THE BREEDING BIOLOGY OF THE ROOK CORVUS FRUGILEGUS L. IN CANTERBURY, NEW ZEALAND

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ABSTRACT

During 1967, Rooks at West Melton and Banks Peninsula rookeries selected mainly *Pinus radiata* for nesting and chose the highest safe sites. Nest construction periods varied from 5 to 20 days, the last nests being completed most rapidly.

Eggs were laid between 30 August and 6 November. Rookeries showed significant differences in laying date, apparently resulting from differences in food availability. The size of eggs varied with laying sequence. The mean clutch size was different at each rookery, ranging between 2.9 and 3.8 eggs, a similar value to that obtained by past workers in Canterbury but smaller than that of Rooks in Britain.

Nestling periods were directly related to brood size. Growth rates of nestlings varied with brood size, hatching sequence, partial brood loss and season. Parental feeding visits were largely independent of brood size and ranged from 1.4 to 3.3 visits per hour.

Failure of the embryo to develop accounted for most egg losses. Most nestling mortality resulted from parents killing the smallest nestling before it died of starvation.

Breeding success varied seasonally and ranged from 38 to 12.7%. Three and four egg clutches occurred most frequently, but larger clutches produced more fledglings.

INTRODUCTION

The Rook (*Corvus frugilegus* L.) is regarded as an agricultural pest on the Canterbury Plains. The many attempts at extermination have been unsuccessful, but numbers have been greatly reduced and fewer than 300 birds now remain. A similar number exists on nearby Banks Peninsula where they are valued by the farmers and are not controlled.

This study of the breeding of Rooks on the Canterbury Plains was made in 1967, following large scale reductions of the population. The population on Banks Peninsula was also examined for comparative purposes. The distribution, abundance and feeding activity of Rooks in Canterbury has been described separately (Coleman 1971).

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METHODS

Nests in West Melton rookeries were visited daily between 1000 and 1200 hr during egg laying and hatching, so that breeding phenology could be recorded. Nests in Banks Peninsula and Sunnyside rookeries were visited weekly, but at Sunnyside the few Rooks present produced only one clutch and this was excluded from the present paper.

Eggs laid each day were serially numbered on one end with a felt marking pen. Nestlings were marked for growth studies by clipping the claws of individual toes, according to the chicks position in the hatching order.

Egg lengths and diameters were measured to the nearest 0.1 mm with vernier calipers. Volumes were calculated from Worth's (1940) expression: $V = K\ pi/6ab^2$, where V = volume, a = length and b = the greatest transverse diameter. K, the mean constant of equality, was taken as 0.983 ± 0.029, a value calculated from a sample of 27 randomly selected eggs of measured volume.

Nestlings were at first weighed to the nearest gram on a 25 g spring balance and later to the nearest 5 g on a 500 g spring balance.

Breeding behaviour was observed from a tree-top hide within 5 m of 19 occupied nests. Observation periods were between 10 a.m. and 3 p.m. on days of similar weather, and during each period the behaviour of birds at four to six nests was recorded. Breeding displays were used to distinguish the sexes.

Unless otherwise stated, "Student's *t*" test was used in all statistical analyses with confidence limits of 0.95 being considered significant.

RESULTS

NEST SITES AND CONSTRUCTION

The location of all Mid-Canterbury rookeries is shown in Figure 1. All are in groves dominated by *Pinus radiata;* Jarman's, Kirwee and Chorlton rookeries are in pure stands, while Robinson's, Okains Bay and Long Look Out Point rookeries occupy groves containing *P. radiata, Eucalyptus* spp. and *Cupressus macrocarpa.* In mixed groves *P. radiata* is preferred for nesting while eucalypts are used only at Okains Bay. Nests were not found in *C. macrocarpa.*

The earliest nests were built at higher levels than later ones (Table 1; $r = -0.36086$, $p < 0.01$). Although high sites were available in peripheral trees, late nesters select sites at lower levels in the centre of the colony, presumably due to gregariousness or for communal protection.

Nests in eucalypts were always below crown level in the crotches of branches. Stead (1946) noted that prior to 1930 Canterbury Rooks preferred eucalypts. He suggested that the change to pines was caused by the death of many eucalypts and, as is still quite apparent, by the unstable whippy branches of those remaining.

TABLE 1: NEST HEIGHT IN RELATION TO THE START OF NEST CONSTRUCTION AT ROBINSON'S ROOKERY

Start of Nest Construction	No. of Nests	Height of Nests (m) Mean	Range	S.D.
Up to 25.8.67	8	18.0	16.5 - 19.6	1.08
26-31.8.67	10	17.9	14.2 - 19.5	1.34
1-6.9.67	23	17.6	15.2 - 19.5	1.08
7-12.9.67	21	16.6	13.7 - 18.9	1.47
13-18.9.67	12	16.4	14.4 - 19.0	1.55
19-24.9.67	11	16.4	13.4 - 18.9	1.73
After 24.9.67	7	16.6	14.9 - 19.2	1.48

Note: Table includes two nests which were never laid in

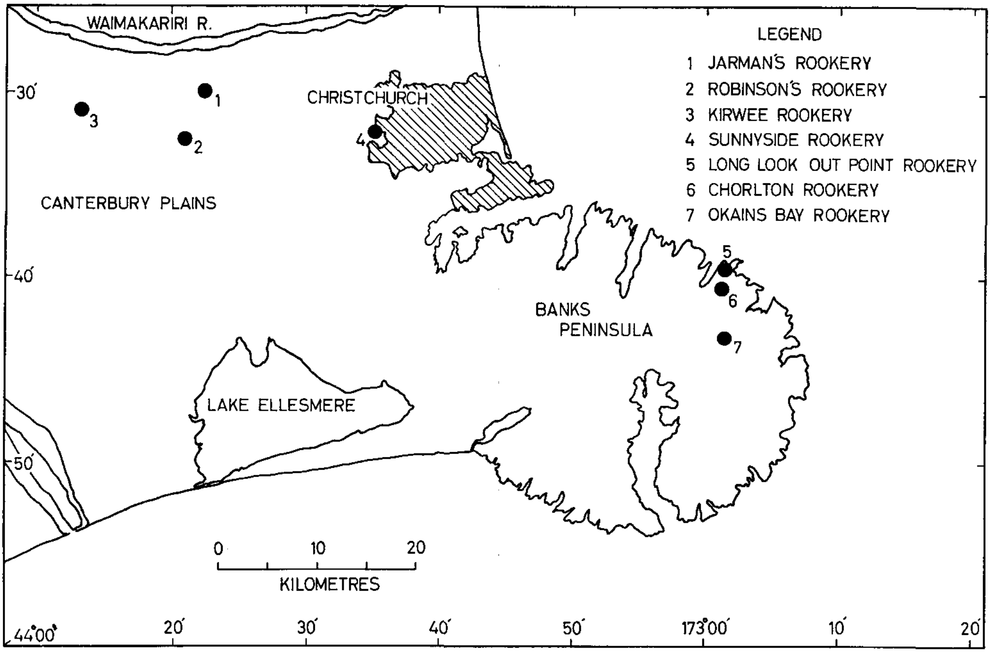

FIGURE 1: Mid-Canterbury, New Zealand, showing the position of rookeries occupied during the study.

At Robinson's rookery nests were built between 17 August and 25 October (Fig. 2A). Only 21% of all nests were started before 31 August when the birds moved from the winter roost to the rookery; thereafter the number of nests increased rapidly. The number of nests started during late September and October was less than that lost from constructional failure or destruction by stick-thieving birds. Of all nests built in Robinson's rookery, 12% were lost during the breeding season.

Rooks placed up to approximately 30 twigs on the first day of nest construction, and nest bases were generally recognisable from ground level 24 hr after the placing of the first twig. Nest construction was therefore considered to have started 24 hr prior to the day of discovery and to have finished when the nest was completely lined. Nest building periods for 56 nests ranged from 5 to 20 days (7.5 ± 2.66). Construction times varied considerably throughout the nesting season, later nests being built more rapidly (shown also by Yeates 1934, Busse 1965).

Several partially collapsed nests containing endangered eggs or chicks were observed, but it seems that only the loss of a clutch or brood will initiate reconstruction of the nest. Limited nest reconstruction occurred during autumn (late March) e.g. at Robinson's rookery seven out of 40 nests examined were roughly reconstructed. Reconstruction was never completed at this time and laying never followed.

THE EGG PHASE

Egg Laying

Eggs were laid between 30 August and 6 November (Table 2), with peak laying in late September in all but the Kirwee and Chorlton rookeries, where laying was significantly later ($p < 0.01$).

TABLE 2: LAYING DATES IN CANTERBURY ROOKERIES

Rookery	No. of eggs	No. of Nests examined	Mean	Laying Date Range	S.D.
Robinson's	382	90(90)	17.9.67	1.9 - 6.11	16.1
Jarman's	78	26(26)	26.9.67	30.8 - 30.10	16.1
Kirwee	68	22(33)	4.10.67	15.9 - 25.10	10.4
Okains Bay	45	14(39)	18.9.67	6.9 - 3.10	5.5
Chorlton	110	30(30)	1.10.67	10.9 - 22.10	10.6
Long Look Out Point	120	45(83)	23.9.67	10.9 - 25.10	12.2

Note: Figures in parenthesis show the total number of nests in the rookery

Eggs from replacement and second clutches included

Eggs were laid between 0700 and 1000 hr at intervals of one to five days, with most (86% of a sample of 183 eggs) being laid within one day of their predecessor. Irregular laying increased with eggs laid later within individual clutches. Of 26 (14%) abnormal laying intervals, 11 were between final eggs of clutches. Six eggs, three of which were infertile, were laid following intervals of three or more days.

Egg Dimensions and Clutch Size

Since volume is biologically the most meaningful dimension of an egg, indicating how much material is contained therein, the following section is limited to this dimension. Volumes of eggs varied with individual laying sequences, but showed a general decrease after the laying of the second egg (Fig. 2B). This phenomenon, together with increasing irregularity of laying of later eggs in individual clutches could have been caused by the depletion of energy reserves directed into egg production. Payne (1965) likewise suggested that the decrease in size of the final eggs of Cowbirds *(Melothrus ater)* resulted from a physiological slowing down in the conversion of food into egg material.

The mean size of eggs did not regress significantly on laying date. However, the regression of clutch size on laying date was highly significant, indicating a seasonal decline in egg production by birds laying later (Table 3; $y = 4.64831 + -0.04018X$; $F = 10.0247$, $p < 0.01$). Egg and clutch sizes of British corvids decreased seasonally, which Holyoak (1967) believed to have resulted from young birds laying later.

The frequency distribution of clutch sizes varied from rookery to rookery (Table 4), and although the ranges in clutch size were similar (1-6 eggs), the means varied between 2.94 and 3.85 eggs. Overall, clutches of three and four eggs were most common (63.2% of all clutches) followed by two (17.6%), five (12.6%), one (3.3%) and six (3.3%) egg clutches. Clutches of one were considered to be incomplete (for Rooks in Britain, Owen 1959) and were omitted from some calculations.

Of the 11 replacement clutches laid at Robinson's rookery, eight followed clutch losses and three followed brood losses. Time lags between first and replacement clutches ranged from 12 to 51 days (30.8 ± 12.64). Replacement clutches were on average smaller (2.92) than the preceding first clutches (3.36), but generally were larger than first clutches laid at the same time. Only one second clutch was laid and that was 46 days after the laying of the first.

The frequency of occurrence of different clutch sizes varied throughout the laying season (Fig. 2C). Clutches of six eggs occurred only during the first two weeks of laying, while those of five were recorded commonly throughout the first half of the laying season. Clutches of three and four eggs were found throughout the laying

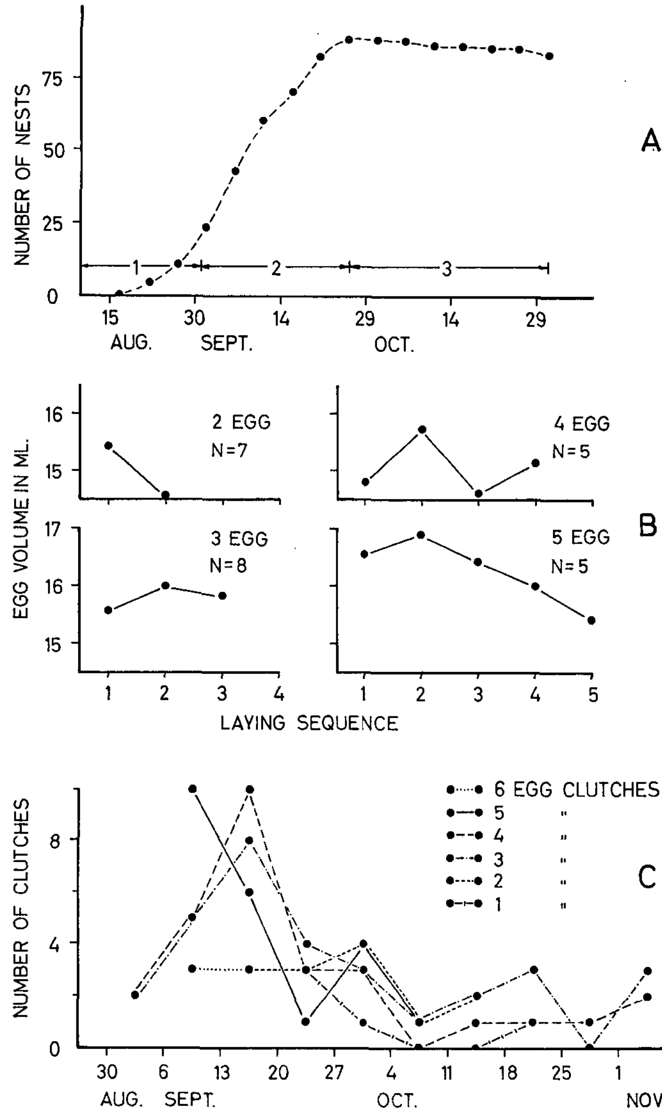

FIGURE 2A: Changes in the number of nests present at Robinson's rookery during the breeding season; 1, 2 and 3 refer to the period before complete rookery re-occupation, the period of maximum nest construction and the period of late nest construction respectively.

FIGURE 2B: Egg volume in relation to laying sequence in different sized clutches at Robinson's rookery. Sample sizes show the number of clutches involved.

FIGURE 2C: Seasonal variations in the frequency of individual clutch sizes laid at Robinson's rookery.

TABLE 3: VARIATION IN EGG AND CLUTCH SIZE WITH LAYING DATE AT ROBINSON'S ROOKERY

Laying Date	No. of Clutches	No. of Eggs	Mean Clutch Size	Mean Egg Volume (ml)
Up to 5.9.67	4	14	3.50	15.26
6-10.9.67	17	77	4.59	15.11
11-15.9.67	18	78	4.33	15.40
16-20.9.67	22	80	3.64	15.50
21-25.9.67	8	20	2.50	13.71
26-30.9.67	12	40	3.33	14.24
1-5.10.67	5	15	3.00	14.38
After 5.10.67	4	11	2.75	15.00

Note: Replacement and second clutches excluded

TABLE 4: SIZE OF FIRST CLUTCHES IN CANTERBURY ROOKERIES

Rookery	Clutch Size						Mean Clutch Size	
	1	2	3	4	5	6	M1	M2
Robinson's	4	12	22	25	21	6	3.72	3.85
Jarman's	2	2	8	9	2	0	3.26	3.52
Kirwee	1	2	15	2	0	1	3.14	3.24
Okains Bay	0	3	2	6	2	0	3.55	3.55
Chorlton	0	5	9	12	1	0	3.35	3.35
Long Look Out Point	0	14	15	10	1	0	2.94	2.94
Total	7	38	72	64	27	7	-	-

Note: M1 - mean clutch size excluding replacement clutches

M2 - mean clutch size excluding replacement and one egg clutches

period, but occurred most frequently during early laying and at the end of the season during the upsurge in relaying. One and two-egg clutches occurred less frequently than clutches of 3-5 and only during later laying.

With the exception of Robinson's and Long Look Out Point rookeries, the mean clutch sizes recorded at individual Canterbury rookeries were similar (Table 4). The mean clutch size at Robinson's rookery was significantly larger ($p < 0.05$) than at Kirwee and Long Look Out Point rookeries, while clutches at Long Look Out Point were significantly smaller ($p < 0.05$) than those at Robinson's, Jarman's and Chorlton rookeries.

INCUBATION AND HATCHING

The incubation period was taken to be the time between the laying of an egg and its hatching. Unless otherwise stated, this measurement refers to the last egg of a clutch. The recorded period may have an error of up to 23 hr because the precise times of laying and hatching were rarely known.

TABLE 5: THE VARIATION IN INCUBATION PERIOD WITH THE SEQUENCE OF EGG LAYING AT ROBINSON'S ROOKERY

Incubation period (days)	Position of egg in laying sequence 1st	2nd	3rd	4th	5th
21	2				
20	2				
19	3	1			
18	8	7			
17	2	7	6	3	
16			4	3	
15	1				3

No. of eggs at each incubation period

Incubation periods decreased with the sequence of laying (Table 5), and, allowing for the maximum possible error, ranged from 14 to 22 days with a mean of 17.4 ± 1.31 days cf. 18.0 days obtained by Yeates (1934) for Rooks in Britain. The shorter incubation period of later eggs of individual clutches resulted from an increase in the intensity of incubation behaviour during laying, with the initial incubatory patterns being easily disturbed. Van Tyne & Berger (1959) considered that birds of many species sat on eggs during early incubation without applying enough heat to affect embryological development.

Hatching, the period during which the chick freed itself from the egg, took approximately 24 hr from the first outward sign of pipping. Depending on clutch size, the hatching period of entire clutches took from 24 to 27 hr; the eggs hatching asynchronously in the order laid.

THE NESTLING PHASE

Nestling Period

As nestlings within broods left the nest together, the nestling period was taken to be the time between the hatching and fledging of first-hatched nestlings; the mean interval for 47 broods raised at Robinson's rookery (Table 6) being 33 ± 1.25 days.

TABLE 6: NESTLING PERIOD IN RELATION TO BROOD SIZE

Brood Size	Nestling Period (days) 26	27	28	29	30	31	32	33	34	35	36	37	38	Total	Mean Nestling Period
1	1				2	3	3		2		2			13	31.9
2	1	1		2		3	4	1		1		1	1	15	31.7
3					2		1	3		5		1		12	33.6
4										1	3	2	1	7	36.4

Nestling periods were directly related to brood sizes; four-chick broods remaining in the nest significantly longer than one ($p < 0.001$), two ($p < 0.001$) or three-chick ($p < 0.01$) broods. Chicks in large broods grew more slowly than those in small broods (see nestling growth rates) and had longer nestling periods.

Brood Size

Brood sizes in Canterbury rookeries ranged from one to six chicks. Four was the most fledged from any brood, with 53% of successful broods losing one or more chicks before the rest fledged. Three pairs raised five chicks to fledging weight, but then lost one or more during the final nestling period. The ranges and frequencies of brood sizes were similar in most rookeries, but large broods were infrequent at the Long Look Out Point colony.

Nestling Growth

The variation in growth rates of all nestlings in all three-chick broods raised at Robinson's rookery is shown in Fig. 3A (nestling growth rates in the following section refer to data collected at Robinson's rookery). Nestlings above or below the mean growth curve of this and other brood sizes generally remained so, except for single-chick broods in which considerable variation in individual growth rates often occurred. Individual nestlings with slower growth rates than their nest-mates risk starvation, and the larger the brood the smaller the weight differences which may affect survival. Typically, newly hatched chicks weighed from 12 to 15 g. At first, weight increases were slow, but later accelerated, with 30 to 40 g being added daily between the 6th and 18th days. Maximum weights (380 to 440 g) were reached by the 23rd day (a 30-fold increase) and maintained thereafter.

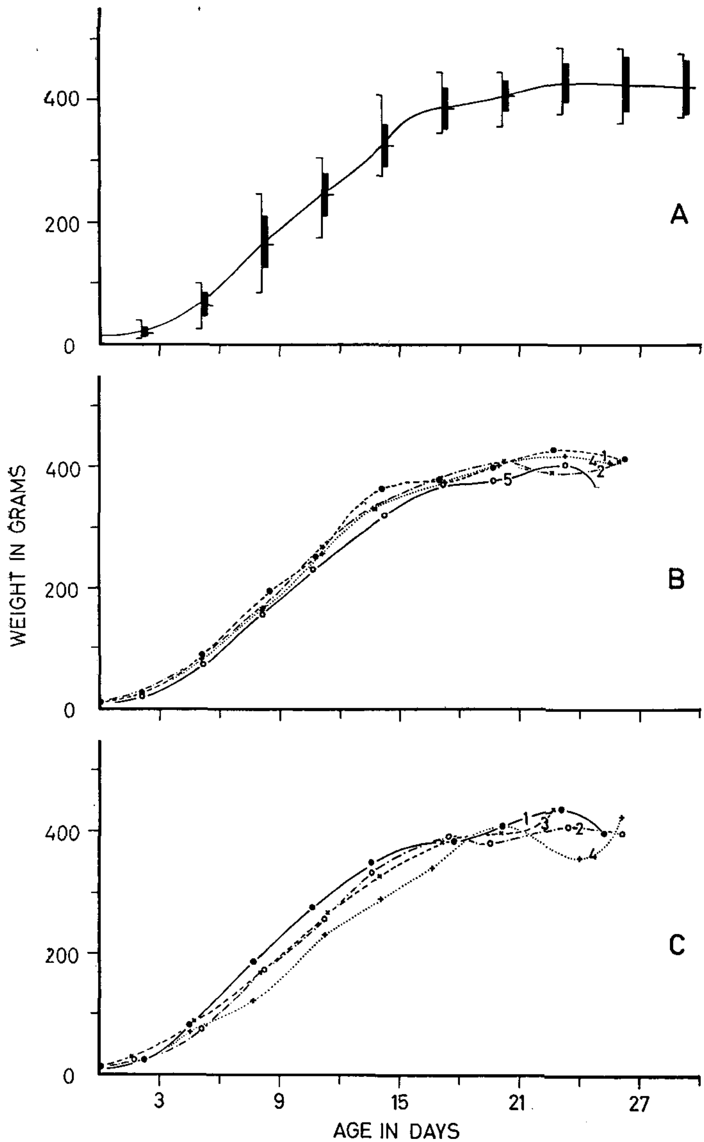

FIGURE 3A: Variation in growth of nestling Rooks in broods of three (N = 13). The curve runs through points of mean growth rate in each sample, the vertical lines show range, and the vertical bars one S.D. on either side of the mean.

FIGURE 3B: Growth of nestling Rooks in broods of one (N = 9), two (N = 13), four (N = 8), and five (N = 2) nestlings.

FIGURE 3C: Growth of the first, second, third and last hatched Rook nestlings in broods of four (N = 9).

The growth curves of the various brood sizes are similar in form, but chicks in smaller broods generally grow faster and fledge at higher weights than those in larger broods (Fig. 3B). During the first four days, however, broods of 1, 2, 3 and 4 chicks have similar growth rates.

Nestling growth rates and fledging weights are generally directly related to hatching sequence, the earliest hatched nestling being most advanced (Fig. 3C).

Nestlings from replacement clutches laid early in the breeding season show similar growth rates to those of 'normal' broods. For example, brood 9B (Fig. 4A) was raised during peak nestling activity and closely followed the mean growth curve for 'normal' broods, while broods 11C and 8A raised during December and after the desertion of the rookery by most other birds, grew more slowly. The effect of season is illustrated further with the growth rates of two-chick broods (Fig. 4B). Excluding the first seven days of the nestling period, later hatched broods grow less rapidly and fledge at lower weights than earlier broods; a trend which coincides with a decrease in availability of some nestling foods during October and November (see Coleman 1968, Fig. 5.3). Also, exceptionally late broods are fed less frequently than earlier broods as their parents forage with the main flock two or three miles away from the rookery rather than nearby.

Surviving nestlings in small broods show dramatic weight gains following the death of brood-mates (Fig. 4C). In large broods no changes in rates of growth were observed however, as there were more nestlings present to share any extra food.

Nestling Feeding Frequency

The frequency of parental feeding visits, while independent of brood size, ranged from 1.4 to 3.3 visits per hr and all chicks normally received food on each occasion (Table 7).

Feeding rates bore little relation to brood age: ten observation periods on seven broods of between one and seven days of age showed a mean feeding rate of 2.07 visits per hr, and on nestlings between 10 and 30 days of age, a mean feeding rate of 2.28 visits per hr.

The weight of food received by 16 nestlings at individual feeds showed a range of 0.02 to 9.4 g. However, the amount of food received per feed varied with the age of the nestling; 10 meals taken from chicks between 5 and 11 days of age had a mean weight of 0.94 ± 0.38 g, while six meals from chicks between 17 and 23 days of age, had a mean of 3.4 ± 2.60 g. During the first 20 days of the nestling period, the female remained at the nest and ate an unknown proportion of the food brought by the male. Later, when the combined needs of the female and chicks were apparently beyond the foraging capabilities of the male, the female also foraged.

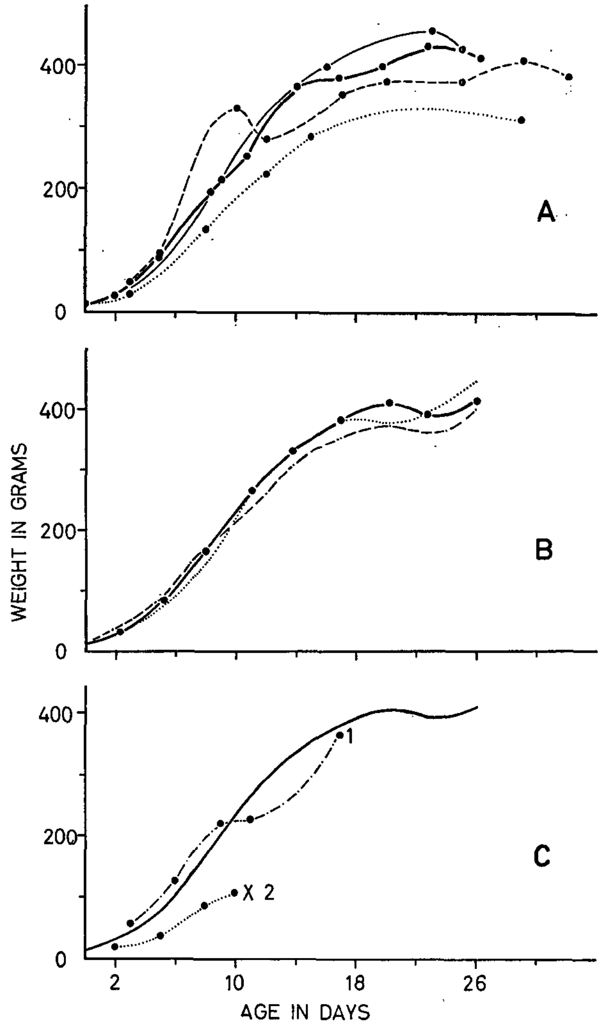

FIGURE 4A: Growth of solitary Rook nestlings from three replacement clutches. The solid line designates a chick raised during peak nestling activity (brood 9B), and the broken and dotted lines (broods 11C and 8A) chicks raised after the desertion of the rookery site by all other Rooks. The heavy line depicts the mean growth of all (13) 'normal' broods of one nestling.

FIGURE 4B: Growth of Rook nestlings in three early (prior to 25 October) and three late fledged (after 15 November) broods of two nestlings (dotted and broken lines respectively). The heavy line shows the mean growth of all (13) broods of two nestlings.

FIGURE 4C: Growth of Rook nestlings in a brood of two, one of which died. The cross indicates the nestling which died, the heavy line the mean growth rate of 13 broods of two nestlings.

TABLE 7: FREQUENCY OF PARENTAL FEEDING VISITS AT ROBINSON'S ROOKEK

Clutch No.	Clutch Size	Total weight of brood (g)	Feeding frequency (visits per hour)
2E	1	80	1.8
	1	280	2.1
2C	2	164	3.3
	2	384	2.0
	1	350	1.8
8B	3	40	1.4
	3	90	3.2
	2	800	3.3
	2	870	2.3
21A	3	925	1.8
	3	1260	2.6
2A	3	371	2.0
2B	4	173	2.6
	4	484	3.2
	3	845	2.7
	3	1250	1.5
5B	4	530	3.2
	4	1600	1.8
	4	1670	2.6

Note: Feeding frequencies determined from observation periods of 5 hr duration between October 3 and 26 inclusive

Similar-aged nestlings in broods of different sizes had meals of about the same weight. Samples collected from nestlings within individual broods varied in composition but often not in weight e.g. nestlings in brood 10 (Robinson's rookery, 6 Nov. 1976) aged eight, nine and ten days received at one feeding, 0.50, 0.65 and 0.64 g respectively. Nestlings within individual broods grew and fledged at different rates however, and probably each chick received a slightly different amount of food.

BREEDING SUCCESS

Egg and Chick Losses

The majority (56%) of egg failures in West Melton rookeries were recorded as 'eggs which disappeared from the nest,' with most lost after full incubation and as complete clutches (Table 8).

TABLE 8: REASONS FOR EGG LOSSES IN WEST MELTON ROOKERIES

Reasons for egg losses	Robinson's 1st clutch	Robinson's Repl.*	Robinson's Tot.	Jarman's 1st clutch	Jarman's Repl.	Jarman's Tot	Kirwee 1st clutch	Kirwee Repl.	Kirwee Tot.
No sign of development	32(23)	4(3)	36	2(2)	0	2	9(6)	0	9
Embryo dead	3(3)	1(1)	4	0	0	0	0	0	0
Embryo died at hatching	7(6)	0	7	0	0	0	0	0	0
Broken by recorder	7(5)	0	7	6(4)	1(1)	7	14(6)	0	14
Cracked by parent	1(1)	0	1	0	0	0	0	0	0
Eaten by parent	4(3)	0	4	1(1)	0	1	1(1)	0	1
Nest collapsed	8(3)	6(2)	14	3(1)	3(1)	6	1(1)	0	1
Eggs buried	2(1)	0	2	0	0	0	0	0	0
Eggs which disappeared from the nest									
Early	12(6)	8(3)	20	3(2)	0	3	4(2)	0	4
Mid-incubation	20(11)	10(4)	30	7(3)	0	7	9(3)	5(1)	14
After full incubation	50(33)	7(3)	57	8(3)	0	8	4(3)	0	4
Total			182			34			47

Note: Figures in brackets denote the number of clutches involved
Repl.* - Replacement clutches

Of all eggs that remained in the nest after complete incubation, 36% showed 'no sign of development.' Many eggs lost from the nest after full incubation probably failed to hatch for the same reason. Of all eggs of known laying order lost through developmental failure at Robinson's rookery, 52% (17) were eggs laid last.

Egg losses resulting from the collapse of nests was rare and usually involved the complete clutch.

Intra- or inter-specific predation of viable eggs was not observed, although some parent birds ate cracked and addled eggs. Clutches which disappeared from nests may have been eaten by other Rooks, but considering the strong territorial defence shown by this species, this could have occurred only after the eggs had been deserted.

The most common losses of nestlings resulted from parents killing their chicks, especially starvelings (Table 9). At Robinson's rookery four neighbouring broods were killed at one time, probably by a rogue bird nesting in the same tree.

TABLE 9: NESTLING LOSSES AT ROBINSON'S ROOKERY

Time of Nestling Loss	Reasons for Nestling Losses: Deserted	Starved	Killed by parent	Killed by recorder	Nest destroyed	Nest collapsed	Fall from nest	Unknown causes	Total
Following hatching: 0-4 days	12	5	6	0	2	0	0	0	25
Mid-nestling: 4-20 days	0	7	20	2	0	12	0	3	44
Prior to fledging: 20-? days	0	0	1	3	0	2	1	0	7
Total	12	12	27	5	2	14	1	3	76
Position in brood:									
First hatched	0	0	0	1	0	3	0	0	4
Mid-brood	0	0	0	0	0	0	1	0	1
Last-hatched	0	11	8	3	0	5	0	0	27
Age unknown	0	1	1	0	0	0	0	0	2
Total brood losses (B/1)	3	0	2	1	0	1	0	0	7
Larger broods	9	0	16	0	2	5	0	3	35
Total	12	12	27	5	2	14	1	3	76

The desertion of broods occurred only immediately after hatching, all nestlings involved ultimately succumbing to chilling or starvation. Losses from starvation in attended broods, however, were confined to the early and mid-nestling periods of last-hatched nestlings.

Some nests collapsed during the mid-nestling period as chicks approached maximum size, and generally the entire brood was lost. Partial brood losses resulting from nest failure were not related to hatching sequence.

Nestlings which hatched last had a higher mortality than their brood mates during the five to seven days between their desertion of the nest and rookery sites respectively (54% of the 13 recorded fledgling losses were last-hatched chicks, see Table 10). Such chicks were generally smaller than their siblings and it was likely that larger broods which fledged smaller nestlings suffered proportionately heavier fledgling losses. Mortality during the first post fledging month of European Rooks also was highest in last-hatched nestlings and was directly related to brood size (Van Koersveld 1958).

Breeding Success

Hatching and nestling success were apparently not related, the lowest hatching and highest nestling success recorded in Canterbury occurring at Chorlton rookery. Hatching success ranged from 34.2% at Chorlton rookery to 62% at Jarman's rookery, while breeding success varied from 22 to 46.5%. Breeding success was not related

TABLE 10: FLEDGLING LOSSES IN RELATION TO BROOD POSITION

Nest No.	1A	1C	4A	4B	5B	6A	9D	12B	17A	38
Brood Size at Fledging	4	2	4	2	4	2	3	3	4	2
Position of Nestling in Brood at Fledging	L	L	1	L	L	1&L	1&L	1	2&3	L

Note: 1, 2, 3 and L indicate first, second, third and last in brood sequence

TABLE 11: HATCHING, NESTLING AND BREEDING SUCCESS IN CANTERBURY ROOKERIES

Rookery	Egg No.	Hatching success (%)	Nestling success (%)	Breeding Success (%) B1*	B2+
Robinson's	382	51.0	63.2	35.5	36.5
Jarman's	78	62.0	63.0	38.0	46.5
Kirwee	68	40.0	31.8	12.7	22.0
Chorlton	110	34.2	66.6	22.8	29.6
Okains Bay	45	52.3	39.2	20.5	25.0
Long Look Out Point	120	50.0	65.0	32.6	42.5

Note: B1* Breeding success excluding those destroyed by the author.

B2+ Breeding success excluding total clutch and brood losses, and those destroyed by the author.

Hatching success = brood size/clutch size; Nestling success = No. fledged/brood size; Breeding success = no. fledged/clutch size.

to colony size, although there may well be a minimum size of rookery below which successful breeding is unlikely to occur e.g. Sunnyside, which had only nine birds, produced no young.

Hatching success at Robinson's and the Banks Peninsula rookeries differed, and the two colonies showed different relationships between clutch size and the average number of nestlings hatched per pair (Table 12). At Robinson's rookery, the number of nestlings fledged increased with clutch size. This was not so at Peninsula rookeries, where nestling success and the number fledged was lowest in the larger clutch sizes.

TABLE 12: HATCHING AND NESTLING SUCCESS IN RELATION TO CLUTCH SIZE

Clutch size	No. of clutches	No. of eggs	No. hatched	% success	Average No. hatched/pr.	No. of Nestlings fledged	% success	Average No. Fledged/pr.
ROBINSON'S ROOKERY								
C/1	6	6	4	66.6	0.66	2	50.0	0.33
C/2	11	22	4	18.2	0.36	3	75.0	0.27
C/3	21	63	35	55.6	1.66	20	57.1	0.95
C/4	25	100	61	61.0	2.44	40	65.6	1.60
C/5	19	95	57	60.0	3.00	35	61.5	1.84
C/6	5	30	18	60.0	3.60	13	72.2	2.60
BANKS PENINSULA ROOKERIES (SUMMED)								
C/2	19	38	22	58.0	1.16	13	59.0	0.67
C/3	25	75	37	49.4	1.48	34	92.0	1.36
C/4	27	108	42	39.0	1.56	21	50.0	0.78
C/5	4	20	10	50.0	2.50	4	40.0	1.00

Note: Eggs from replacement and second clutches and those broken by the author are excluded.

TABLE 13: HATCHING, NESTLING AND BREEDING SUCCESS IN RELATION TO LAYING DATE AT ROBINSON'S ROOKERY

Laying Date	Eggs laid	Hatching success (%)	Nestling success (%)	Breeding success (%)
up to 11.9.67	26	60.0	93.0	55.8
11-15.9.67	81	58.0	81.0	47.0
16-20.9.67	93	66.7	72.5	48.3
21-25.9.67	54	66.7	47.2	31.4
26-30.9.67	26	42.4	27.3	11.6
1-5.10.67	30	23.4	43.0	10.0
6-10.10.67	12	50.0	16.6	8.3
after 10.10.67	13	30.7	50.0	15.4

Note: Eggs from second and replacement clutches excluded

Hatching, nestling and breeding success at Robinson's rookery was greatest for birds laying early in the season (Table 13) when food was abundant (see Coleman 1968, Fig. 5.3). This was so also for tits, *Parus* spp. (Lack, Gibb & Owen 1957).

Breeding success at Robinson's rookery was also considerably greater in first (36.5%) than in replacement clutches (6.4%) (Coleman 1968), largely because the latter (12.5% of all clutches) were laid at a later and probably less favourable time for food gathering and concomitant egg production.

DISCUSSION

Egg Laying

Laying at the Kirwee rookery on the Canterbury Plains and at the Chorlton rookery on Banks Peninsula was significantly later than at neighbouring rookeries. Although there was no obvious reason for this at the Kirwee rookery, laying at the Chorlton rookery, sited 380 m above sea level, was probably retarded by the low temperatures and food availability experienced during the early part of the breeding season; snow lay about the rookery for three to four days during early laying.

The ability of the Rook to replace lost clutches or broods depends on the date at which the loss occurs and on the length of the preceding incubation or brooding period. Marshall & Coombs (1957) considered that Rooks were capable of relaying for two to three weeks after the hatching of the first chick. Excluding the anomalous clutch laid after a first brood was successfully fledged, Canterbury birds replaced only lost clutches or newly hatched broods, and these only during the first half of the laying season. As the sexual activity of Rooks waned during late incubation and hatching, so also their re-laying ability apparently decreased, especially in later breeding (presumably younger) birds and this may also partly account for the difference in the size of first and replacement clutches.

The mean clutch sizes which I recorded in 1967 resemble those recorded by past Canterbury workers, but are smaller than those of Rooks in Britain (see Lockie 1955; Owen 1959, Table 14). In Canterbury, Stead (1946) recorded a smaller range of clutch sizes than was observed during this study but failed to give any mean clutch size, while Crequer's (cited by Bull 1957) Canterbury data are similar to those of the present study. Niethammer (1970) reported that the " smaller clutches in New Zealand [of many introduced passerines including the Rook, compared with those recorded in Britain] can be attributed to high population density and to the subsequent mutual disturbance of breeding pairs, causing diminished use of available food." If this were so, the mean clutch size in Canterbury now should be larger than before the recent poisonings and should be directly related to rookery size, neither of which is true. Clutch sizes of many European birds vary with location however, and are larger in high than low latitudes (Lack 1947). Oxford at 51°45′N (Owen's and Lockie's study areas) is latitudinally higher than Mid-Canterbury at 45°30′S and the difference in day-length between these stations presumably accounts for the differences in recorded clutch sizes.

TABLE 14: COMPARISON OF CLUTCH SIZES IN CANTERBURY AND BRITAIN

Source	Locality	Year	Sample Size	Mean Clutch Size
Stead (1946)	Canterbury	c.1946	'large'	- (3-5)
*Crequer	West Melton	1956	40	3.4
Coleman	Canterbury	1967	215	2.94- 3.85
Owen (1959)	Britain	1952-57	292	4.2 - 4.7
Lockie (1955)	Britain	1945-53	151	4.3 (normal)
			20	3.5 (late)

Note: * cited by Bull (1957)

Nestling Growth

The discrepancy between the growth curves of individual chicks and the mean growth curves for particular brood sizes results from either differences in the hatching order of individual chicks, or from differences in the amount of food brought to broods by their parents. Differences in size of siblings generally result from asynchronous hatching, which is later enhanced by differential feeding. Older chicks beg more strongly, obtain more food, and grow more rapidly than their smaller brood-mates. The amount of food brought to the nest varies with seasonal availability and with the food-gathering ability of the parents: nestlings in large or late broods received less food than those in small or early broods and grew less rapidly.

Breeding Success

Excluding eggs lost from the nest, most egg failures were due to lack of embryo development and occurred most commonly in eggs laid last. As chilling would most often affect the first egg of clutches (as incubation intensity increases with laying), the major causes of failure of last-laid eggs were probably infertility, or early embryonic death from causes other than chilling. The eggs of the Shag *Phalacrocorax aristotelis* showed a drop in fertility with laying sequence, a result of either a decrease in copulatory activity coincident with the onset of laying and incubation, or the small size of final eggs (Snow 1960). Rooks also showed a decrease in sexual activity and egg size with laying sequence and this may have brought about the drop in survival noted.

Nestlings at Canterbury rookeries died from a variety of causes. However, excluding total brood failures, those lost were mostly last-hatched nestlings, which either starved to death or were killed by their parents. Lockie (1955) similarly found that 90% of partial brood losses were last-hatched chicks; apparently due to asynchronous hatching which, as an adaptation to a fluctuating food supply, frequently resulted in the death of the smallest nestlings.

Lack (1966) considered the most frequent clutch size in any particular bird species to be that which, on average, gave rise to the greatest number of surviving offspring. If clutch size is partly under genetic control, it is reasonable to suppose that the largest clutches, which in the present study hatch the greatest number of nestlings per pair, should occur most frequently. As this was not so, then either larger clutches must be selected against at some later stage (nestling, fledgling or sub-adult), or a seasonal or age trend exists within the population which affects all clutch sizes and hatching successes. Large broods at Peninsula rookeries were apparently disadvantageous, four-chick broods occurring infrequently, and five-chick broods being absent. At Robinson's rookery larger broods fledged greater numbers of nestlings than smaller, more frequently occurring broods. Large broods, however, fledged smaller chicks which perhaps incurred a higher mortality after fledging.

Clutch size and nestling success varied seasonally, as large clutches were laid early in the season when food was abundant, whereas smaller clutches, including replacements, were generally laid later and the resultant chicks raised during less favourable periods.

Both factors, in conjunction with the presumed higher fledgling mortality of nestlings from larger broods, explain the predominance of the apparently less successful three and four-egg clutches at Robinson's rookery.

Small clutches of one and two eggs occurred infrequently (Table 12), produced fewer nestlings than larger clutches, and hence could be expected to disappear from the population. Owen (1959) suggested that such small clutches may have been maintained by years of food shortage when small clutches produce more surviving young than do large clutches. While it is conceivable that such conditions may result in three-chick broods leaving more offspring than four and five-chick broods, conditions would have to be unusually severe and occur very often to account for the occurrence of one and two-egg clutches. Lockie (1955) suggested that small clutches may have resulted from birds laying an egg (or eggs) away from the nest. However, as females rarely left the nest site after nest completion, this is unlikely. Clutches of one are laid only in West Melton rookeries and at a time when most other birds are feeding broods and demands on local food supplies are presumably heaviest. These rookeries appear to contain birds breeding in their first year which, being inefficient food gatherers (Lack 1947), lay small eggs and clutches; this together with a lower fledgling mortality in smaller broods (Van Koersveld 1958) may account for the retention of smaller clutch sizes.

Rooks usually mature and breed in their second year (Yeates 1934; Coombs 1960), and only rarely do they breed in their first (Giban 1947); most yearling birds form a non-breeding component within each breeding colony. Non-breeding components existed at rookeries on Banks Peninsula but were absent from those at West Melton (Coleman 1971). It appears that birds at West Melton may breed in their first year, while those in Peninsula rookeries do not do so until their second year.

Following reductions by large scale poisonings in 1956 and 1957, and further small scale poisonings in subsequent years, the West Melton Rook colony now shows signs of growth. Partial brood mortality occurs in large numbers of West Melton broods, but from past population sizes (approx. 10,000 in Mid-Canterbury) it seems that rookeries are capable of supporting higher numbers than occur at present. Young birds at these rookeries appear to be breeding at an earlier age than is usual, either because of an increase in food availability through reduced competition, or from an absence of interference by mature birds (see Ashmole 1963). Rookeries on Banks Peninsula have not been controlled in any way in recent years, and the birds rarely breed in their first year.

The breeding of Rook populations on the Canterbury Plains following large scale reductions appears to be an example of a reproductive response to a 'crash,' and contrasts with the 'control' population on Banks Peninsula. The birds on the Plains seem to have responded to a decrease in numbers by breeding at an earlier age, and not by increasing their clutch size and have thus increased the breeding potential of the population. Although food was abundant near Plains rookeries, it seems that individual Rooks do not have the capacity to increase their reproductive rate.

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REFERENCES

ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103*b:* 458-473.

BULL, P. C. 1957. Distribution and abundance of the Rook (*Corvus frugilegus* L.) in New Zealand. Notornis 7(5): 137-161, figs 1-3, tables 1-4.

BUSSE, P. 1965. Nest building dynamics of a breeding colony of the Rook (*Corvus frugilegus* L.). Ekologia Polska (A) XIII (25): 491-514, figs 1-12, tables I-IX.

COLEMAN, J. D. 1968. Aspects of the ecology of the Rook *Corvus frugilegus frugilegus* Linnaeus in Canterbury. M.Sc. thesis, University of Canterbury.

——— 1971. The distribution, numbers, and food of the Rook *Corvus frugilegus frugilegus* L. in Canterbury, New Zealand. N.Z. Journal of Science 14(3): 494-506, figs 1-3, tables 1-8.

COOMBS, C. J. F. 1960. Observations on the Rook *Corvus frugilegus* in southwest Cornwall. Ibis 102(3): 394-419, text-figs 1-9.

GIBAN, J. 1947. Donnees fournies par le baguage sur la biologie du Freux (*Corvus frugilegus* L.) en France et sur la migration de l'espece en Europe occidentale. Annales des epiphyties, n.s. 13(1): 19-41, 6 figs.

HOLYOAK, D. 1967. Breeding biology of the Corvidae. Bird Study 14(3): 153-168, 6 figs, 9 tables.

LACK, D. 1947. The significance of clutch-size [parts I-II]. Ibis 89(2): 302-352, tables I-II, appendices I-VII.

——— 1966. Population studies of birds. Pp. vi + 1-341, frontis., figs 1-31 and text-illus., tables 1-50. Oxford: Clarendon Press.

——— GIBB, J.; OWEN, D. F. 1957. Survival in relation to brood-size in tits. Proceedings of the Zoological Society of London 128: 313-326.

LOCKIE, J. D. 1955. The breeding and feeding of Jackdaws and Rooks with notes on Carrion Crows and other Corvidae. Ibis 97(2): 341-369, figs 1-5, tables 1-5, appendices 1-3.

MARSHALL, A. J.; COOMBS, C. J. F. 1957. The interaction of environmental, internal and behavioural factors in the Rook, *C. f. frugilegus* Linnaeus. Proceedings of the Zoological Society of London 128: 545-589.

NIETHAMMER, G. 1970. Clutch sizes of introduced European passeriformes in New Zealand. Notornis 17(3): 214-222, fig. 1, tables 1-3.

OWEN, D. F. 1959. The breeding season and clutch-size of the Rook *Corvus frugilegus*. Ibis 101(2): 235-239, tables 1-6.

PAYNE, R. B. 1965. Clutch size and numbers of eggs laid by the Brown-headed Cowbird. Condor 67(1): 44-60, figs.

SNOW, B. 1960. The breeding biology of the Shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. Ibis 102(4): 554-575, figs 1-2, tables 1-22.

STEAD, E. F. 1946. The Rook *(Corvus frugilegus)* in New Zealand. Oologists' Record 20: 43-44.

VAN KOERSVELD, E. 1958. A few data on the reproduction of the Rook, *Corvus f. frugilegus* L. Ardea 46: 58-62.

VAN TYNE, J.; BERGER, A. J. 1959. Fundamentals of ornithology. Pp. xi + 1-624, text illus. New York: John Wiley; London: Chapman Hall.

WORTH, C. B. 1940. Egg volumes and incubation periods. Auk 57: 44-60.

YEATES, G. K. 1934. The life of the Rook. Pp. 1-96, text-figs 1-2, pls 1-16. London: Philip Allan.

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