	Clapper Rail eggs	Normal eggs
f.	4	Lighter gull eggs	Bird hesitated; finally sat on light eggs and rolled its own eggs in with them.

The artificial eggs of Experiment 14a were made exactly the same size and approximately the same weight as genuine eggs. Size is thus eliminated as a factor. Weight can have no bearing on a selection which is made on the basis of visual cues. The surfaces of these plaster of Paris substitutes for eggs were varnished and later painted with oil colors. Number was controlled in two cases by making the artificial clutch of the same number as the original clutch while the alternative set of genuine eggs was in one case, one over, in the other case, one under, the number of eggs that the bird had been incubating.

It is apparent that the rejection of the artificial eggs which so closely resembled normal eggs in color must have been due to some characteristic of color or texture that we were unable to control. Since the birds failed to distinguish light from dark gull eggs, this rejection of the artificial eggs seemed remarkable (Experiment 14f). It is also possible that odor may have played a rôle, but of this we have no information.

Kirkman (1937) found that his Black-headed Gulls, which would not be disturbed by gull eggs painted various colors including red, were disturbed by red wooden eggs of the same size and shape. This, again, may have been due to texture or odor. In order to control the factor of the odor of the oil colors, tests were made with lacquers of different colors with the results discussed below. When the eggs were painted the colors were approximately Flaming Maple red, Bluebird blue and Cadmium yellow of Maerz and Paul (1930). In this series of experiments artificially colored gulls' eggs were introduced into the nests of brooding birds and their reaction to the situation was noted.

Experiment 15

Some eggs of a clutch painted.

a. With blue spots (lacquer). Two eggs in nest; one painted.

b. With yellow spots (lacquer). Three eggs in nest; one painted.

c. Completely red (lacquer). Three eggs in nest; two painted.

d. Cross-banded with red (oils). Three eggs in nest; two painted.

Result: In a, b, and c, bird sat, after more or less hesitation. Hesitation greatest in c (red). In d, one red egg was found thrown out of the nest next day and the nest was abandoned. The bird had previously shown fear of the blind, which was only seven feet from the nest, but there is little doubt that it returned and removed the egg.

Experiment 16

All eggs in clutch painted.

a. Completely blue (lacquer). Experiment repeated twice on different birds.

b. Completely yellow (lacquer). Repeated twice on different birds.

c. Completely red (lacquer).

Result: In a, the bird sat with slight hesitation. In b, one bird sat after slight hesitation, the other returned, stood at nest, but did not sit during twenty minutes of observation. In c, the bird was not seen for the rest of the day, but was found sitting next morning.

Experiment 17

One set of normal eggs substituted for another.

a. Two very pale eggs substituted for two very dark ones.

b. Two very dark greenish eggs substituted for one pale and one dark one.

c. Two very dark brown eggs substituted for two very light ones.

In every case the number of introduced eggs was the same as that of the original clutch.

Result: All birds incubated without hesitation.

It may be added that there was some variation in the responses of any one bird, as well as among the responses of different birds. The experiments clearly show, however, that red is most disturbing, blue much less so. The experiments with yellow are not clear, but suggest that the disturbance caused by it is intermediate between blue and red. Further tests were therefore devised to test the disturbing effect of artificially coloring a gull's egg.

It has been shown above (Experiment 1) that a Laughing Gull, given a normal nest and eggs on the site, will not incubate eggs in an extra nest off the site. A nest with eggs offers some attraction to the gull, but a nest with eggs on the site offers considerably more. If coloring the eggs renders them less attractive, the gull presented with colored eggs on the site and uncolored eggs in a nest off the site should select the latter. We have therefore tested a series of gulls in such a double nest situation.

Experiment 18

Two nests, one on the site, one off the site.

Contents *Nest on site*	*Distance* *Nest off site*	*Remarks*	*Reaction*
a. Red-spotted	20 inches	No other nest in 3 feet	Lands, stands at original nest, walks to extra nest, sits, walks back to original and returns. After thirty minutes, finally incubates red-spotted eggs on site.
b. Red	18 inches	No other nest in 2 feet	Sits on original ten minutes, starts to turn eggs; is immediately disturbed, alternates between nests, etc.; settles on red eggs on site after two hours.
c. Yellow	12 inches	Repeated twice on different birds	As in a.
d. 1 blue, 1 yellow	14 inches		Next day only normal eggs off site are warm.
e. Yellow	24 inches	(See Note 1)	Bird sits at once on normal eggs off site.
f. Red	30 inches	Nest in 6-ft. open site	Bird stands over red eggs ten minutes, then walks to normal eggs and sits; flies off. Returns and repeats (four times in one hour); sits on red eggs the fifth time; incubates seven minutes, then frightened off; returns at once to red eggs.
g. Yellow	30 inches		Stands over eggs on site, but does not incubate. Shows no interest in nest thirty inches away. No record of bird sitting.
h. Yellow	32 inches	(See Note 1)	Sits on yellow eggs.

Note 1.—When the positions of the eggs were reversed, the bird sat on the normal eggs on the site.

The disturbance caused by the abnormal colors is clear. If the eggs in the nest on the site had been normal, the birds would have paid no attention to the extra nest. In eight experiments only two birds sat on the artificially colored eggs on the site without first sitting on the normal eggs off the site.

Of the three experiments where the nests were thirty inches or more apart, in only one did the bird notice the extra nest; in this experiment the nests were in a 6-foot open space in the grass. In the others, the nests were built on the grass. It is apparent that the tendency to move to an extra nest is less, the farther away it is from the site. There is obviously considerable individual variation, however, among different birds.

A further test of the disturbing effect of artificially coloring the eggs of a gull was made by studying the rolling reactions of gulls presented with such eggs.

Experiment 19

Artificially colored eggs outside an empty nest.

	Number	*Color*	*Distance*	*Reaction*
a.	2	Blue-spotted	10 inches	Rolled in after at least two hours.
b.	2	Red-spotted	12 inches	Bird sits nervously all afternoon without touching eggs; found rolled in next morning.
c.	2	1 normal, 1 blue	2 inches	Only normal egg rolled in.

Experiment 20

Artificially colored eggs outside a nest containing eggs.

	Number in nest	*Number outside*	*Color*	*Distance*	*Reaction*
a.	2	2	Red-spotted	On rim	Rolled in after at least one hour.
b.	1	3	Yellow	2 inches	None rolled in.
c.	1	5	3 red, 2 normal	On rim	None rolled in.
d.	2	3	Red	2 inches	None rolled in.
e.	1	4	1 red, 3 normal	Just over rim	Two of the normal eggs rolled in.

Artificial colors on the eggs have, therefore, a marked disturbing effect on the rolling reaction of the Laughing Gull. In Experiment 19c, the normal egg was rolled in, whereupon the situation became that of Experiment 20, and the blue egg was not rolled in. The rolling of colored eggs into empty nests always took much longer than with normal eggs. The only time colored eggs were rolled into a nest already containing eggs, they were actually on the rim of the nest at the beginning of the experiment (20a).

The question remained if the shape and texture of an egg had an influence on the incubation response of the Laughing Gull.

Experiment 21

Two lumpy eggs placed in a nest in place of the bird's clutch. These eggs are made by attaching (with rubber cement) two-thirds of a shell to the end of a normal egg and one-third of the same shell to the other egg of the clutch. There is a distinct edge where the two shells meet. This experiment was repeated twice, on different birds.

Result: The bird incubates the eggs; neither egg is disturbed.

This change in shape does not disturb the bird to the extent of interrupting incubation.

Experiment 22

Three eggs removed from the nest and replaced by one egg with a hole broken into one end.

Result: Bird returns but refuses to brood.

Experiment 23

All eggs in the nest covered with a layer of rubber cement. This experiment was repeated twice, on different birds.

Result: a.—Bird returns and touches eggs many times but does not incubate. After some time sits and broods for twenty minutes; then gets up and tries to move eggs, then flies away. Back in five minutes and tries to brood again. Finally settles down for thirty minutes. At this time many small sticks are stuck to the eggs and they are drier.

b.—Bird later found brooding.

The rubber cement, which dries very rapidly, was very disturbing to the birds at first, but they gradually became used to it. At first it is very soft and wet; it gradually becomes drier and harder. The gradual drying and hardening of the egg probably removes some of the source of the bird's disturbance (since it will brood eggs of abnormal shape more readily than these wet eggs); in addition, the bird's drive to brood may be overcoming its hesitation. It is not apparent how much of the change is due to either factor.

Experiment 24

Nest in low grass moved two feet to one side of the site and extra nest placed two feet to the other. Eggs in the original nest covered with sticky rubber cement.

Result: Parent goes to the foreign (normal) egg in foreign nest, after having inspected the original eggs. Broods only foreign eggs.

When the position of the nest is reversed, the bird follows the normal eggs to the other nest.

Experiment 25

Eggs in the nest covered with rubber cement, then bits of dry grass stubs stuck into the cement, giving the eggs a 'whiskered' appearance.

Result: Bird broods the eggs, but later throws out one of them.

The 'whiskered' eggs are apparently disturbing but not enough so to prevent the bird from sitting on them.

Experiment 26

Extra nest with normal eggs twelve inches away from nest on site. Of the eggs in the nest on the site, one has projecting teeth of dentist's cement, the other has 'whiskers' of long wood chips.

Result: Bird sits on site, seems disturbed, gets up and goes to extra nest. Keeps going back and forth, finally settles on the 'whiskered' eggs. Frightened off the nest, it goes through the same performance on its return.

Here the disturbance caused by 'whiskered' eggs is demonstrated in the same way as that caused by color (Experiment 18).

EVIDENCE OF LEARNED BEHAVIOR IN INCUBATION

In the course of experimentation it became apparent that the birds could quickly become adjusted to new incubating situations. Experiments were therefore devised to test the extent to which place habits could be acquired in a short time. A bird was tested in two experimental situations and the influence of the first trial in modifying the response in the second determined.

Experiment 27

a.—Nest with three eggs moved twelve inches.

Result: Bird sits on it all day.

b.—Next day, the bird is still sitting. Another, similar nest with three eggs is placed on the site.

Result: The bird was extremely disturbed and did not settle down all afternoon. Next day, four eggs were found in the off-site nest, two in the on-site nest, but only the on-site nest was warm and only it was seen incubated thereafter.

This indicated that the bird first sat on the off-site nest but that the attraction of the nest on site was suffiicent to make it roll one egg into the off-site nest from it. Finally, the attraction of the site-nest induced the bird to return there, after which the four eggs in the extra nest were not moved. The bird was very much disturbed by the situation, which it would not have been if the first situation had not been experienced (Experiment 1).

Experiment 28

a.—Extra nest placed 18 inches from nest. Eggs from nest placed in extra nest.

Result: Bird sits on extra nest after some hesitation.

b.—After the bird has been brooding for six hours, an extra set of eggs is placed in the original nest in addition to those in the duplicate nest.

Result: Bird sits thirty minutes on duplicate, then gets up and goes to original nest. Still there, three hours later, when observations were discontinued. (Note: If the bird is presented with a nest with eggs on the site versus a nest with eggs off the site without any previous disturbance, it normally sits on the site without reacting at all to the extra nest with eggs—see Experiment 1.)

Experiment 29

a.—Nest moved 18 inches with eggs.

Result: Sits on nest with eggs after some hesitation.

b.—After four hours of incubation, grass at original site flattened, set of eggs put there.

Result: Bird lands, stands hesitating between the two spots, flies off; does this four times, then settles on nest with eggs. (It would normally sit on eggs on site—Experiment 3.)

c.—Eggs on original site, placed in nest (still on original site).

Result: Bird sits on off-site nest all afternoon, but nest on site is the only one warm next morning and is the only one seen incubated thereafter. (See note, Experiment 28.)

Experiment 30

a.—Nest moved 12 inches, eggs left on site.

Result: Bird sits on eggs.

b.—Eggs added to nest (in addition to those on site).

Result: After hesitating and alternating for over three hours, the bird finally settles on nest. Next morning, nest warm, eggs on site slightly so; only the nest seen incubated that day in the morning but it is deserted for the site later in the day; only the site seen incubated thereafter. (Note: If the bird is presented with eggs on site versus nest with eggs, without any previous disturbance, it goes to the eggs on site—see Experiment 3.)

Experiment 31

a.—Nest and eggs each 12 inches from site, on opposite sides.

Result: Bird spends over one hour going from nest to eggs and back. It sits on nest for two minutes, appears uncomfortable, gets up and walks to the eggs, sits, gets up in thirty seconds, walks to nest, etc. Finally settles on eggs and scoops out a hollow under them.

b.—Set of eggs added to nest.

Result: Bird sits on nest with eggs with practically no hesitation. (Normal; see Experiment 6.)

c.—Nest with no eggs placed on site.

Result: Bird hesitates 30 minutes between the two nests; finally sits on eggs (walking past site to do so); gets up after 30 minutes, walks past site to nest with eggs (off site); settles there.

d.—Eggs placed in nest on site.

Result: Bird sits on off-site nest with eggs, after 45 minutes hesitation, for four hours, then moves to nest and eggs on site. Sits there all the rest of the afternoon with occasional standing up and looking at the off-site nest. (See note, Experiment 28.)

Experiment 32

a.—Nest moved 12 inches, eggs left on site.

Result: Bird sits on eggs, hollows out nest around them.

b.—Eggs moved to moved original nest; hollowed-out new nest left in position.

Result: Bird sits on nest with eggs.

c.—Eggs (extra) added to the new nest on site.

Result: Bird sits on nest and eggs off site. (See note, Experiment 28.)

DISCUSSION

The different species of gulls apparently exhibit marked difference in their tendency to roll back displaced eggs into the nest. *Larus ridibundus*, according to Skrebitzky and Bibikova (1936), will roll eggs back into its empty nest from distances of at least a meter. If there are some eggs in the nest, this species will roll them back only from distances less than 15 cm. away. Kirkman (1937) has shown in this species that if the nest is empty all the eggs will be rolled back from a distance of 20 cm. but that only 80 per cent will be rolled back if there are some eggs in the nest. *L. argentatus*, which builds a more elaborate nest than either *L. ridibundus* or *L. atricilla*, is more attracted by the nest than are these species. Tinbergen (1936a) found that if its eggs are placed outside the nest, the bird tends to sit on the empty nest, instead of on the displaced eggs. Steinbacher (1937) and Goethe (1937) agree with Tinbergen that the Herring Gull does not often roll its eggs back into the nest. There is, however, considerable variation of this tendency within this species. Goethe (1937) found that if the eggs are placed more than 20 cm. from the nest the bird will sit on the empty nest. Steinbacher secured different results. At 20 cm., three clutches which he experimented with had a new nest built around them, while four other clutches were rolled back into the empty nest. At a distance of 40 cm. from the nest, three clutches were rolled back, one deserted and six accepted on the new site. At one meter, 29 clutches were accepted at this distance from the nest, four were rolled back and 34 were deserted. This discrepancy between the findings of Goethe and Steinbacher may be due to the fact that the experiments were performed with gulls at different stages of incubation.

It is apparent that gulls and terns building shallow nests roll their displaced eggs more than do birds building deeper nests. Goethe (1937) states that *L. argentatus* very rarely knocks an egg out of the nest when leaving it. Kirkman (1931) finds that, in *L. ridibundus*, this happens "not infrequently." We found no certain case of this in *L. atricilla*, although displaced eggs were seen four or five times. Hence, gulls which build shallow nests have greater opportunities of rolling back displaced eggs than do species building deep nests. Just as Herring Gulls which build deep nests, tend to ignore displaced eggs, so passerine birds, which build even more elaborate nests, ignore their young when these are thrown beyond the rim of the nest by a parasitic cuckoo (Chance, 1922). In both Herring Gull and passerine bird, the extensive work which has gone into the nest construction seems to take the attention of the bird away from the biologically more significant object.

The different results secured by different workers with a single species of gull may be due in some cases to different methods of testing. For example, Skrebitzky and Bibikova (1936) placed a series of eggs and nests of *L. ridibundus* on opposite sides of the original nest site and 20 cm. from it. In 85 per cent of the cases (number not stated) the birds sat on the site and eventually rolled the eggs to it. In the other 15 per cent of the cases they sat on the eggs and built a new nest around them. Kirkman (1937) placed the nest, eggs and site at the respective apices of an equilateral triangle. Sixty per cent of a series of twenty birds sat on the eggs and built a new nest around them. In 10 per cent of the cases they rolled the eggs to the site and in 5 per cent of the cases they rolled the eggs to the nest. In the remaining 25 per cent of the cases they sat on the empty nest. In brief, Kirkman, unlike Skrebitzky and Bibikova, had proved that the nest was of some attraction to the parent birds of *L. ridibundus*. The difference in the results is probably due to the fact that the strength of the attractions of nest, eggs and site, respectively, in the two experiments is different because of the arrangement of the incentives. At least a gull standing in the center of a triangle having 18-inch sides would have its head only a few inches from the nest.

In some cases the differences between the results secured by different workers may be due to differences in the activity of other birds in the immediate vicinity. For example, Skrebitzky and Bibikova found that if the nest with its eggs of *L. ridibundus* is moved from 20 cm. to one meter away from the site the bird is attracted more by the nest and eggs than the site and broods in the new location. Kirkman, however, noted that if a nest of this species is moved close to that of another gull, the owner of the first nest will move its eggs out of the nest and back to the site in spite of the fact that the bird's first reaction is the same as that reported by Skrebitzky and Bibikova.

When due consideration is given to the different methods that have been employed in studying the reactions of gulls to the several factors in the nest situation, it still seems that there are constant species differences. The Herring Gull is not only more attracted by its nest than is the European Black-headed Gull but it seems to be more attracted by the nest site. Goethe (1937), for example, found in one case that when he moved the nest and eggs of a Herring Gull 28 cm. the bird ate the eggs. Skrebitzky and Bibikova (1936) assumed that the site was more attractive than the nest in the case of *L. ridibundus* because when they moved the nest of this species 20 cm., leaving the eggs on the site, the bird incubated the eggs and hollowed out a new nest around them. It is probable, however, that the parent birds were in this case responding to the eggs and not to the site at all. If the eggs are placed in the nest instead of on the site, in the otherwise same situation, the bird sits on the nest. Tinbergen (1936), on the other hand, found that if the eggs of the Herring Gull are placed only a short distance from the site while the empty nest is left on the site, the parent will brood them only if a nest form is built under them. It may, therefore, be concluded that the nest hollow itself is attractive to the Herring Gull, irrespective of its relation to the site.

It was shown above that artificially coloring the eggs of a Laughing Gull would seriously modify the incubation behavior of a parent bird. The Laughing Gull builds crude nests and similarly the terns, which build simple nests, are disturbed by a change in color of their eggs. Dircksen (1932) found that in the case of *Sterna sandvicensis* the substitution of fowl eggs, colored either red or blue or left white, caused considerable hesitation in brooding. Eventually the parent would settle on the nest except in some cases when red eggs were employed. Marples and Marples (1934), experimenting with *S. hirundo*, also found that red or blue eggs were definitely disturbing, although they were usually later accepted. Similarly coloring the eggs of *S. fuscata* caused a marked hesitation (Watson, 1908). The Noddy Tern, *Anous stolidus*, unlike these other terns, builds well-formed nests in bushes and Watson found that coloring the eggs produced little change in the behavior of the parents. The extreme stage of sensitivity to slight differences in the eggs is found in the Atlantic Murre as reported by R. A. Johnson (personal communication). This species builds no nest, laying eggs on the surface of ledges on the rocky cliffs of its nesting colonies. When Johnson interchanged the eggs of three individuals sitting close together, the birds, on their return, each rolled its own egg back to the original site and sat on it, thus restoring the situation to what it was before the experimenter disturbed it.

From such data as the above we might expect that the gulls which build poor nests would be very sensitive to changes in the color of their eggs while, conversely, the better nest builders would ignore these changes. These correlations do not seem to work out in detail. As shown above, *L. atricilla*, a poor nest builder, is very sensitive. *L. ridibundus*, another poor nest builder, according to Skrebitzky and Bibikova, and Kirkman, will accept eggs of a great variety of colors without hesitation. On the other hand, a better nest builder, *Larus argentatus*, hesitates before yellow, green or blue eggs (Goethe, 1937) but most birds would brood them. When normal eggs were placed with blue eggs on the edge of the nest only the normal eggs were rolled into the nest. In the double nest situation (two nests on the original site) with the normal eggs in one nest and colored eggs in the other, Booy and Tinbergen (1937) failed to secure a marked preference for the normal eggs. Only red eggs were markedly disturbing in this situation and in the single nests. This, therefore, is a clear-cut difference between these two species of gulls and, oddly, the better nest builder is the more disturbed by the red eggs.

In view of our experiments with *L. atricilla*, it becomes even more apparent that species differ in the attention they pay to the details of the egg regardless of the elaborateness of the nest. *L. atricilla* in a double nest situation can distinguish its own eggs from models that resemble them closely. Similarly, the North American Cowbird, *Molothrus a. ater*, parasitizes successfully many species of passerine birds but the European Cuckoo, *Cuculus canorus*, apparently meets with greater resistance from its hosts. Rensch (1925) found that in the case of several European passerines complete clutches of eggs painted red were accepted far more often than single red eggs introduced into a nest of normal eggs. Into one nest of *Sylvia borin*, from which the eggs had been removed, Rensch placed the same number of *Sylvia curruca* eggs. The latter eggs were accepted but when later the parent laid a single egg this was rejected, apparently because it was unlike the other eggs. It is, therefore, not surprising that the cuckoos that parasitize *Sylvia borin* must lay eggs which resemble the eggs of that species closely, as Makatsch (1937) has shown. All this attention to discordant eggs in the clutch is far more precise than the behavior of gulls even though the nests of passerine birds are more elaborate.

Although passerine birds are disturbed by changes in the clutch as a whole, other birds seem to pay attention to details in the eggs *per se*. The Ringed Plover, *Charadrius hiaticula*, will accept spotted eggs of a variety of colors but will fail to incubate unspotted eggs (Koehler and Zagarus, 1937). Although the eggs of *Larus atricilla* are spotted, the gulls will incubate eggs uniformly lacquered yellow or blue. Hence the species respond to different cues, whether these are learned or innate.

Tinbergen (1936) found that a tern, which had incubated eggs in a new location for only three minutes, returned to this site when the eggs were moved back to the original nest site. We have shown above that *L. atricilla* quickly learned a new site in which its eggs were placed. Although it is impossible to tell from the data available on gulls how much of the incubation behavior is learned and how much innate, it is interesting that two species as closely allied as *L. atricilla* and *L. ridibundus* and building essentially similar nests should differ so considerably in their reaction to the eggs. *L. ridibundus* will roll and incubate eggs of many different colors; *L. atricilla* is disturbed by foreign colors, especially red, and the intensity of its egg-retrieving behavior is greatly lessened by these colors.

Within the species, however, there are variations, some of which may be correlated with sex. Skrebitzky and Bibikova (1936) and Kirkman (1937) found that *L. ridibundus* would incubate objects having a great variety of shape and form. Our experiments with *L. atricilla* were in agreement so far as they went. Any object having a sharp edge or corner was removed from the nest unless it was small and could be worked into the nest. Booy and Tinbergen (1937) found that *L. argentatus* would incubate sharp-edged eggs (parallelopipeds) even when the normal eggs were adjacent to them. In the same species Goethe (1937) found that males hesitate or refuse to incubate polyhedral eggs. The female, however, although hesitant is less 'critical' than the male and accepts them sooner.

Text-figure 1 shows the reactions of the birds to visual cues, namely, the birds' first reactions, based on what they see. The subsequent behavior may be affected by tactile cues. In Experiment 8, where a bird sat on a spot where there were no eggs, the birds were seen to become steadily more uneasy; finally the birds, when the eggs were 12 inches from the nest, rolled them in; when they were 32 inches away, the bird, after brooding the empty nest twenty minutes, went to the eggs.

The marked difference between the egg-rolling behavior of birds incubating eggs and that of those sitting on empty nests is apparently a result of difference in tactile stimuli. In *L. argentatus* and *L. ridibundus* also, birds on nests with eggs are less persistent in egg rolling than those on empty nests. Our experiments are not sufficiently extensive to show conclusively whether this difference is an 'all-or-none' one, or whether a bird with, for example, two eggs would roll more than one with three eggs. Judging from Experiment 13e, in which the bird rolled three eggs into a nest already containing two, as well as from the remarkable persistence of *L. ridibundus*, which will roll in enough to make a total as high as nine (Kirkman, 1937), differences in the number of eggs in the nest (within the normal range) would presumably not modify the reaction.

The apparent inconsistency in Experiment 14, where the birds were shown to be able to distinguish artificial eggs closely resembling normal eggs in size, shape and color from the latter, but were unable to distinguish other gull eggs from their own even when they were distinctly different in tone and pattern, may have been due to either odor or tactile cues. Although workers with other species of gulls have shown the importance of tactile cues in certain situations, there is no clear evidence that olfactory cues enter into the response of any gull to its eggs.

The retrieving behavior of an incubating bird has been extensively studied in the case of the Grey-lag Goose, *Anser anser*, by Lorenz and Tinbergen (1938). They find that only objects with an unbroken surface are rolled back into the nest. The retrieving movements in this species are far more stereotyped than in the case of the Ringed Plover as described by Koehler and Zagarus (1937). This species may use its wing, feet, breast or bill to move the egg. In other species, such as *Sterna fuscata* (Watson, 1908) or *Larus argentatus* (Tinbergen, 1936), the return of the egg to the nest site appears to be the result of the way the bird facing away from the nest site tucks the eggs under her breast feathers in settling upon it. Kirkman (1937), however, considers the reaction a definite attempt to restore the egg to the nest and this appears to be true in *L. atricilla* when the egg is not far from the nest. When the egg is far from the nest the rolling seems to be more accidental.

CONCLUSIONS

1. *Larus atricilla* is able to distinguish its own eggs from artificial eggs which resemble them closely in form and color. It fails to distinguish its own eggs from other Laughing Gull eggs which have a decidedly different color tone or pattern.

2. Incubating birds of this species will accept and incubate eggs of various colors when placed in the nest. Red causes more hesitancy than either blue or yellow and some individuals may remove red eggs from the nest. In this antipathy to red, *L. atricilla* differs conspicuously from *L. ridibundus*.

3. Artificially coloring the eggs will disturb the retrieving reaction to displaced eggs more than it will the brooding reactions. Merely marking the eggs with different colors will disturb the incubating reactions as experiments with double nests on the nest site show.

4. Broody Laughing Gulls are attracted by (a) the eggs, (b) the nest site, and (c) the nest. At short distances the attraction of the eggs is greatest, of the nest site less, and of the nest least. This order of attraction is different in species which build more elaborate nests.

5. The retrieving reaction toward displaced eggs is stronger when all the eggs have been removed from the nest. It is greater when the number of eggs outside the nest is larger. This reaction is also stronger the nearer the eggs are to the edge of the nest.

6. Broody Laughing Gulls are more attracted by deep nests than by shallow ones, but they distinguish between them only by settling down in them. The number of eggs in the nest does not seem to modify the response provided some eggs are present.

7. Eggs of abnormal shape will be incubated but not one having a hole punctured in it. Roughening the surface of the eggs by gluing small pieces of hay to them disturbs but does not prevent the incubation behavior. A

covering of soft, rubber cement, however, will inhibit the incubation behavior.

8. A Laughing Gull will learn a new position of the nest very quickly and return to this place after the nest has been returned to the original site.

9. In general, the more elaborate the nest the more a parent bird is attracted by it but different species of gulls having essentially similar nests may differ considerably in the degree of disturbance in their behavior that a modification of their eggs will produce.

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