CLUTCH SIZE AND INCUBATION BEHAVIOR IN
BLACK-BILLED GULLS (*LARUS BULLERI*)

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THE Black-billed Gull is endemic to New Zealand. It is a small gull which typically breeds inland on open shingle margins, or islands, of river beds. For general descriptions of the species the reader should see Stead (1932), Guthrie-Smith (1936), Oliver (1955), Moon (1960), and Soper (1963).

Dwight (1925) placed the Black-billed Gull in the subgenus *Hydrocoloeus* of his genus *Hydrocoloeus* together with the Black-headed Gull of Europe (*ridibundus*), the Brown-hooded Gull of South America (*maculipennis*), and Franklin's Gull (*pipixcan*) of North America. The other subgenus, *Cirrocephala*, included the other small gull common in New Zealand, the Red-billed Gull (*novaehollandiae scopulinus*). In discussing similarities of behavior between Hartlaub's Gull (*novaehollandiae hartlaubi*, a South African representative of the *Cirrocephala*) and the Black-headed Gull, Tinbergen and Broekhuysen (1954) hinted that Dwight's classification might need revision. Moynihan (1959) has used behavioral criteria to make such a revision. In this all the gulls are contained in the single genus *Larus*, which is divided into 10 groups. Of these, Group 5 contains *ridibundus, maculipennis, novaehollandiae*, and *bulleri*. The question of whether the closest relative of *Larus bulleri* is at least as far away as South America (as is implied by Dwight's division) is left open. In any case it is clear that the Black-billed Gull and the Black-headed Gull are considered to be closely related, which is the point I want to make.

In recent publications (Beer, 1961–1963) I presented data showing that the incubation and nest-building behavior of the Black-headed Gull is influenced by the number of eggs in the nest. The most common clutch of the Black-headed Gull is three eggs, at least in western and northern Europe (e.g., Goodbody, 1955; Ytreberg, 1956), and three eggs in a nest proved to be the "optimal" situation for incubation behavior: with more or fewer than this number the gulls were more restless and repeated the

TABLE 1

COUNTS OF CLUTCHES IN THREE GULLERIES ON THE TAIERI RIVER

Gullery	Date of count	Numbers of clutches with various numbers of eggs[1]				Total clutches
		1	2	3	4	
I	28 October 1962	60 (30.6)	106 (54.1)	29 (14.8)	1 (0.5)	196 (100.0)
II	29 October 1962	66 (28.9)	138 (60.5)	22 (9.7)	2 (0.9)	228 (100.0)
III	23 October 1963	134 (26.6)	321 (63.7)	46 (9.1)	3 (0.6)	504 (100.0)
	Totals	260 (28.0)	565 (60.9)	97 (9.9)	6 (0.5)	928 (100.0)

[1] Per cent of total in parentheses.

rising and settling movements more often during an incubation bout (Beer, 1961).

I shall show presently that the most common clutch in the Black-billed Gull is two eggs. The possibility suggested itself that this species differs from *ridibundus* also in the way different numbers of eggs in the nest affect incubation behavior. Observations and experiments to test this possibility are the main subject of this paper.

CLUTCH SIZE

According to Black (1955) the normal clutch of the Black-billed Gull is two eggs. In the seasons of 1951 and 1952 he found, in a gullery on Lake Rotorua (North Island), that only 15 per cent of nests contained three eggs and only 10 per cent contained one egg.

In Table 1 are listed the scores for three counts that I made at three different breeding colonies on the Taieri River, Otago (South Island) during the 1962 and 1963 seasons. Two-egg clutches were clearly in the majority in each case. There was good evidence that laying was largely completed in each of these gulleries when the counts were made. The figures for three-egg clutches could be lower than the numbers of three-egg clutches laid, because of loss of eggs from nests, but there is no evidence that eggs are more likely to be lost from three-egg clutches than from two-egg clutches. In any case, it is most unlikely that this source of error could falsify the conclusion that three is not the most common clutch size in this species.

INCUBATION BEHAVIOR

Methods of observation.—The observations to be reported were made from a canvas hide set up in a gullery on the Taieri River during the

breeding season of 1963. I recorded the behavior at a sample of nests:
for each nest a watching period lasted half an hour. Some nests were
watched more than once (always on different days) but the number of
these is not large (e.g., in Table 2: 27 of the 125 watches were made at
nests that had previously been watched) and I assume that all the one-
half hour watches can be treated as independent (except in the case of
experiments in which the same nests were observed as experimentals and
as controls). The observations were made between 0900 hours and 1630
hours, and the weather also varied, although it did not included rain.
Watching periods of the different natural and experimental situations to
be described were more or less evenly distributed between differences in
time of day and weather. Variation in neither time of day nor weather
showed any consistent influence on the records of the behavior I shall
discuss.

Settling sequences and sitting spells.—In gulls the two parents take
more or less equal shares in incubation of the eggs and brooding of the
young. In *bulleri* one of the parents sits uninterruptedly throughout the
night, but during the day the two relieve one another every two hours
or so (Beer, MS). The intervals between nest reliefs I refer to as incuba-
tion or sitting *bouts*. During an incubation bout a gull on its nest usually
rises and resettles at least once, often several times. The interval between
settling and rising I call a sitting *spell*.

Settling consists of a sequence of up to three movements. If we start
with a gull standing in its nest with eggs in front of its feet, settling begins
with the bird erecting the ventral feathers to expose the brood-patches,
and then dropping forward to rest its chest on one side of the nest. In
this position the legs are still partly extended so that they prop up the
rear end of the body and press the feet against the other side of the nest.
The eggs lie in the space between breast and feet. From this position the
bird may bend its legs and bring its feet forward under itself so as to
lower its tail and sit with its body horizontal in the nest; it may return
to a standing position; or, more usually, it passes into the next movement
of the settling sequence: *waggling* (Figure 1). Starting from the chest-
dropped position, the bird treads or pushes backwards with its legs, one
leg and then the other in alternation a number of times. As the foot on
one side presses down or back the rear end of the bird's body is pushed
towards the other side, the breast acting as a pivot. Thus the tail end
swings from side to side in phase with the leg movements. Often waggling
starts with vigorous leg movements and wide-amplitude tail swings, with
the feet pushing back into the material piled up at the rim of the nest,
and then the leg and tail movements decline in vigor and amplitude, and
perhaps increase in frequency, as the feet move in toward the center of

Figure 1.   Black-billed Gull settling on eggs: waggling.

the nest (i.e., farther under the bird) and press downwards onto the nest material instead of backwards against the rim. In the varieties of its forms waggling is essentially continuous with the movement which gulls (and other charadriiform birds) use to shape the nest into a saucer in the pre-laying period (Beer, 1961, 1963a) and which has been called "scraping" (e.g., Moynihan, 1953: 60). At the end of waggling, the bird may again stand, or it may flex its legs and lower its rear to sit in the nest. It may then sit on without any immediate further movement, or it may add the third movement of the settling sequence: *quivering*. This is a rapid shaking or shivering of the whole body, often accompanied by slight side-to-side rocking movements. From observations made from below transparent nests (Beer, 1961: 70–71) I found, in Black-headed Gulls, that, just before or at the start of quivering, the ventral feathers are relaxed and so fold over the brood patches. At the end of quivering a gull usually remains sitting quietly in the nest. Sometimes a gull will make quivering movements in the course of sitting spells without attendant rising and resettling (for a more detailed description of the incubation movements see Beer, 1961).

In what follows I shall distinguish two categories of settling sequence, *incomplete settling*, which consists of dropping the chest or dropping the

TABLE 2[1]

SETTLING SEQUENCES AND SITTING SPELLS

Number and size of clutches	Settling	Spell length					Totals[2]
		Less than 10 seconds	*10 seconds to 1 minute*	*More than 1 minute*	*More than 5 minutes*	*More than 10 minutes*	
One-egg	incompl.	68	29	24	11	7	121
(42)	compl.	1	7	40	35	23	48
	total	69	36	64	46	30	169
Two-egg	incompl.	23	6	7	3	2	36
(53)	compl.	2	6	56	50	44	64
	total	25	12	63	53	46	100
Three-egg	incompl.	7	1	0	0	0	8
(24)	compl.	0	0	15	12	10	15
	total	7	1	15	12	10	23
Four-egg	incompl.	18	7	0	0	0	25
(6)	compl.	0	2	9	6	5	11
	total	18	9	9	6	5	36
Totals	incompl.	116	43	31	14	9	190
(125)	compl.	3	15	120	103	82	138
	total	119	58	151	117	91	328

[1] In column 2 of the table: incompl. = incomplete settling sequences, compl. = complete settling sequences, total = incomplete plus complete settling sequences. The number of one-half hour watches in each sample is included in parentheses in column 1.
[2] Column 3 + columns 4 and 5.

chest plus waggling; and *complete settling* which consists of all three movements—dropping the chest, waggling, and quivering. Quivering that occurs not as part of a settling sequence I shall refer to as *quivering-while-sitting*.

In addition to variation in the composition of settling sequences there is variation in the length of sitting spells: these may last anything between less than 10 seconds and an hour or more. In Black-headed Gulls I found that relatively long sitting spells were usually begun with complete settling sequences, and that relatively short sitting spells were usually begun with incomplete settling sequences; that is, complete settling usually led to a relatively long sitting spell and incomplete settling to a relatively short sitting spell (Beer, 1961: 72–73; 1962a: 285–286). Does this connection between spell length and settling sequence obtain in Black-billed Gulls?

The figures in Table 2 indicate that it does. They were collected from 125 one-half hour watches (distributed between 98 nests). Within each clutch size category they show association between incomplete settling and short spells and between complete settling and long spells. Taking over-all totals for the different categories of spell length and settling sequence: incomplete settling began 97.5 per cent of spells under 10 seconds, 67.3 per cent of spells under 1 minute; complete settling, 79.6 per cent of

spells over 1 minute and 89.9 per cent over 10 minutes; 61.1 per cent of incomplete settlings led to spells less than 10 seconds, 83.7 per cent to spells less than 1 minute; 87.1 per cent of complete settlings to spells over 1 minute, 58.0 per cent to spells over 10 minutes.

There is thus essential agreement between observations of Black-headed Gulls and Black-billed Gulls: it appears that, in both species, performance of the complete settling sequence is usually required before a gull will sit on its eggs for any length of time. There is evidence from Black-headed Gulls (Beer, 1961) that waggling effects the fitting of eggs into brood patches and that unless it achieves this, quivering is unlikely to be performed. I suggested that quivering, in its turn, effects intimate contact between the surfaces of the eggs and the loose vascular skin of the brood-patches, and that the resulting stimulus situation is usually necessary for a gull to sit incubating. All this appears to be equally applicable to Black-billed Gulls.

CLUTCH SIZE AND INCUBATION BEHAVIOR

Clutch size and settling.—The usual clutch in Black-headed Gulls, at least in the regions where I studied them, is three eggs. In this species (Beer, 1961), three normal eggs in an undisturbed nest produced incubation behavior composed of the maximum proportion of complete settling sequences, the minimum number of risings and resettlings, and hence the longest average sitting spells. Any difference or alteration in tactile features of eggs or nest, compared with this "optimal" situation, affected the incubation pattern in the direction of greater restlessness. In particular, for the present context, gulls with less than three eggs (either because eggs had been removed from nests or because the completed clutch was less than three), and gulls whose clutches had been increased from three to five by the addition of egg models, completed proportionately fewer of their settling sequences, rose and resettled more often and hence sat on the average for shorter spells. Baerends (1959) has reported similar observations on Herring Gulls (*L. argentatus*).

We have seen that the clutch size in Black-billed Gulls is less than three in the majority of cases. Is there a corresponding difference in the "optimum" tactile situation for incubation behavior in this species compared with the Black-headed Gull? In Table 2 the scores for watches of gulls with different clutch sizes are separated (only watches which were uninterrupted by nest relief or other disturbance are included). Clutches of three produced the highest proportion of complete settlings (65.2 per cent). By Chi-square test this figure is significantly different ($P < .05$) from those of the other categories except for two-egg clutches. The proportion of relatively long sitting spells was highest in watches of

TABLE 3[1]

RESPONSES TO CLUTCHES OF DIFFERENT SIZES

Number and size of clutches	Proportion of settlings completed	Mean number of settlings	Proportion of s.w.b. completed	Mean number of s.w.b. movements	Mean number of shiftings	Shifting/ settling ratio	Mean number of q.w.s.
One-egg (42)	48/169 = 28.4 %	4.02	144/322 = 44.7 %	7.67	0.67	28/169 = 0.17	1.07
Two-egg (53)	64/100 = 64.0 %	1.89	127/245 = 51.8 %	4.62	0.51	27/100 = 0.27	0.83
Three-egg (24)	15/23 = 65.2 %	0.96	14/50 = 28.0 %	2.08	0.25	6/23 = 0.23	0.17
Four-egg (6)	11/36 = 30.6 %	6.00	65/152 = 42.8 %	25.33	2.33	14/36 = 0.39	3.17

[1] In columns 4 and 5 of the table, s.w.b. = sideways-building; in column 8, q.w.s. = quivering-while-sitting. The figures in parentheses in column 1 refer to the number of one-half hour watches making up each sample.

three-egg clutches also, and again, if we take the proportions of spells more than one minute long, the differences between three-egg clutches and the other clutch sizes are significant ($P < .05$) with the exception of two-egg clutches. Differences in average sitting spells are better reflected by numbers of settlings per one-half hour watch; the means of these scores are included in Table 3. The lowest figure was produced by three-egg clutches: by Mann-Witney U test (e.g., Siegel, 1956: 116–127) it is significantly less than the figures for each of the other categories ($P < .01$ in each case).

In Table 4 are set out the results of experiments in which the number of eggs in a clutch was altered. In these experiments nests were watched for half an hour beginning at least half an hour but not more than 1½ hours after the alterations in clutch size had been made. The same nests with their original contents were watched as controls. The control watches were begun two hours before (half) or after (half) the beginnings of their corresponding experimental watches. The symmetry is not complete because some watches had to be discarded because of interruptions by nest reliefs or colony "panic" flights.

The results of these experiments confirm that three eggs in a nest tend to produce more uninterrupted sitting than any other number. Increasing two eggs to three reduced the number of settlings ($P < .006$), and increased the proportion of complete settlings although not significantly ($P > .10$); reducing four eggs to three eggs reduced settling ($P < .01$) and increased the proportion of complete settlings ($P < .02$); reducing three eggs to two increased rising and settling ($P < .001$) and decreased the proportion of complete settlings ($P < .01$). This last result shows a

TABLE 4[1]

Effects of Altering Clutch Size

Number and size of clutches	Proportion of settlings completed	Mean number of settlings	Proportion of s.w.b. completed	Mean number of s.w.b. move-ments	Mean number of shiftings	Shifting/settling ratio	Mean number of q.w.s.
2–3 (13)	7/9 = 77.8 %	0.7	3/16 = 18.8 %	1.23	0.4	5/9 = 0.56	1.3
2 (13)	22/32 = 68.8 %	2.5	55/126 = 43.7 %	9.7	0.8	10/32 = 0.31	1.0
4–3 (6)	4/5 = 80.0 %	0.8	3/11 = 27.3 %	1.8	0.3	2/5 = 0.40	0.2
4 (6)	11/36 = 30.6 %	6.0	65/152 = 42.8 %	25.3	2.3	14/36 = 0.39	3.2
3–2 (11)	20/78 = 25.6 %	7.1	107/229 = 46.7 %	20.8	1.6	17/78 = 0.22	3.3
3 (10)	8/11 = 72.7 %	1.1	13/37 = 35.1 %	3.7	0.2	2/11 = 0.18	0.2

[1] In column 1: 2–3 = 2-egg clutches made up to 3, 4–3 = 4-egg clutches reduced to 3, 3–2 = 3-egg clutches reduced to 2; for each of the samples of altered clutches the row following contains the scores for control-watches of the same nests in their unaltered condition (2-eggs, 4-eggs, 3-eggs). Other points as in Table 3.

greater difference in restlessness than we noted between untampered nests of two eggs and three eggs; hence the effect of the number of eggs in the nest can be influenced by change *per se* in number, at least if the change is a reduction. This is no doubt of selective value: restlessness caused by reduction of the number of eggs in a nest will favor the probability that an egg that has rolled from the nest will be retrieved (see Beer, 1962b: 394).

Again we find essential agreement between Black-billed Gulls and Black-headed Gulls: in spite of the fact that clutches of three eggs probably amount to less than 15 per cent of the total clutches laid by Black-billed Gulls, three eggs still provide the "optimum" situation for incubation.

Choice tests.—There is no evidence that visual stimuli play an important immediate role in control of the responses we have been considering. However, I have one experimental result which shows that Black-billed Gulls are visually attracted more by three eggs than by two. At nine nests, each of which contained two eggs, I set up a choice test consisting of two nests side-by-side sharing the site of the original nest, one containing two eggs and the other three. Neither the nests nor the eggs used in a choice test belonged to the birds concerned but were borrowed from other pairs and replaced after the test. The test was offered twice at each nest, with the clutches exchanged in the second test, to reduce the possible influence of position preference. Half the tests began with the two-egg

clutch in the right-hand nest and half with the two-egg clutch in the left-hand nest. When the gull owning the site returned to find the test situation, I recorded which nest it stepped into first and which it settled in first. The majority of the gulls returned to their nest sites and settled in one of the nests within two minutes of my returning to the hide after setting up a test. Four of them showed signs of fear (long thin neck, "alarm" calls, repeated hovering flights, and balked approaches to the nests) and one of these failed to reach the nests in 10 minutes and so the test was discontinued. In the remaining 16 tests the three-egg nest was stepped into first in 13 and sat in first in 15. The gulls were clearly more attracted by the larger clutch.

However, there may be little or no connection between visual preference, as shown in these choice tests, and the differences produced in rising and settling behavior by differences in clutch size. It may be that gulls would choose a larger rather than a smaller number of eggs irrespective of whether the former was the "optimum" for incubation or not. This appears to be the case (Tinbergen, 1951: 45) for Oystercatchers (*Haematopus ostralegus*). Black-headed Gulls presented with a choice between their own eggs and a model egg several times as large as a normal egg chose the large model in spite of the fact that it was almost impossible to settle on and incubate (Beer, 1961: 86). If it were found that four or five eggs are visually more attractive to gulls than three eggs it would be interesting to repeat the tests with the same birds a number of times to see if experience could alter the preference in favor of the clutch size that is "optimal" for incubation.

Quivering-while-sitting.—In my study of incubation in Black-headed Gulls I suggested that quivering-while-sitting is caused by stimuli of a sort tending to disrupt sitting but insufficient to cause rising. Such stimuli may result from slight disturbances of the contact between eggs and brood-patch, by, for example, the making of vigorous calls. Any change in the tactile features of eggs or nest tended to increase the quantity of quivering-while-sitting; conditions which increased the likelihood of rising and settling tended also to increase this response.

In Tables 3 and 4 I have included the means for the number of times quivering-while-sitting occurred in a one-half hour watch. As with rising and settling, the score for this response was significantly lower in watches of three-egg clutches than in watches of larger or smaller clutches ($P < .05$ in each case).

In the experiments (Table 4), increasing two eggs to three increased quivering-while-sitting, but not significantly ($P = .20$); reducing four eggs to three produced marked decrease ($P = .006$); and reducing three eggs to two produced marked increase ($P = .002$).

Figure 2.   Black-billed Gull shifting eggs.

Again we have agreement with what obtains in Black-headed Gulls. The reduction from four eggs to three was a change in the tactile situation, which produced less instead of more quivering-while-sitting (cf. the Black-headed Gull), but this was accompanied by a large reduction in the amount of rising and settling. As in Black-headed Gulls, many of the quiverings-while-sitting of Black-billed Gulls occurred just after performance of calling or nest-building movements.

Shifting.—Between rising and resettling on the nest, a Black-billed Gull, like other gulls, often performs one or more of a number of actions. It may walk from the nest a distance of one to three meters, turn, defecate, walk back to the nest (at no time have I seen the defecation flights which are the usual thing in incubating Black-headed Gulls); it may alter its orientation by stepping sideways to one side or the other around the center of the nest, and this is usually performed with the body axis inclined—head down, tail up—in an attitude I have called "stooping" (Beer, 1961: 66) and often with a rapid treading that I have called "trampling" (*ibid.*); it may move the eggs about in the nest by means of a movement (Figure 2) called *shifting* (e.g., Tinbergen, 1953: 137–139; Beer, 1961: 66–67). Shifting consists of bending the head down so that the under-side of the bill is placed against an egg between the bill

and feet; the feet are usually trampled at this time. This rolls the egg against the feet and usually turns it about the short axis also so that it slides off the bill to one side or the other to lie with its long axis more or less parallel with the long axis of the bird. With three eggs in the nest, shifting tends to arrange the eggs—two in front and one behind—so that they match the arrangement of the brood-patches of the gull standing over them. This obviously helps the fitting of the eggs into brood-patches when the bird settles. Shifting also serves to effect the agitation of the eggs, providing a certain amount of rotation and shaking, which is requisite for efficient development and hatching of the embryo (e.g., Randles and Romanoff, 1950; New, 1957; Lind, 1961: 94–96).

In Tables 3 and 4 I have included the means for occurrences of shifting per one-half hour watch and also the ratios of occurrences of shifting to occurrences of settling (since shifting can occur only between rising and settling and is rarely performed more than once in the interval between a rising and settling). Statistical tests of the shifting/settling ratios show significant differences between one egg and two eggs ($P = .05$), one egg and three eggs ($P < .05$), and one egg and four eggs ($P < .01$). In each case the larger clutch produced the larger shifting/settling ratio. The ratio for four eggs was higher than those for three eggs and two eggs but these differences were not significant. The consistent trend was for relatively more of the occurrences of rising and settling to be accompanied by shifting in watches of larger than in watches of smaller clutches, irrespective of which was the more "satisfactory" for incubation sitting.

This result is consistent with what I found in Black-headed Gulls (Beer, 1961: 100–102). The evidence from that species suggested that contact of the edges or upper surfaces of the feet with the eggs, or obstruction by the eggs to movement of the feet, stimulates shifting. The greater the number of eggs in the nest the greater the chance these conditions will arise.

Nest building.—Black-headed Gulls continue to show nest-building behavior throughout the incubation period (e.g., Kirkman, 1937). The same is true of Black-billed Gulls. This behavior consists of two patterns: (1) *collecting trips*, in which a gull picks up twigs, pieces of dried grass, or other suitable nest material in its bill, some distance from its nest, and walks or flies with the accumulated bundle to drop it at the edge of the nest; (2) *sideways-building movements*, which are performed in the nest by a sitting gull (occasionally a standing gull will show the movement also). Here the gull reaches out to pick up a single piece of nest-material in its bill and then it may bend its head round to one side or the other to place the piece of material along its body. In what follows I shall mention two categories of sideways-building movement: (1) *incomplete*

Figure 3.   Black-billed Gull building nest: the complete sideways-building move-
ment.

sideways-building, which consists of the first part of the full movement,
e.g., leaning towards or pecking at a piece of nest-material, and perhaps
drawing it towards the breast, but without sideways bending of the head;
(2) *complete* sideways-building, which consists of the full movement with
sideways bending of the head (Figure 3).

Except on two occasions, all the collecting trips I saw were performed
at nest reliefs, either by an incoming bird or a bird just relieved. The
numbers of nest reliefs that I recorded for each sample of observations
were small and there were no significant differences between the samples
in the numbers of collecting trips per relief.

Moynihan (1953) found that the number of sideways-building move-
ments performed in a standard time by an incubating Black-headed Gull
could be increased by removal of eggs from the nest, and that this in-
crease was greater the more eggs that were removed. In my observations
of Black-headed Gulls I found that sideways-building was increased by
all the natural and experimental situations that increased rising and set-
tling, that is, that there was high positive correlation between the number
of settlings and the number of sideways-building movements in a one-half
.hour watch within each sample of watches and in all the watches taken

together, and that most of these sideways-building movements were made just before or just after rising to resettle or settling (Beer, 1963b).

In Tables 3 and 4 I have included the means for the numbers of side-ways-building movements per one-half hour watch and also the per-centages of complete sideways-building movements for each sample of watches of Black-billed Gulls. The lowest numbers of sideways-building movements occurred in the watches of three-egg clutches: the differences between three eggs and four eggs ($P < .001$) and between three eggs and one egg ($P < .001$) are significant but the difference between three eggs and two eggs is not ($P = .18$). In the experiments: increasing two eggs to three decreased sideways-building ($P = .07$); reducing four eggs to three also decreased sideways-building ($P = .01$); reducing three eggs to two increased sideways-building ($P = .002$). Thus differences in numbers of sideways-building movements per watch closely parallel the differences in numbers of settlings per watch. Tests for correlation between settling and sideways-building scores did not show significant association of varia-tion in the smaller samples but did in the watches of one- and two-egg clutches: Spearman Rank Correlation tests (e.g., Siegel, 1956: 202–213) gave $r_s = 0.73$ for one-egg clutches ($P < .001$), and $r_s = 0.65$ for two-egg clutches ($P < .001$). Thus, in these two samples at least, the more often a bird rose and resettled the more often it performed sideways-building.

The majority of sideways-building movements were performed just before or just after settling. This can be seen in Table 5. If the occur-rences of sideways-building were random relative to the occurrences of settling, one would expect the temporal association to be considerably less than it appears in the table. For example, since the average number of settlings per watch for one-egg clutches was about 4, a chance distribution would put about 26 per cent of the sideways-building movements within one minute of settling, which is well below the 75.5 per cent score of our sample; four-egg clutches had the highest mean for settling (6.0) and the lowest percentage of sideways-building movements within one minute of settling (70.4) but the latter is still markedly higher than the figure to be expected in a random distribution (about 40 per cent).

A number of the sideways-building movements that did not occur within one minute of settling took place just before or just after quivering-while-sitting: from Table 5 it can be seen that over 60 per cent of sideways-building movements not accompanied by settling were within one minute of quivering-while-sitting.

Three-egg clutches produced a lower proportion of completed sideways-building movements than did two-egg clutches ($P < .01$), one-egg clutches ($P < .05$), or four-egg clutches ($P < .10$). In the experiments: reducing four eggs to three lowered the proportion of completed movements ($P <$

TABLE 5

TEMPORAL ASSOCIATION OF SIDEWAYS-BUILDING MOVEMENTS WITH SETTLING AND
QUIVERING-WHILE-SITTING[1]

Time of movement	Nature of movement	Clutch size				Totals
		1-egg	*2-egg*	*3-egg*	*4-egg*	
S.w.b. within	incompl.	128	105	26	61	320
1 minute	compl.	115	115	13	46	289
of settling	total	243	220	39	107	609
S.w.b. outside	incompl.	50	13	10	26	99
1 minute	compl.	29	12	1	19	61
of settling	total	79	25	11	45	160
S.w.b. outside	incompl.	20	5	1	24	50
1 minute	compl.	21	9	0	19	49
of settling within 1 minute of q.w.s.	total	41	14	1	43	99

[1] Occurrences of incomplete (incompl.) and complete (compl.) sideways-building movements (s.w.b.) are sorted according to whether they took place within 1 minute before or after occurrences of settling or not; the numbers of the latter group which took place within one minute before or after quivering-while-sitting (q.w.s.) are listed in the third set of rows. "Total" = incomplete plus complete s.w.b. in each group.

.05); increasing two eggs to three also lowered the proportion of completed movements ($P = .10$); decreasing three eggs to two raised the proportion of completed movements, but the difference is not significant ($P > .20$).

Thus, when the conditions are most satisfactory for incubation sitting (rising and resettling are at a minimum and the proportion of complete settling sequences at a maximum) it appears that the total number of sideways-building movements performed and the proportion of these movements completed are at a minimum. In this respect also, Black-billed Gulls are like Black-headed Gulls.

DISCUSSION

On all the points of behavior in the incubation period that I observed or tested, Black-billed Gulls proved to be similar to Black-headed Gulls. In my study of Black-headed Gulls I emphasized the fact that the "optimal" number of eggs for incubation sitting corresponds with the number of brood-patches. Black-billed Gulls also have three brood-patches, as, I believe, do all other species of gulls.

The clutch size listed for most species of gulls is three. Cullen (1957: 291) listed three exceptions with smaller clutches but the nesting habitat of each of these is somewhat peculiar. In view of the number of brood-patches possessed by gulls it is a reasonable assumption that three eggs is the primitive clutch size for all gulls and that a smaller clutch is a derived

condition. If this is so then we can regard the "optimal" character of three eggs for incubation sitting in Black-billed Gulls as a behavioral relict—an ancestral trait that has remained unchanged in spite of the evolution of a different average clutch size. The discrepancy between the most common clutch size and the clutch size "optimal" for incubation behavior, in Black-billed Gulls, probably affects the efficiency of incubation very little and hence has not tended to be reduced by selection.

Note.—Various New Zealand birds have smaller clutches than corresponding species in other parts of the world. For example the Red-billed Gull lays two eggs (Cunningham, 1946; Fleming, 1946; Stidolph, 1947; pers. observations). The South Island Oystercatcher (*Haematopus ostralegus finschi*) usually lays a clutch of two and occasionally three (Oliver, 1955: 246; Williams, 1963: 54; pers. observations), while the European subspecies (*H. o. occidentalis*) usually lays three eggs and not uncommonly four (Witherby *et al.*, 1943: 417). The Banded Dotterel (*Charadrius bicinctus*) lays two or three eggs (Potter, 1949; Oliver, 1955: 260), the New Zealand Dotterel (*C. obscurus*) lays three eggs (Oliver, 1955: 257), and the Wrybill Plover (*Anarhynchus frontalis*) lays two eggs, very rarely three (Oliver, 1955: 268), all of which are less than the usual clutches of most small Charadriidae from the Northern Hemisphere: e.g., the Ringed Plover (*C. hiaticula*) and the Little Ringed Plover (*C. dubius curonicus*), both of which normally lay four eggs (Witherby *et al.*, 1943). Pheasants (*Phasianus* sp.) introduced into New Zealand appear to have acquired a reduced clutch (Westerskov, 1956: 74–84) and the same is true of introduced European Blackbirds (*Turdus merula*) and thrushes (*T. ericetorum*) (Bull, 1946). The breeding ranges of these birds are closer to the equator than those of their representatives that have been studied in the Northern Hemisphere. Differences in day length and available food supply are obvious candidates for the role of ultimate factors underlying these differences in clutch size (see Lack, 1954: 22; Westerskov, 1956: 81).

In my paper on incubation nest-building in Black-headed Gulls (Beer, 1963b), I suggested that rising to resettle and sideways-building were both caused by discrepancy between the stimulus pattern that an incubating gull is "set" to receive from its eggs and nest, and the stimuli actually fed back, particularly from the brood-patches. If there could be differences of degree of such discrepancy then a low degree might activate incomplete sideways-building, a slightly higher degree complete sideways-building, and a still higher degree rising and subsequent resettling. The observations of incubation nest-building in Black-billed Gulls also fit this interpretation. For example, taking the over-all totals in Table 5, a higher proportion of complete sideways-building movements occurred within one minute of settling (82.6 per cent) than was the case for incomplete sideways-building (76.4 per cent) and the difference is significant ($P <$ .05). This is what one would expect if the closer conditions are to the threshold for rising the more likely they are to cause complete rather than incomplete sideways-building. It is to be hoped that advances in neuro-

physiological studies of birds will make possible the formulation of this hypothesis in terms of nervous structure and function and hence the testing of it by means other than the behavioral relationships we want it to explain.

SUMMARY

In three breeding colonies of Black-billed Gulls (*Larus bulleri*) the commonest clutch size was found to be two, instead of three which is the usual size in most other species of gulls, including the closely related Black-headed Gull (*L. ridibundus*).

In Black-billed Gulls, as in Black-headed Gulls, long sitting (incubation) spells are usually initiated by complete settling sequences, and short sitting spells by incomplete settling sequences.

Observations of incubation on clutches of different sizes, and on nests in which the number of eggs had been reduced or increased, showed that the effects of egg number on incubation behavior in Black-billed Gulls are similar to those in Black-headed Gulls (see text for terminology):

(1) three eggs in the nest produced less rising and settling, a higher proportion of complete settlings, less sideways-building, and a lower proportion of complete sideways-building movements, and less quivering-while-sitting, than did more or less than three;

(2) the number of settlings and the number of sideways-building movements per watch were positively correlated in the two largest samples, and the majority of sideways-building movements (significantly more of the complete than the incomplete) took place in close temporal proximity to occurrences of rising and settling;

(3) the chances of shifting during rising and resettling tended to be greater the more eggs there were in a nest.

It is concluded that the discrepancy between the most common clutch size and the "optimum" number of eggs for incubation sitting in Black-billed Gulls has probably arisen because natural selection has acted on the laying processes without affecting the role of tactile stimuli in the control of incubation behavior.

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