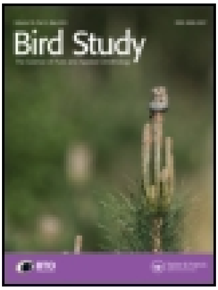

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Egg shell removal by the Black-headed Gull (Larus r. ridibundus L.) II. The effects of experience on the response to colour

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Egg shell removal by the Black-headed Gull (Larus r. ridibundus L.)

II. The effects of experience on the response to colour

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INTRODUCTION

Black-headed gulls remove the empty egg shell shortly after the hatching of the chick. An investigation into the survival value of this response and of the stimuli eliciting it (Tinbergen *et al.*, 1962) yielded the following results. An empty egg shell at a distance of 4 inches from a single egg laid out in the dunes renders such an egg more vulnerable to predation by Carrion Crows (*Corvus corone*) and Herring Gulls (*Larus argentatus*); this suggests that egg shell removal may help to reduce predation.

The response can be elicited throughout the incubation period by a variety of objects in the nest or on its rim, in fact by 'any object which does not resemble an egg, a chick, or nest material' (*loc. cit.*) although the egg shell itself is optimal. In systematically conducted tests with dummies, it was found that colour, shape, size and distance between nest and shell affected the response.

These results suggested, therefore, that this seemingly trivial response, which normally takes no more than 20 seconds each year of a bird's time, contributes to the survival of the brood; and they showed that it is controlled by a complicated and well-adapted mechanism.

A pilot test, in which the response to black and khaki models was tested in birds which had been prevented from laying any eggs that season and had been sitting instead on black eggs, showed that such gulls responded more to black models than control gulls who had been incubating their own, khaki-coloured eggs. It was decided to investigate this with larger numbers of gulls and with green eggs as well, and also to examine whether this increased response was due to a learning process or to the birds carrying objects of a colour which at the moment of the test matched the colour of its eggs. In addition, we decided to use these same birds to investigate the effect of this type of experience on egg rolling, or retrieving.

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METHODS

On 18 April 1961, when very few gulls had started to lay, we selected 120 empty 'scrapes'. In 60 of these we put a plaster-of-paris dummy of a Black-headed Gull's egg painted a matt black; the other 60 received a similar egg dummy painted 'sage green' (for reflection graphs of the colours used in egg and egg shell dummies, as well as of the colour of the natural eggs, refer to Figs. 6, 8 and 9 of Tinbergen *et al.*, 1962). A number of gulls accepted these dummy eggs and incubated them; these received a second egg dummy on the next day, and a third dummy on the third day. Other pairs deserted the nest as a consequence of our interference; the dummies from such nests were taken away and deposited in another empty scrape. Since such desertions occurred at a number of scrapes, the days on which incubation finally started on the individual nests varied considerably. On 9 May we stopped selecting new scrapes; between then and 12 May when we started testing, some nests were deserted and not replaced; hence the final numbers of nests tested in each group were slightly below 60, namely, 56 nests with black eggs and 53 nests with green eggs. Some of these pairs were inhibited from laying by accepting our dummy eggs (see Weidmann, 1956) and thus had no naturally coloured eggs of their own in 1961; this was so with 15 pairs which had received black eggs and with 20 pairs which had accepted green eggs. In all, scrapes which received black eggs were deserted in 43 cases, those which had received green eggs were deserted in 32 cases. Hence, it seems that green eggs were more readily accepted than black eggs. The 41 ($=56-15$) pairs with black eggs which were not prevented from laying were always robbed by us of any natural egg that appeared in their nests; the same was done with the 33 ($=53-20$) pairs which started laying after having received a green egg. Our two groups were thus partly composed of birds which had not laid eggs in 1961, partly of birds which had laid but had only had brief experience with their own eggs. The mean time during which the pairs had been incubating when our tests began was 16.2 days for the 'black-egg-birds' and 17.6 days for the green-egg-birds' (the normal incubation time is approximately 24 days (Beer, 1961; Ytreberg, 1956)).

Our third group, consisting of control birds which had been allowed to keep their own eggs, had not been checked as to their time of laying; however, since the peak of egg laying occurred at about 25 April, they must be assumed to have incubated on the average during approximately the same time as the black-egg and green-egg groups.

In the experiments each nest received three differently coloured egg shell dummies, one at a time. Six tests were done at each nest, so that each model was offered twice. As egg shell dummies we used strips of thin metal measuring 2×10 cm. and bent in a flat cylinder ('small rings' of our previous experiments); these cylinders had about the same diameter as real eggs. The three colours used were khaki (which resembles very closely the ground colour of real eggs), the same black paint as used for the black egg dummies, and the same green colour as used for the green egg dummies. The six tests were arranged as given in Table I. Each model was left on the nest's rim for one hour, after which models were scored as either 'carried away' or 'not carried'.

TABLE I—TEST SCHEDULE FOR THE THREE SUB-GROUPS, A, B, AND C, OF EACH OF 60 NESTS

	Test 1	*2*	*3*	*4*	*5*	*6*
A	green	khaki	black	khaki	green	black
B	black	green	khaki	green	black	khaki
C	khaki	black	green	black	khaki	green

This method was not ideal. The three main flaws were (1) the birds had to be disturbed for each test, and this may in some cases have caused them to desert the clutch. That this actually happened was indicated by the fact that even towards the end of our test period freshly laid eggs appeared in some of the nests, which must have been laid by new birds which had replaced the original owners. (2) At the end of each test several of our rings were found in the nest. This, as we know from direct observations from hides, may occur in different ways. A bird may take up a model without carrying, and drop it again on the spot when it may roll into the nest; this is probably a low-intensity carrying response. A bird might also roll a ring into the nest as if it were an egg. Finally, a ring (or an egg) may be accidentally kicked into the nest when the bird shifts its clutch or scrapes while settling, or when it flies off the nest in panic. We had no means of deciding between these possibilities and therefore scored as 'carried' only those models which had been actually removed. Eggs were scored as 'rolled in' when they had moved into the nest. There is no reason to suppose that the three groups differed substantially in the incidence of such doubtful responses. We would no doubt have obtained purer results if we had observed every single test from hides; this, however, would have been so time-consuming that it would have been totally impossible to obtain scores fit for statistical treatment. (3) Both sexes incubate, and in these mass tests we had no means of deciding which partner had been subjected to our test situation. This again was cancelled by the large number of nests in each group.

The differences in the scores for khaki and black between the real egg group (*Rr*)[3] and the black egg group (*Bb*) were significant at the .01 level; those in the scores for khaki and sage green between

[3]In the symbols characterising the birds at the moment of the test ('*Rr*', '*Bb*', '*Gg*', etc.) the first (capital letter refers to the colour of the eggs they had been sitting on before they were tested; the second to the colour of the eggs they had in their nests during the test.

the real egg group (*Rr*) and the green egg group (*Gg*) were significant at the .001 level; and those in the scores for black and sage green between the black egg group (*Bb*) and the green egg group (*Gg*) were significant at the .02 level.

RESULTS

Table II summarises the results of this first experiment. The significance of the differences was tested with the Mann-Whitney U-test, as described in Siegel (1956).

TABLE II—NUMBERS OF KHAKI, BLACK, AND GREEN RINGS REMOVED BY THE THREE GROUPS. N=NUMBER OF PRESENTATIONS

Group of nest	*Model presented*	*Carried*	*Number*	*Percentage carried*
Real-egg-group (*Rr*)	Khaki	71	120	59.0
	Black	50	120	41.5
	Green	34	120	28.5
Black-egg-group (*Bb*)	Khaki	42	112	37.5
	Black	51	112	45.5
	Green	42	112	37.5
Green-egg-group (*Gg*)	Khaki	41	106	38.5
	Black	40	106	38.0
	Green	52	106	49.0

When tested in this way, therefore, each group carried more shell dummies of their own eggs' colour than the other groups did, and even more of their own colour than of the other colours. This result could have been effected in either of three ways: (1) the birds could have been conditioned to their 'own' egg colour and had transferred this to the shell-removal response; or (2) the birds could, at the moment of testing, have matched the shell dummy's colour against that of the eggs present in the nest at that moment, and removed preponderantly matching shell dummies; or (3) both effects were operating. In order to test this, we repeated the tests, but with this difference, that the birds were given, during the test only, the eggs of a different colour from those they had been incubating. For practical reasons (exchanging eggs, in addition to depositing shell dummies, disturbed the birds for a much longer time than in the first experiment) we did this experiment with the black egg group and the green egg group only. The results are set out in Table III.

The differences in scores for black and green between the two groups in this experiment were significant at the .02 level; those in scores black-green between *'Bg'* and *'Gg'* (Table III) are not significant ($P=.086$); those in scores black and green between 'Gb' and 'Bb' are not significant either ($P>.08$).

TABLE III—NUMBERS OF BLACK AND GREEN RINGS REMOVED BY THE BLACK EGG BIRDS AND THE GREEN EGG BIRDS WHEN SITTING ON THE 'WRONG' COLOUR

Group of nests	*Model presented*	*Carried*	*Number*	*Percentage carried*
Black egg group,	black	42	110	38.0
green eggs during test (*Bg*)	green	37	111	33.5
Green egg group,	black	29	95	30.5
black eggs during test (*Gb*)	green	38	95	40.0

Therefore, having the 'wrong' colour of eggs in the nest during the test did not significantly alter the colour preference, and the birds kept removing predominantly the models which matched the colour of the eggs they had been sitting on before the test. We must conclude that our first hypothesis is correct, i.e. that having incubated on khaki, black or green eggs results in a change of the birds' responsiveness to the colour of the egg shells when they remove them; in other words, that experience gained during incubation is transferred to another response. As in normal birds, the response is not strictly confined to one colour, but neither is it confined to a particular shape, nor size (Tinbergen *et. al.*, 1962).

Effect of experience on egg-retrieving

We used the same three groups of birds to test whether experience with abnormally coloured eggs would also influence the birds' egg retrieving response. Each nest was given, immediately after each egg shell removal test, a natural, black or sage green egg on the nest's rim. The distance between egg and centre of the nest was 15 cm. and, when necessary, a sand platform was built so that the egg would have to be rolled over a horizontal surface. This egg had the same colour as the shell dummy which had been presented immediately before. After 30 minutes all nests were inspected and those where the egg was found in the nest were marked 'rolled in'. The results are given in Table IV.

TABLE IV—NUMBERS OF NATURAL, BLACK AND GREEN EGGS ROLLED IN BY THE THREE GROUPS

Group of nests	*Egg model presented*	*Rolled in*	*Number*	*Percentage rolled in*
Real egg group (*Rr*)	natural	89	120	74.0
	black	48	120	40.0
	green	39	120	32.5
Black egg group (*Bb*)	natural	80	112	71.5
	black	61	112	54.5
	green	51	112	45.5
Green egg group (*Gg*)	natural	74	106	70.0
	black	31	106	29.0
	green	66	106	62.5

Again, there is a clear shift towards the colour of the eggs on which the birds had been sitting, but this shift is far less pronounced than in the shell-removal responses. The differences in the scores for natural and green between *Rr* and *Gg* are significant at the .01 level; those in the scores for black and green between *Bb* and *Gg* are significant at the .02 level, and those in the scores for natural and black between *Rr* and *Bb* at the .04 level.

It is striking that, while in spite of the shorter test time, the scores for rolling and removal are of the same order as far as the black and green models are concerned, the retrieving score for khaki is much higher than the removal score for the same colour; in the retrieving tests 'natural' was preferred even by the 'Black-egg birds' and the 'Green-egg birds'. The most likely explanation would seem to be that the real eggs provide some stimuli (such as dotting and shell texture) which were not provided by the black and green eggs. While dotting does effect egg retrieving, at least in the Herring Gull (Baerends, 1957) there are no indications that it affects egg shell removal in the Black-headed Gull (Tinbergen *et al.*, 1962).

Next we investigated whether the shift in colour preference is really the result of experience. As in the shell removal tests, the Black-egg birds and the Green-egg birds were tested with black and green eggs while they were, for the duration of the tests, sitting on eggs of the 'wrong' colour. These tests gave the results presented in Table V.

TABLE V—NUMBERS OF BLACK AND GREEN EGGS ROLLED IN BY THE BLACK-EGG BIRDS AND THE GREEN-EGG BIRDS WHILE SITTING ON THE 'WRONG' COLOUR

Group of nests	*Egg model presented*	*Rolled in*	*Number*	*Percentage rolled in*
Black egg group,	black	79	107	74.0
green eggs in test (*Bg*)	green	76	112	68.0
Green egg group,	black	67	95	70.5
black eggs in test (*Gb*)	green	72	96	75.0

The differences in black-green scores between the two groups in this experiment are not significant (P = .56), but neither are those between *Gb* (Table V) and *Bb* (Table IV) (P = .24). However, *Bg* (Table V) has significantly different scores from *Gg* (P = .005). This means that the scores for black and green, which were different in Table IV, rather levelled out (though not completely) when the birds were put on the 'wrong' eggs. This might be due to a 'matching effect' in the last experiment, but, since these experiments involved 1½ hours' exposure to the 'wrong' eggs every time the birds were tested for both shell removal and egg retrieving (six times in all, i.e. a total of 9 hours' exposure) it is also possible and, in fact, rather more likely that the conditioning to black and green eggs was gradually broken down. That this conditioning was real is indicated by the fact that *Bg* responded very differently from *Gg*. Why the effect is not equal in both groups cannot be said with certainty, but it would seem to be significant that in the tests of Table IV the 'Green-egg group' had a high score for green eggs, while the 'Black-egg birds' rolled in hardly more black eggs than green eggs. The entire effect might well be due to a high valence of green eggs (which Baerends, l.c. demonstrated in the Herring Gull). As pointed out by Tinbergen *et al.* (1962), the low valence of green in *shell removal* must have survival value because it prevents the birds from removing leaves of the surrounding cover. No such pressure against responding to green eggs by retrieving can be expected.

Our results therefore show that a few weeks' incubation on abnormally coloured eggs influences the colour preferences shown in both egg retrieving and egg shell carrying. It is peculiar that this effect should be as clear in egg shell removal as in egg retrieving, because it is sitting on and shifting of the eggs which are directly involved in the birds' experience with the abnormal eggs, not shell removal—the response to which the conditioning is transferred.

We do not believe that these results can be correctly described by saying that the response to colour in egg shell removal is normally conditioned. Our experiments with a wider range of colours presented to normal birds (see Tinbergen *et al.*, 1962) do not merely show a high score for khaki (the colour of the eggs on which such birds had been incubating) but also for white—a colour of eggs the birds have not had during incubation; moreover, such birds have an extremely low score for green. For a complete evaluation of the part played by experience, it is further of great interest that three individual birds which were given an egg and, on a separate occasion, an egg shell on the nest rim before they had had any experience with eggs or shells (i.e. birds in immature plumage which were tested when their first scrape was still empty) showed both removal response and egg retrieving quite normally, although colour preferences have not been tested in these birds. We hope to be able in the future to test such birds on a much larger scale.

The only conclusion which seems warranted at the moment is that colour preference in egg retrieving and in egg shell removal can be influenced by forcing the gulls to incubate abnormally coloured eggs; this experience increases their responses to the colour of the 'adopted eggs'.

SUMMARY

1. An attempt was made to influence the valence of different colours for the elicitation of egg shell removal (see Tinbergen *et al.*, 1962) by forcing the birds to incubate abnormally coloured eggs. In addition, the effects of this treatment on colour preference in egg retrieving were studied.

MODELS → / ↓ IN NEST	KHAKI	BLACK	GREEN	NAT L.	BLACK	GREEN
NAT L.	59%	41.5	28.5	74	40	32.5
BLACK	37.5	38 / 45.5	33.5 / 37.5	71.5	74 / 54.5	68 / 45.5
GREEN	38.5	30.5 / 38	40 / 49	70	70.5 / 29	75 / 62.5

FIGURE 1. A graphic summary of the results, giving the percentages mentioned in the four tables. The highest figures in each column are underlined. The smaller figures in the upper right corners of eight compartments refer to the scores of Tables III and V, when the nests contained eggs of the 'wrong' colour.

2. One hundred and eighty nests were divided in three groups of which one retained the eggs laid by the birds themselves, another received black egg dummies, and a third was given green egg dummies. After about 17 days' incubation the responses to egg shell dummies coloured 'khaki', black, and green were recorded in these three groups, as well as the retrieving of black, green and real eggs.

3. In both test series the gulls showed an increased response to dummies of the colour of their 'adopted' eggs.

4. This effect was retained when the birds were given, during the tests only, eggs of a different colour from those they had been incubating. This showed that the birds' responses were affected by experience rather than by similarity between the dummies and the clutch in the nest at the moment of the test (Fig. 1).

5. Three immature gulls which were given egg shells and eggs on the rim of their scrapes before they had laid eggs showed normal removal and retrieving responses to the appropriate object. This shows that the response it not entirely acquired.

6. While the experiments show that the effect of colour on these two responses can be influenced by experience during incubation, neither the high score for white nor the low score for green in the removal of normal birds can be explained by this experience.

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