MARSHALL, Incubation Behavior of Common Tern

Hartert (Nov. Zool., 32: 147, 1925) says: "This peculiar bird is known only from the type specimen. It is very peculiar, the crown to the base of the upper bill nearly black, underside heavily striped. I am not sure about its relationship."

Hartert and Steinbacher (Vögel pal. Fauna, Ergänzungsband, 4: 374, 1935) says: ". . . das man für ein melanistiches stück halten möchte, doch hebt der Autor den schlankeren und spitzeren Schnabel noch besonders hervor."

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FACTORS IN THE INCUBATION BEHAVIOR OF THE COMMON TERN¹

BY NELSON MARSHALL

THE publications of Watson (1908) and Lashley (1915) contributed, among other things, an initial demonstration of the use of the egg, nest, and nest locality as subjects for controlled experiments on incubation behavior. Since their work on the Noddy and Sooty Terns, *Anous stolidus* and *Sterna fuscata*, respectively, many recent studies have centered on the relation of such factors to the incubation instinct. Though much of this research has been confined to members of the family Laridae, the accumulation of knowledge has not enabled the formation of generalizations applying throughout. Species differences occur within this family, as is clearly illustrated in the discussion by Noble and Lehrman (1940).

One might suggest that comparable experimental results of much greater value would be available if certain techniques were adopted as standards. The triangle test evolved by Kirkman (1937), working on the Black-headed Gull, *Larus ridibundus*, in which the eggs, the nest, and the nest site were offered as alternatives to the adult, is an example of a test worthy of repetition where possible. In practice, however, specific differences with respect to behavior and habitat often prevent such duplication. My program of experimentation on the Common Tern, *Sterna hirundo hirundo*, was greatly influenced by the methods of others, but the final program could not be planned till various techniques were actually tried in the field.

The research to be discussed was conducted from the F. T. Stone Laboratory of Ohio State University, Put-In-Bay, Ohio. Dr. C. F. Walker of the Laboratory staff has contributed with help and suggestions which have added greatly to the progress of the work.

¹ Contribution from the F. T. Stone Laboratory of Ohio State University.

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Colonies located on nearby islands, particularly Starve Island, were used for observations. Starve Island is located in the western end of Lake Erie, approximately one-quarter mile southwest of South Bass Island. The island is composed almost entirely of solid rock with limited stretches of large, loose gravel and with little vegetation. In 1939 the work was spread over late June and early July. Continued study during late May and early June, 1940, enabled me to check conclusions reached during the previous year and to attempt additional experiments suggested by the 1939 results.

Color banding was considered as a means of distinguishing experimental birds. The method would have limited the number of birds that could be observed. Also, I have noted that these shortlegged birds tend to obscure color bands when near the nest. It was discovered, however, that when observing from short distances, it is possible to distinguish birds by minute individual differences in color pattern. Throughout my experiments such distinctions were used with considerable success. Observations were made from a canvas blind and 8-power binoculars were used.

Recognition of the Nest Complement

The first set of experiments to be discussed involves the individual bird's ability to recognize the number of eggs present in its nest. The method merely consists of temporarily adding a desired number of eggs taken from another nest, or removing a desired number of eggs without emptying the nest. Frequently the experiments were run

 TABLE 1

 Experiments Involving Alteration of Number of Eggs in Nest

(Sequi	ence of Trials Is I	NDICATED BY NUMBERS IN PAREN	THESES)
Individual bird	No. of eggs in nest	No. of eggs added	No. of eggs subtracted
Α	1	(1) 1; (2) 2; (3) 3; (4) 4	,
в	3		(1) 1; (2) 2
С	3	(1) 1	(2) 2
D	1	2	
\mathbf{E}	3	(1) 1	(2) 2
F	2	(1) 1	(2) 1
G	4	(2) 1*	(1) 3
H∫	4		(1) 3, (2) 1*
I	2	(1) 1	(2) 1
J	3		2
ĸ	3	2	
L	3		2
м	3		1
N	3	1	

A-J trials were made in late June and early July, 1939; K-O, late May, 1940. G and H attended the same nest. Results were uniform; the adults incubated the altered number.

* The nest contained only 3 eggs when this experiment was made.

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in pairs; the eggs that were subtracted from one nest were added to another. Table 1 gives an account of the results. It shows that eggs were added to a total of nine different nests involving nine different birds. They were removed from a total of nine different nests, involving ten different birds; two adults were tried on one of the nests. Though there was a frequent short and varied period of adjustment to the new situation, in all such cases the attending adult incubated quite normally.

Additional experiments involved emptying the nests and also replacing the eggs by an equal number of egg-shaped rocks. The results, shown in Table 2, reveal that under both these experimental

TAB	LE 2
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BEHAVIOR OF ADULT COMMON TERNS AT EMPTIED NESTS AND AT NESTS WITH EGGS Replaced by Rocks. (Sequence of Trials Is Indicated by the

NUMBERS	IN	PARENTHESES)

Individual bird	No. of eggs in nest	Nest emplied	Eggs replaced by equal number of egg-shaped rocks
Α	1	(2) Settled on nest	(1) Settled on rocks
в	3	Failed to settle	
С	3		Failed to settle
D	1	(1) Settled on nest	(2) Settled on rocks
Ę	3		Failed to settle
\mathbf{F}	2	(1) Failed to settle	(2) Failed to settle
G	4	(2) Settled on nest but restless	(1) Failed to settle
I	2	Settled on nest	(2) Settled on rocks
J	3	Failed to settle	
N	3	Settled on nest	
0	3	Failed to settle	

A-J trials made in late June and early July, 1939; N and O, late May, 1940.

conditions some birds actually attended their nests as though incubating, while others did not. If of value for no other reason, these responses suggest the existence of individual differences and possibly, to some extent, sexual differences, phases of tern behavior to be discussed below.

Normal nest attendance was thus observed in all cases of decrease or increase in the number of eggs present except when the nest was emptied completely. Several trials were run long enough to establish the bird's attendance for over ten minutes, but it might be questioned that this constitutes normal attendance. As a check, fifteen nests known, by observations from the blind, to be attended were subjected to a variety of rearrangements in egg content involving increase, decrease, and exchange of eggs. Two days later I observed these nests from the blind and noted that they were attended, with the following two exceptions: the only one that had been emptied completely, and the only one in which a rock had been substituted for the single

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egg present. In the remaining thirteen nests the terns had accepted the altered complement of eggs.

The trials show that a Common Tern is not markedly disturbed by an alteration of the number of eggs in its nest and will attempt to incubate all eggs present. In considering situations where this might have some bearing on the nesting behavior, the following circumstances and probable behavior are described:

(1) A Common Tern will not forsake its nest when an egg is broken or removed by a predator. On occasions I have seen attending terns removing pieces of broken eggs from their nests.

(2) It is not unusual for a misplaced egg to be left a short distance outside a nest for a prolonged period, then later be rolled into the nest. The rolling of such an egg, likely as not addled by the time it is rolled, is probably done by one adult. The mate, however, will not forsake the nest because of the addition.

(3) It is quite possible, as can be seen from experiments described below, that a tern might roll a foreign egg (misplaced from a nearby nest) into its own nest. If such an egg were more advanced than the original-nest eggs, its hatching might alter the adult's nesting behavior and prevent proper incubation of the younger eggs.

(4) Should another adult, behaving abnormally, lay an egg in a foreign nest, attendance at this nest would not be interrupted. Such a parasitic egg would probably receive improper attention unless it hatched with, or soon after, the other eggs of the nest.

The first two of the above conditions are known to exist. As to the third, Marples and Marples (1934: 185, 186) described an experiment in which two nests of three eggs each were moved till they were 18 inches apart. One pair of adults took possession of all eggs by rolling the neighboring three over into their own nest. A nest of six eggs I once observed at Middle Island, Ontario, may have resulted from a similar situation in nature. The fourth condition described above remains theoretical.

EGG ROLLING AND EGG RECOGNITION

Common Terns have a definite tendency to roll their eggs when these become displaced from the nest, either by a natural accident or by the hand of an experimenter. The avian egg-rolling behavior involved is essentially like that described by Lashley (1915) for the Sooty Tern, and by Tinbergen (1934) for the Arctic Tern, *Sterna paradisaea*. An adult, after it has returned to the nest, may notice such a displaced egg. It may then walk toward the egg, but sometimes it turns back and makes several partial approaches before reaching it. When it can reach the outside egg with its beak, it stops and rolls the egg under its body. Since the bird is almost invariably facing away from the nest, eggs are thus rolled closer to the nest each time this complex reaction is completed. No evidence of implicit behavior can be detected. To learn more concerning the factors involved in egg-rolling by the Common Tern, experiments were devised as described below.

One type of trial involved placing the entire set of eggs six inches outside the nest, the measurement being taken from the center of the nest in all experiments. Trials were continued, for varying periods of time, until the adults exhibited some definite reaction toward either their nests or eggs. These reactions are recorded in the third column in Table 3. The experiments were carried out on a total of sixteen different nests involving eighteen different birds, since on two of the

TABLE 3

EGG ROLLING EXPERIMENTS ON THE COMMON TERN WITH AND WITHOUT A COMPLETE SET OF EGGS IN NEST. (SEQUENCE OF TRIALS IS INDICATED BY NUMBERS IN PARENTHESES)

	No. of eggs		Nest eggs placed	
	comprising		6 inches outside;	Substitute eggs placed
Individual	nest com-	Nest eggs placed	substitute eggs placed	6 inches outside;
bird	plement	6 inches outside	in nest	nest eggs left in place
I)	2	(1) Stood near nest		
11	2	(1) Settled on nest	(2) Incubated at nest	
m	1	(1) Incubated egg		
		(2) Rolled egg		
IV	1	(1) Rolled egg	(3) Incubated at nest	
		(2) Settled on nest		
v	1	(1) Settled on nest	(3) Incubated at nest	
		(2) Settled on nest		
VI	3	(1) Settled on nest	(3) Incubated at nest	
		(2) Settled on nest		
VII	3	(1) Rolled eggs	(3) Rolled eggs	(5) Rolled eggs
		(2) Rolled eggs	(4) Rolled eggs	
VIII	1	(1) Rolled egg	(3) Incubated at nest	(5) Rolled egg
		(2) Rolled egg	(4) Rolled egg	
IX	2	(1) Rolled eggs		
X	4	(1) Rolled eggs		
XI	4		(2) Incubated at nest	(1) Incubated at nest
XII	2	(1) Rolled eggs	(3) Incubated at nest*	(2) Incubated at nest
\mathbf{XIII}	2	(1) Settled on nest		(2) Incubated at nest
XIV	2	(1) Rolled eggs	(2) Incubated at nest	
$\mathbf{x}\mathbf{v}$	2	(1) Rolled eggs	(3) Incubated at nest	(2) Incubated at nest
XVI	1	(1) Rolled egg		(2) Rolled egg
XVII	3	(1) Rolled eggs		(2) Rolled eggs**
XVIII	3	(1) Attended eggs after attempting to roll them		
XIX	3	(1) Rolled eggs		(2) Incubated at nest or rolled eggs
$\mathbf{X}\mathbf{X}$	3			(1) Incubated at nest
XXI	3			(1) Rolled eggs

I-XVII trials made in late June and early July, 1939; XVIII-XXI, late May, 1940. Brackets indicate adults attending the same nest.

* The nest complement consisted of 1 egg when this experiment was made. ** The nest complement consisted of 2 eggs when this experiment was made.

nests both the attending adults were the subjects of tests. In one instance the adult merely stood near its nest. In two trials the adults, after first going to the nest, incubated the eggs in the changed locations. However, the behavior of these two adults differed markedly; whereas bird III incubated without any attempt to accomplish an easy roll into the nest (it did roll its egg when tested two days later), bird XVIII tried in vain to roll its eggs over a rough surface before commencing to incubate them. In seven trials the adult did not roll the outside eggs but settled in the empty nest as though incubating. Actual rolling occurred in fourteen, the majority of trials.

In a second type of experiment, the nest eggs were placed six inches outside the nest and substitute eggs were placed in the nest. As in the first type, the trials were conducted until definite reactions were displayed and these results are recorded in the fourth column of Table 3. The experiments involved a total of twelve different nests and twelve different birds. In nine trials the adult incubated the eggs in the nest, but did not roll the outside eggs. In three trials the adult not only incubated the eggs in the nest but also rolled the outside eggs toward the nest.

A third type of experiment involved leaving the nest eggs in place and putting an equal number of eggs (taken from another nest) six inches outside. The fifth column in Table 3 indicates reactions displayed by the adults in trials conducted as described above. The experiments involved a total of eleven different nests and eleven different birds. In five trials the birds incubated the nest eggs but did not roll the additional eggs toward the nest. In five trials the birds not only incubated the nest eggs but rolled the additional eggs from outside. It will be noted that in experimenting with the bird labeled XIX it was not possible to tell whether the bird would roll the outside eggs. It made preliminary gestures at rolling and then hesitated at length. Fear that rolling the eggs over rough terrain might result in breakage caused me to discontinue the trial after eight minutes.

It is possible that learning might influence the reactions of a bird subjected to more than one of these experiments. The results shown in Table 3, where the sequence of trials is given, yield only negative information as to the effect of the learning process and possible modifications due to learning cannot be detected.

In this demonstration of egg rolling, the existence of marked variations is brought to attention again, as in the last of the experiments involving the nest complement. Kirkman (1937) has discussed egg rolling as a test of individual capacity in the Black-headed Gull. He considers the variations exhibited as being based primarily on differences in innate capacity. The variations I have recorded in eggrolling experiments on the tern are also very suggestive of individual differences in innate capacity. It seems necessary, however, to consider other factors which might contribute to variation in behavior. Such factors are:

(a) The extreme irregularity of the island surface is such that the task of rolling eggs, or even seeing them, differs. This variable would have less significance on habitats of smoother surface.

(b) The proximity of other nests is a probable factor that has been mentioned by Palmer (1941).

(c) The direction a bird approaches the nest and sits on it, once it has arrived, affects the possibilities of this bird being attracted by an egg outside the nest. It seems probable that such a cause for variation would be effective in other species; however, in such birds as the Sooty Tern where the existence of a definite path of approach to the nest has been established (Lashley 1915), such error might be counteracted.

(d) No data are available as to the stage in the nesting cycle and the state of other physiological factors. Such an objection would seem to apply to Kirkman's interpretations as well.

(e) As in most Laridae, the sex of the adult Common Tern cannot be detected in the field. Some differences in behavior may be partially or wholly associated with the sex of the birds.

Noble and Lehrman (1940) discuss the fact that the retrieving action toward displaced eggs is greater in the case of birds sitting on empty nests. Palmer (1941) writes as follows: "... it may be said that Common Terns roll eggs farther to empty nests than to those containing part of a clutch." This generalization, though apparently based on observations, is not accompanied by experimental data. In my egg-rolling experiments, the birds rolled eggs in fourteen out of twenty-four experiments, or 58% of the trials when the nest was empty, but in experiments in which the nest was not empty, the birds rolled eggs in nine (one of which is questionable) out of twenty-three, or roughly 40%, of the trials. It thus seemed worth while to design experiments for a further analysis of this question. In doing so, nests were selected having three eggs, the predominant nest complement for the Common Tern, and situated on comparatively open, smooth terrain where variables in the difficulty of rolling would be minimized. First, all three eggs were placed twelve inches from the center of the nest. Next, one egg was placed twelve inches outside and two were left in the nest. If anything, the bird's experience from rolling three eggs would tend to lessen the time required to attempt rolling the one egg in the trial that followed.

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In the following descriptions of the experiments (Table 4), the time indicated was recorded from the moment the bird first alighted

EGG ROLLI	ing of the Common Tern in Comple	TELY AND PARTIALLY EMPTIED NESTS
Individual bird	Three eggs 12 inches outside	One egg 12 inches outside, two eggs in nest
1	Bird started to roll eggs in 2 minutes.	Bird flew three times on general alarm flights during the 14 minutes under observation and on three occa- sions it approached the outside egg but did not roll it.
2	In about 2 minutes bird sat on outside eggs. Started to roll eggs 9 minutes after first alighting.	Bird was observed to incubate at nest quietly for 12 minutes with no noticeable expression of an interest in the outside erg.
3	Bird flew on two general alarm flights after first alighting but in 6 minutes it started to roll its eggs.	Bird flew on five general alarm flights during the 13 minutes under observa- tion, but it incubated well when at nest with no noticeable expression of an interest in the outside egg.
4	Bird flew on one general alarm flight after first alighting but started to roll its eggs in 2 minutes.	After 6 minutes of incubating very quietly and facing in the direction of the outside egg, the bird went to the latter and rolled it.
5	Bird started to roll eggs in 3 minutes. One egg immediately rolled into nest and the bird incu- bated this, keeping its head turned away from the remaining outside eggs during the next 7 minutes it was observed.	Bird incubated on the nest, facing away from the direction of the out- side egg for the 7 minutes it was under observation.

TABLE 4

near the nest after the eggs had been arranged. In the left-hand column is a description of the bird's behavior when all its eggs were outside the nest; opposite that description is an account of the behavior of the same bird at the same nest when only one of its eggs was placed outside. In each trial the observations were continued long enough to note some distinctive behavior in comparison with the behavior exhibited in the contrasting experiment. Unfortunately, 'up-flights' (flights of general alarm involving many individuals) were frequent, but that is always true in the colony shortly after I enter my blind. Some of the experimental birds, however, remained at their nests during such up-flights, so I doubt that the rearrangement of eggs was the cause for alarm.

The conclusion is that an incubating Common Tern has a distinctly greater tendency to roll outside eggs when the nest is empty than when it is partially full. The results are quite in accord with the generalization made by Noble and Lehrman and with the behavior exhibited by the Arctic Tern in Tinbergen's (1934) experiments.

In their rolling performances, Common Terns respond as though

unable to recognize their own eggs. The fact that additional eggs were rolled into the nest, even though the full nest complement existed, greatly strengthens this view. It will be noted from Table 3 that the two birds known to roll their own eggs from outside when substitute eggs were in the nest also rolled additional eggs from outside when their own eggs were in the nest. Thus the experimental results are in accord with the generalization made by Tinbergen (1934) to the effect that investigators working with colonial birds are unanimously of the opinion that the birds do not recognize their own eggs. When we consider, however, that Johnson (1941) discovered an exception to this in the Atlantic Murre, Uria aalge aalge, it seems possible that we may be dealing with an indifference rather than a lack of recognition on the part of the majority of the birds studied.

A generalization made by Goethe (1939: 34) for the Laro-Limicolae states that the nest and nest site play a greater rôle than the egg itself. Noble and Lehrman (1940) designed experiments to evaluate the relative attraction of the nest, the site, and the eggs as each affected the incubating reaction of the Laughing Gull. They conclude as follows: "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." In discussing the observations of other workers, these authors demonstrate the existence of species differences within the family; so it is interesting to consider the attraction of these factors to the broody Common Tern.

From experiments involving moving the eggs of the Common Tern in excess of the maximum retrieving distance, Marples and Marples (1934) found that terns accepted their eggs in the new locality. The time required for such acceptance was greatly decreased when the nests were moved with the eggs. These authors conclude as follows: "It would seem, from these results, that a Tern will follow its eggs and that it is the eggs, as is proper, rather than the site of the nest which loom largest in the bird's affections."

The same authors conducted experiments in which the eggs were buried in the sand at the nest site, inevitably destroying the nest structure; yet the Common Terns found their nest locations and, in the majority of trials, uncovered their eggs. In the egg-rolling experiments that I conducted, the terns invariably went to the nest location first. Some of the nests involved were of elaborate structure and some were, in effect, structureless; furthermore, since adults were repeatedly picking up sticks and dropping them in the direction of the nests, they must be considered as distinctly dynamic structures. Nevertheless, an approaching tern exhibited further reactions only after going onto the nest location. In view of these facts it seems logical to designate not the nest but the nest site as the source of attraction. This view is further supported by my experimentation on factors of recognition, discussed below.

It does not follow, however, that the nest site, which is first to attract the approaching adult, is necessarily the greatest source of attraction to an incubating tern. The nest and nest site would be abandoned if no eggs were available either in, or to be rolled in, for incubation. It thus seems difficult, with respect to the Common Tern, to isolate these factors and decide which has the greatest attraction.

Recognition of the Nest

A fascinating topic in a colony of nesting birds is the question of nest recognition. Working on Starve Island on July 11, 1939, I attempted to confuse the birds by disturbing various distinctive aspects of the scenery close to their nests. In only one of seven such cases did the attending bird give evidence of being confused as to its nest site. In this instance a large clump of weeds was removed from next to the nest, and a board was shifted from the west to the east side of the nest. The bird involved failed to find its nest until the conditions were restored as well as possible. It is noteworthy that in one case I moved a flat stone block, with an area of approximately four square feet from a position close to one nest to a corresponding position near another nest 4 feet, 8 inches away. The attending bird (I was watching the one at the first nest mentioned) went to its nest without delay or evidence of confusion.

At a later date I experimented with six nests by moving all of the nest material six inches away from the nest site but leaving the eggs on the site. The birds involved went directly to their eggs and incubated well, and in only one trial the attending adult picked at the moved nest sticks.

On July 13, 1939, I had an opportunity to make comparable tests in a colony at Middle Island, Ontario, Canada. In contrast to the habitat at Starve Island, this colony was established on a long gravel bar, vegetation was practically absent, and in many cases only the debris present distinguished one stretch of the bar from another. At first I placed my blind in a region where there was considerable beach debris and where the surface consisted of rounded rocks about three inches in diameter. Here I experimented with two nests but failed to confuse the adults. Later I placed the blind farther out on the gravel bar where there were nests situated on fine gravel with comparatively little debris about them. This was a favorable place to work, for there was little differentiation in the appearance of one small area from the next. Experiments were conducted as follows:

Nest F-1 contained two brownish eggs placed in a shallow cup in the fine gravel. Sticks were absent from the nest but a few "nest sticks" were noticed just to the north of it.

(A) The surroundings were altered by scraping gravel all about the nest, making an especially large hollow to the northeast and a mound of gravel to the north of the nest. The position of some small rocks was also altered. In three minutes the bird arrived and went directly to the nest.

(B) The nest surroundings were left as described under A. The eggs were replaced by two eggs of a light blue background color, and the bird's own eggs were placed in an artificially-made depression one yard to the west of the nest. In two minutes the bird came to the nest and incubated the foreign eggs.

(C) The proper eggs were returned to nest F-l and the substitute eggs removed. The surroundings were left as altered under A, except that the nest sticks mentioned as being just north of the nest were moved about seventeen inches westward and the west side of the nest depression was leveled off. When the bird alighted from the west it went to the sticks first, but soon went to its eggs.

Nest F-2 contained three light-brown eggs, and was composed of considerable stick material. Two larger sticks were on each side of the nest but there was no other debris within four yards of the nest site.

(A) The sticks from the nest were placed about sixteen inches westward and the two small debris sticks mentioned were removed. The bird went to the nest in one minute and without hesitation.

(B) The nest sticks were left as placed in A. The two debris sticks which had been removed in A were then placed so that they had the same relation to the nest sticks as had existed before the latter were removed. In about one minute the bird alighted at the nest sticks. Then it went from the nest sticks to the eggs and back three times, after which it went to the eggs and incubated normally.

Nest F-3 contained two light-brownish eggs, one of which was cracked. I noted that the bird would alight at a point from which it approached its nest by going over a small log. The log almost undoubtedly prevented the bird from seeing the nest from the alighting place. A much larger log in the background was conspicuous as a landmark.

(A) The small log was moved about sixteen inches westward, thus making the nest visible from the alighting place. In four minutes the bird arrived and went directly to the nest without hesitation.

Nest F-4 contained three brown eggs. It was just west of the large log mentioned in F-3.

(A) The small log mentioned in F-3 was moved about sixteen inches farther to the west. This log then had the same relation to F-4 that it originally had to F-3. The bird came to its nest immediately.

Nest F-5 contained three light-brownish eggs located in a small depression in the gravel with small nest sticks around, but not in the center of, the nest depression.

(A) The nest sticks were moved about sixteen inches eastward. In one minute the bird came and incubated the eggs.

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(B) Some debris, which had been lying with its closest end about a foot from the nest, was moved so that it regained its original relation to the moved nest sticks. In two minutes the bird returned to the nest and incubated the eggs.

(C) The eggs of nest F-5 were placed in the newly constructed nest (A and B). Within one minute the bird landed at the old nest site. It acted confused, flew off, and soon returned to a spot between the new nest and the old nest site. It went to the new nest, then to the nest site, then flew. It returned, alighted at the old nest site, walked to the new nest, and repeated walking back and forth. Soon another bird came and approached the new nest, but the first bird drove it off. This happened three times, with apparently the same intruder involved in each case. Then the first bird flew off, returned to the old nest site, then to the new nest, and was walking back and forth when I closed the experiment after six minutes of such observation.

Nest F-6 contained three light-brownish eggs, one of which was broken. The eggs were in a small gravel depression which had a few nest sticks about it. The nearest debris consisted of a small stick and a small block of two-by-four-inch timber, about twelve inches and sixteen inches away, respectively.

(A) The nest sticks were moved about sixteen inches to the northwest. The bird alighted in about one minute and proceeded to attend the eggs.

(B) In addition to the change made in A, I placed the stick and piece of timber so that they resumed their original relation to the moved nest sticks. The bird alighted to the westward and then went to the eggs. Soon it flew and alighted again, less to the westward than before, and went to the eggs. It soon flew again and returned well to the northwest. As it walked toward the eggs, it hesitated a while at the nest sticks and then walked to the eggs.

Two more nest recognition experiments were conducted on Starve Island, May 25, 1940. It was known from experience that pronounced changes would be necessary to confuse the adults in such well-marked surroundings as exist on Starve Island. In the following experiments outstanding changes were made with this in mind.

Nest L-2 contained three brownish eggs and was of average size. Most conspicuous landmarks were a ten-foot, three-by-four-inch timber situated thirty inches east of the nest, and half of a barrel about five feet away.

(A) The 'three-by-four' was moved so that it lay close to the eastern edge of the nest; the barrel was covered with a blue sweater. The bird was confused to the extent of sometimes entering another nest, but in four minutes it incubated its own eggs normally.

Nest L-3 contained three light-brownish eggs and was of average size. It was conspicuous for the accumulation of debris about it.

(A) I cleared the surroundings of debris which consisted of a short 'two-by-four' timber, a plank, a few small boards, a broken baseball bat, and a rusty can. The bird alighted and went directly to its nest.

A patently subjective method has been used in the above experiments. Since nest recognition undoubtedly involves some learned behavior, variables, such as the amount of time a tern has attended the nest and the bird's familiarity with natural changes in the vicinity, probably affected the experimental results. There are, however, certain general observations to be made from these trials. The terns were more easily confused by rearrangement of nest surroundings in the relatively uniform gravel bar of Middle Island than in the highly differentiated terrain of Starve Island. This leads to an analysis of the experiments conducted on Middle Island.

In F-5 experiment C, the bird found its nest and eggs arranged quite normally, but this new nest arrangement was sixteen inches away from the original nest site. The bird apparently retained, by means of some gross landmarks, a recognition of its old nest site, but by minor landmarks it recognized the newly constructed one. The eggs, as objects to be incubated, must have added greatly to the attraction of the new nest site, but in the short time allowed, the bird did not settle on them. In nest F-1 experiment B, the bird's eggs were placed in a newly made nest a yard from the original nest site, but substitute eggs were in the original nest site and these were readily accepted.

Nest F-6 experiment B, illustrates quite clearly the relation between larger and smaller landmarks in nest recognition. With the nest sticks and the surrounding debris moved sixteen inches to the northwest, we note that the bird alighted farther to the westward as it approached. It seems apparent that the nest sticks and the debris influenced this. On noting that the bird paused at the nest sticks between its alighting place and the nest, it seems highly probable that the nest sticks alone effected this pause.

Studies have not proven conclusively that any birds fail to recognize their own eggs, but it has been repeatedly proven that many colony-nesting birds act indifferent to such recognition if, perhaps, it does exist. Quite likely, Common Terns have a brief memory of the number of eggs in their nest, but the stimulus for incubation is effective when the number has been altered. It has also been stated that in all my experiments in which eggs were placed outside the nest, the bird returned to its nest site before reacting to the disturbed nest conditions. With these facts and the above nest recognition experiments in mind, it appears that a given locality is the object of recognition. This locality consists of eggs; often a depression in the sand, gravel, or even in the rock; often a variable amount of sticks under and about the eggs; and all surrounding landmarks from the small pieces of debris nearby to such things as large trees or rocks or the distance to the water. There is no evidence that any one of these things has any greater significance as a constituent in the recog-

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nition of this locality than the simple part it plays in composing the landscape.

SUMMARY

Reduction of or addition to the number of eggs existing in a Common Tern nest does not alter the normal attendance of the adults, if at least one egg remains.

Some Common Terns will roll eggs into their nests when the latter are empty. Some will roll their own eggs into their nests even if a normal complement of substitute eggs has been placed there; moreover, terns are known to roll additional eggs into their nests even if their own eggs are in normal position. Great variation exists in eggrolling performances. Possible causes for such variation are mentioned; however, these appear complex and have not been fully analyzed.

The tendency to roll displaced eggs is strongest when all the eggs have been removed from the nest.

The nest site, rather than the nest itself or the eggs, exerts the initial attraction to the broody Common Tern as it alights in the colony.

Responses of the Common Tern show that it either fails to recognize its own eggs or acts indifferently to such recognition. The total appearance of the locale is used by an approaching tern in finding its eggs. The eggs, the nest, and the immediate and the more distant landmarks are the constituents of this landscape, and it is merely as such constituents that each serves in 'nest recognition.'

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