

THE EFFECTS OF ADULT FECAL MATERIAL ON EGG HATCHABILITY IN GLAUCOUS-WINGED GULLS (*LARUS GLAUDESCENS*)

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ABSTRACT.—The effect of gull and cormorant feces applied to naturally incubated Glaucous-winged Gull eggs upon hatching success was studied on Mandarte Island, British Columbia. Gull feces, but not cormorant feces, significantly reduced the hatching success of treated eggs below that of control eggs. Eggs treated with gull feces lost significantly less water during incubation than either control eggs or eggs treated with cormorant feces. Eggs that were covered with gull feces but that nevertheless hatched had a significantly longer incubation period than did control eggs. The removal of the fat from the feces with ether before application to the eggs did not significantly improve hatching success. Received 9 May 1983, accepted 24 April 1984.

DURING incubation, some birds leave the nest to defecate, whereas others eject feces while remaining on or near the nest. The young of altricial and semi-altricial birds produce fecal sacs, which are removed by the parents or ejected over the rim of the nest. The various reasons for this behavior that have been proposed include keeping predators, flies, and disease away from the nest, preventing the feathers from sticking together, and promoting more efficient incubation. What has not been stressed is the direct effect that feces smeared on the egg may have on the proper development of the egg. Having spent some time in colonies of various gulls (*Larus argentatus*, *L. fuscus*, *L. glaucescens*), I had the impression that eggs that were accidentally smeared with feces by the parents or, possibly, conspecifics tended not to hatch. In contrast, cormorant eggs commonly are covered with feces, and this does not appear to harm the developing embryo. A recent paper by Sobey (1977), in which he reported on the defecating behavior of Herring Gulls (*L. argentatus*), prompted me to pursue this matter further on Mandarte Island, Strait of Georgia, British Columbia. As the gulls defecate away from their nests (Sobey 1977, pers. obs.), my hypothesis was that they did so because defecation in the nest was somehow detrimental. The object of this study was to test experimentally what effect, if any, the application of gull and cormorant feces has on the hatching success of gull eggs.

METHODS

Eggs of Glaucous-winged Gulls (*L. glaucescens*) were numbered with India ink in the order in which they

were laid and on the day on which they were laid in 1979 and 1980. In addition, some of these eggs were weighed with a Pesola balance.

Cormorant feces were scraped off the rocks in cormorant (*Phalacrocorax auritus*, *P. pelagicus*) roosts. The feces were dried, and foreign matter, such as bits of grass, was removed. Enough fresh water was added to the feces to make a thick paste. Gull feces were collected fresh at a gull club (Tinbergen 1953) and were thoroughly mixed. Nothing was added to the material except fresh water when needed. Control eggs were wetted with plain fresh water and left to dry. Feces were applied to the eggs in the field with paint brushes. Each type of treatment had its own brush; brushes were not mixed. The first treatment was given on the day the third egg in a clutch was laid. Only clutches with three eggs were used, and, if one of the eggs in a clutch disappeared, that clutch was not used in the analysis of the data. All treatments were applied to the entire egg surface.

To study the effect of feces on gull eggs, I conducted a number of experiments, the rationale and methodology of which are outlined below.

Hatching success, egg weight, and weight loss of untreated eggs during incubation.—The third egg (*c* egg) in Glaucous-winged Gulls is typically smaller than the first (*a* egg) or second (*b* egg), and, because of this, it could conceivably be less viable than the others. If this were the case, it might influence the experimental treatments described below. To determine whether or not there was an intrinsic difference in the hatching success of *a*, *b*, and *c* eggs in untreated clutches, the fate of the eggs in clutches of three was followed in 1979 and 1980 on Meadow III (Fig. 1) until all eggs had hatched or had had ample time to do so. These eggs were handled twice, once to number and weigh them on the morning of the day they were laid and again to weigh them 22 days after the day the *c* egg in the clutch was laid. At this time the first egg in the clutch was about ready to start

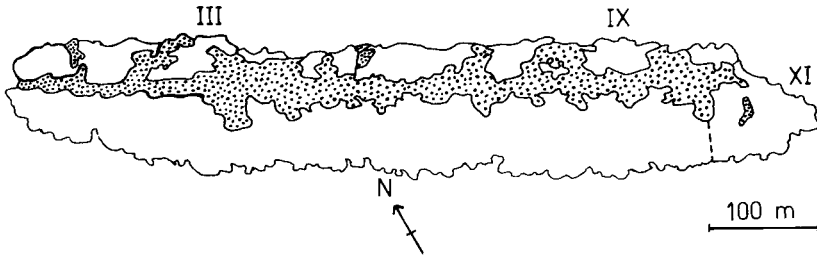


Fig. 1. Mandarte Island, showing the three gull meadows (III, IX, and XI) where the research was carried out. The stippled area indicates shrubs and trees; the blank area is grass.

pping. Effective incubation in gulls usually does not start until the third egg in the clutch is laid (Beer 1962, Vermeer 1963, Drent 1970).

Hatching success of eggs that were rubbed or left untreated.—Two aspects of eggs and incubation were studied in this experiment. First, when a gull egg is laid, it is coated with a thin, opaque, slippery substance. This layer soon dries and becomes invisible to the naked eye. Bits of nest material may be stuck by this substance to the egg, but in the course of incubation such materials are usually abraded. I considered that, besides lubricating the egg on its passage down the oviduct, the substance might possibly be of some value to the eggs in the nest. Second, the question remained whether or not the control procedure (wetting the eggs with water) used throughout this study could have influenced the hatchability of the eggs. To test these two aspects, I treated one egg in clutches of three with water, I removed the mucous layer from another egg by rubbing it with a wet cloth, and I took the remaining egg out of the nest but did not otherwise treat it in any way; it served as the control. The treatments were repeated four times at weekly intervals on Meadow IX (Fig. 1) in 1980.

Hatching success, egg weight, and weight loss of eggs treated with gull or cormorant feces or paint.—Each nest contained one control egg and two other eggs, one of which was coated with gull or cormorant feces and the other with an oil-based paint. I treated control eggs and those coated with feces four times at weekly intervals, starting on the day the third egg in the clutch was laid. The painted egg received only one coat of paint on the day it was laid.

To test whether or not eggs treated with feces lost less weight than control eggs, because the fecal material might have plugged the pores in the egg shell, I weighed the eggs. Eggs were weighed and numbered on the day they were laid and reweighed 22 days after the day the third egg in the clutch was laid. This experiment was done on Meadow IX (Fig. 1) in 1979.

Hatching success of eggs treated with gull or cormorant feces.—In this experiment, *a*, *b*, and *c* eggs were used,

but the treatment was varied among the eggs. The object of this experiment was to verify that each treatment indeed had the same effect, regardless of which egg in the clutch was involved. Thus, in some clutches, eggs *a* and *b* served as controls and egg *c* was coated with gull feces. In other combinations, *a* was the control and *b* and *c* were treated, *b* and *c* were the control and *a* was treated, or *c* was the control, and *a* and *b* were treated. In another series of clutches, a similar procedure was followed with cormorant instead of gull feces. This procedure was repeated four times at weekly intervals in 1979 on Meadow XI (Fig. 1).

Hatching success of eggs treated once with feces.—In a number of clutches on Meadow XI in 1979, one egg per clutch was used as a control, one was covered with gull feces, and one was covered with cormorant feces. The eggs were so treated once on the day the third egg was laid. The object was to test what the consequences were of one application as compared with four in all other experiments in this study.

Hatching success of eggs treated with modified feces.—The object of this experiment was to test to what extent, if any, the fat content of the feces affected the hatching success of eggs treated with gull or cormorant feces. The feces were placed in a separating funnel and treated four times with ether to extract the fat. I then applied the modified feces to the eggs four times at weekly intervals, starting on the day the third egg was laid. This experiment was done on Meadow XI in 1980.

RESULTS

Hatching success of untreated eggs.—The hatching success among *a*, *b*, and *c* eggs did not differ significantly (χ^2 test, $P > 0.05$) in either year (Table 1). Parsons (1970) found the same to be true of Herring Gulls. The hatching success in 1980, however, was significantly lower than in 1979 (χ^2 test, $P < 0.01$), probably because of very wet and cold weather in 1980. The difference amounted to 12.5% (Table 1).

TABLE 1. Hatching success of three-egg clutches in 48 nests in which the eggs were numbered and weighed (Meadow III, 1979 and 1980).

Egg	1979			1980		
	Number of eggs	Number of eggs hatched	Percentage hatched	Number of eggs	Number of eggs hatched	Percentage hatched
<i>a</i>	48	43	89.6	48	36	75.0
<i>b</i>	48	40	83.3	48	36	75.0
<i>c</i>	48	44	91.7	48	37	77.1
All	144	127	88.2	144	109	75.7

Hatching success of eggs that were rubbed or left untreated.—Eggs from which the mucous layer was rubbed off and those that I wetted hatched as well as those that remained untreated (Table 2). The percentage of eggs that hatched was lower in 1980 than in 1979, but not significantly so (χ^2 test, $P > 0.05$) (Table 1). Applying the 12.5% adjustment resulting from bad weather in 1980, I derived a hatching success of 86.4%, similar to that of all eggs in 1979 (Table 1). The normal control procedure and the removal of the mucus thus did not affect hatching success.

Hatching success of eggs treated with gull or cormorant feces or paint.—The hatching success of control eggs did not differ significantly (χ^2 test, $P > 0.05$) from that of eggs treated with cormorant feces (Table 3), nor was it significantly lower (χ^2 test, $P > 0.05$) than that of untreated eggs in 1979 (Table 1). None of the eggs treated with one coat of paint hatched. The hatching success of eggs covered with gull feces was significantly lower than that of either control eggs (χ^2 test, $P < 0.001$) or those covered with cormorant feces (χ^2 test, $P < 0.001$) (Table 3).

Hatching success of eggs treated with gull or cormorant feces.—The hatching success among *a*, *b*, and *c* eggs treated with gull feces did not differ significantly (Fisher exact probability test, $P > 0.05$). The same was true of *a*, *b*, and *c* eggs treated with cormorant feces or used as con-

trols (Table 4). Control eggs and those treated with cormorant feces had an equal hatching success. The combined hatching success of control eggs and those treated with gull or cormorant feces in this experiment did not differ significantly (χ^2 test, $P > 0.05$) from their respective counterparts in the previous (Table 3) experiment.

Hatching success of eggs treated once with feces.—The hatching success of eggs treated once as controls and of eggs treated once with cormorant feces was lower (Table 5) than that of eggs treated four times (Table 3), but not significantly so (χ^2 test, $P > 0.05$ and Fisher exact probability test, $P = 0.25$, respectively). Eggs treated once with gull feces had a better hatching success (Table 5) than those treated four times (Table 3), but the difference was not significant (χ^2 test, $P > 0.05$).

Egg weight and weight loss of untreated eggs during incubation.—The mean fresh weights of *a* and *b* eggs combined differed significantly (ANOVA, $F = 7.64$, $df = 1,141$, $P < 0.01$) from the mean weight of *c* eggs, but *a* and *b* eggs did not differ significantly from each other (ANOVA, $F = 0.62$, $df = 1,94$, $P > 0.05$) (Table 6). The mean weight loss of *a*, *b*, and *c* eggs in 48 clutches during incubation was about 10% (0.45 g/day) (Table 6). Mean weight loss did

TABLE 2. Hatching success of eggs that were wetted, rubbed, or untreated (Meadow IX, 1980).

Treatment	Number of nests	Number of eggs hatched	Percentage of eggs hatched
Wetted	23	17	73.9
Rubbed	23	17	73.9
Untreated	23	17	73.9

TABLE 3. Hatching success of control eggs and those treated with gull or cormorant feces or paint (Meadow IX, 1979).

Treatment	Number of eggs	Number of eggs hatched	Percentage hatched
Control	26	22	84.6
Cormorant feces	16	14	87.5
Gull feces	19	5	26.3
Paint	17	0	0.0

TABLE 4. Hatching success of eggs in which egg *a*, *b* and *c*, or *c* in a clutch served as the control eggs, while the other egg or eggs in the clutch were covered with gull or cormorant feces (Meadow XI, 1979).

Egg	Treatment	Gull feces applied			Cormorant feces applied			
		Number of eggs	Number of eggs hatched	Percentage hatched	Treatment	Number of eggs	Number of eggs hatched	Percentage hatched
<i>a</i> egg	Feces	12	3	25	Feces	12	10	83
	Control	10	9	90	Control	10	8	80
<i>b</i> egg	Feces	11	1	9	Feces	12	10	83
	Control	11	9	82	Control	11	7	64
<i>c</i> egg	Feces	10	2	20	Feces	11	8	73
	Control	12	11	92	Control	12	11	92
Total	Feces	33	6	18	Feces	35	28	80
	Control	33	29	88	Control	33	26	79

not differ significantly between *a* and *b*, *a* and *c*, or *b* and *c* eggs.

Egg weight and weight loss of eggs coated with water, feces, or paint.—Eggs treated with gull feces lost significantly less weight than either eggs treated as controls ($t = 2.53$, $df = 44$, $P < 0.02$) or eggs treated with cormorant feces ($t = 3.03$, $df = 34$, $P < 0.01$). Eggs treated with paint lost very little weight (Table 7).

Hatching success of eggs treated with modified feces.—The hatching success of the control eggs treated with water (Table 8) did not differ significantly (χ^2 test, $P > 0.05$) in 1980 from that of other control eggs that were only weighed and numbered (Tables 1 and 2). To compare the hatching success of eggs treated with normal feces in 1979 (Table 3) with that of eggs treated with modified feces in 1980 (Table 8), I must account for the effect that the bad weather had on hatching success in 1980. The hatching success of eggs treated with modified gull feces in 1980 was 32.1% (Table 8) plus 32.1% of 12.5% (= calculated hatching failure due to bad weather in 1980). This amounts to 10 eggs hatched instead of the 9 given in Table 8. Us-

ing the same reasoning, I assume that all eggs treated with modified cormorant feces (Table 8) would have hatched. Taking the bad weather into account, I found, nevertheless, that the recalculated hatching successes of eggs treated with normal (Table 3) and modified feces (Table 8) did not differ significantly ($P > 0.05$) from each other.

DISCUSSION

The experimental results of this study have identified a heretofore unsuspected reason as to why birds do not defecate in their own nests. When Glaucous-winged Gull eggs were totally covered with gull feces (to simulate repeated defecation in the nest), they had a significantly lower hatching success than that of eggs treated as controls (Table 3), and this result was independent of which egg in the clutch was treated (Table 4). Eggs treated once with gull feces had a reduced hatching success compared with controls (Table 5), but, in contrast to those that were treated four times (Table 3), the difference was not significant. The fecal material that was applied only once may have worn off by abrasion in the nest, especially because it was applied early in the incubation period. Eggs treated with cormorant feces, however, had the same hatching success as control eggs (Tables 3, 4, and 5). There may be several reasons for this difference between species.

First, the eggs in untreated clutches lost about 0.45 g per day during incubation (Table 6), which was essentially due to the evaporative loss of water (Drent 1970). Herring Gull eggs

TABLE 5. Hatching success of eggs treated once with water (control) or with cormorant or gull feces (Meadow XI, 1979).

Treatment	Number of eggs	Number of eggs hatched	Percentage hatched
Control	16	10	62.5
Cormorant feces	16	12	75.0
Gull feces	16	9	56.3

TABLE 6. Mean fresh weight (g) of eggs and weight loss of those eggs 22 days after the third egg in the clutch was laid (Meadow III, 1979).

Eggs	Number of eggs	Fresh weight		Weight loss of egg		Percentage loss of original weight
		Mean weight	SD	Mean weight	SD	
<i>a</i>	48	94.5	8.56	9.7	2.78	10.3
<i>b</i>	48	91.9	7.92	9.1	2.16	9.9
<i>c</i>	48	86.1	7.93	8.5	2.26	9.8

TABLE 7. Mean fresh weight (g) and weight loss of those eggs 22 days after the third egg in the clutch was laid. The eggs were treated with water, gull or cormorant feces, or paint (Meadow IX, 1979).

Treatment	Number of eggs	Fresh weight		Weight loss of egg		Percentage loss of original weight
		Mean weight	SD	Mean weight	SD	
Control	27	96.2	4.86	10.0	2.10	10.4
Cormorant feces	17	94.6	5.34	10.2	2.52	10.8
Gull feces	19	94.6	6.25	8.5	1.89	9.0
Paint	18	93.4	5.65	0.6	0.58	0.6

are of about the same weight as those of Glaucous-winged Gulls and lose a similar amount of water per day (0.47 g, Harris 1964; 0.45 g, Drent 1970). Eggs treated with gull feces, however, lost significantly less weight during incubation than did either the control eggs or those treated with cormorant feces (Table 7). This suggests that the gull feces, but not the cormorant feces, prevented the effective loss of water from the eggs, a loss necessary to the normal development of the embryo (Rahn et al. 1979). The gull feces on the eggs may also have affected the proper exchange of oxygen and carbon dioxide between the embryo and the environment, but I have no measure of that.

Second, it is of interest that the mean incubation period of the 11 eggs that were treated with gull feces but that nevertheless hatched

(Tables 3 and 4) was 29.7 days, as compared with a mean of 28.4 days (Verbeek MS) in untreated eggs. These values were obtained by taking the mean of the incubation periods of *a*, *b*, and *c* eggs, because all of these were represented in the sample of 11 eggs. The difference of 1.3 days is significant ($t = 2.91$, $df = 126$, $P < 0.01$). Apparently a sufficient number of pores remained open in these 11 eggs to allow the exchange of gases and the loss of water necessary to embryonic development, but the development was slowed down. The difference of 1.3 days was not due to a reduction in the willingness of the adults to incubate soiled eggs, because all experimental clutches contained untreated control eggs, and the mean incubation period of these (*c* eggs in Table 4) did not differ significantly ($t = 1.07$, $df = 64$, $P > 0.05$) from that of those (*c* eggs in 1979 in Table 1) in clutches in which all eggs were untreated.

Third, Double-crested Cormorant eggs (pers. obs.) and those of Northern Gannets (*Sula bassanus*, Nelson 1978) are pale blue and smooth when laid but are soon covered with a rough layer of chalky, fecal material. Apparently, this layer is sufficiently porous so that the development of cormorant (this paper) and gannet (Nelson 1978) embryos does not appear to be affected. Such "porous feces" may be typical of species of seabirds that habitually defecate on

TABLE 8. Hatching success of eggs treated four times with water (control eggs) or with modified cormorant or gull feces from which the fat content had been removed with ether (Meadow III, 1980).

Treatment	Number of eggs	Number of eggs hatched	Percentage hatched
Control	28	20	71.4
Cormorant feces	28	25	89.2
Gull feces	28	9	32.1

their eggs and may be associated with a purely marine diet that includes fish. The feces of Glaucous-winged Gulls often contained apparently undigested membranous or fibrous material, which, when dried, had a felt-like appearance. Indeed, Northwestern Crows (*Corvus caurinus*) were often seen to eat gull feces or to feed them to their nestlings. Presumably, this felt-like material helped to plug the pores in the egg shells. Cormorant feces did not appear to contain undigested, edible material.

A fourth reason for the detrimental effect of gull feces on the hatching success of eggs is that the fat contained in the feces may have helped to plug the pores in the shell. Some studies have indicated that a slight application of oil to the surface of eggs greatly reduces the hatching success of those eggs (Kopischke 1972, McGill and Richmond 1979). The fat content of gull and cormorant feces was determined from samples derived from 20 droppings. These samples were oven dried for 2 days at ca. 70°C and then treated three times with chloroform. Samples of gull feces obtained in 1979 and in 1980 contained 2.10% and 2.14% fat, respectively, whereas two samples of cormorant feces contained 2.76% and 0.80% fat. When this small amount of fat was removed, it did not significantly improve the hatching success of the eggs (Table 8).

ACKNOWLEDGMENTS

I am indebted to J. Morgan, L. Legendre, L. Graf, A. Stuart, J. Smith, M. Yang, and Y. Yom-Tov for assistance and discussion. The fieldwork was carried out on Mandarte Island with permission from the Tsawaout and Tseycum Indian Bands of Saanich, British Columbia. The study was supported by the

Natural Sciences and Engineering Research Council of Canada. I thank Jaap Kruijt and the Ethology Group of the University of Groningen, Netherlands, where this paper was written, for their kind hospitality and help. I appreciate the helpful comments I received from J. P. Hailman, D. E. Miller, R. Pierotti, and two anonymous referees.

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