

A Model of Clutch Size Determination in Birds

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Summary. This paper tests the hypothesis that the timing and the size of bird clutches are determined by (1) a tendency to delay reproduction so that the female can store enough internal resources for laying a large clutch; (2) a tendency to breed early because survival of offspring late in the breeding season might be lower than early. These factors are approximated by linear functions in a model. The model predicts that there will be a correlation between early breeding females and those that have large clutches. This agrees with published data for several bird species. Predictions from the model are also made of clutch size and the impact on final clutch-size if one egg is removed or added during the laying. These predictions were compared with data from a crow (*Corvus cornix*) population and were supported if it is assumed that the formation of an egg is a relatively costly process. More precisely, the model is supported if the formation of an extra egg requires a delay of about four or five days before laying can begin.

1 Introduction

The question “What determines clutch size in birds?” has given rise to several hypotheses. Some are only concerned with factors operating within one breeding season (e.g. Lack 1954); recently, others have related clutch size to the whole life history strategy of the individual (e.g., Ricklefs 1977). This paper presents a model of the former class and deduces from it some predictions. It also accounts for a field experiment involving the removal of eggs from and the addition of eggs to the nests of Hooded Crows (*Corvus cornix*) during the egg-laying period and compares the influence of this manipulation on final clutch size with that predicted by the model.

The hypothesis to be modelled states that the number of eggs laid is the outcome of a balance between two factors. One is the amount of resources stored by the female before egg-laying that are available for egg production. For any particular female, a later date for the start of egg-laying means that she will be able to lay a larger clutch. The other factor is the proportion of eggs that survive to become fledged or mature young. It is assumed that eggs and young in late clutches have a lower survival than those in early ones. This could be because predation is heavier later in the season, less food is available for the feeding of nestlings, or younger subadults are less able to survive the winter. Various factors can affect survival in different species. These two forces have been suggested to be of importance for the clutch size determination by Murton and Westwood (1977 p. 186–188).

Thus, the starting point of the study is a previously suggested hypothesis for the determination of clutch size in birds. The hypothesis is formalized into a numerically testable model. It is tested, mainly with respect to its applicability for a population of the hooded crow.

2 The Model

2.1 Unmanipulated Clutches

Abbreviations

- a* A constant related to the rate at which a given female is able to store nutrients that can be used for egg formation.
- b* A constant related to the rate at which breeding success decreases as the breeding season progresses.
- $\left. \begin{matrix} d \\ K \end{matrix} \right\}$ Auxiliary constants that are explained below.
- e* Number of eggs laid by a female.
- s* The survival rate from egg to mature bird.
- t* The date of the first egg.
- t'* The date of laying the last egg and start of incubation.
- p* Production of fledged or mature young.

It is assumed that, during the period when egg-laying is optimally begun, the two factors influencing this timing can be approximated by linear functions

$$e(t) = at, \quad (1)$$

and

$$s(t') = 1 - bt'. \quad (2)$$

t and *t'* are measured on a common scale (e.g., days) but might have different origins. Assuming that these differ by *K* units, that one egg is laid per unit time (e.g. day) and that brooding is started when the last egg is laid, the relation

$$t' = t + K + e \quad (3)$$

holds. To simplify computations, $1 - bK$ is substituted by *d*, and Eq. (2) can now be rewritten as

$$s(t) = d - bt - abt. \quad (2')$$

The production is the product of the number of eggs laid and their survival (Fig. 1);

$$p(t) = at(d - bt - abt). \quad (4)$$

is inserted (from Eq. (5)) and $1-bK$ substituted by d , the optimum value of E can be found in the usual way;

$$\hat{E} = \frac{2d + 2ad - 2b - 2ab - 1}{4b + 4ab} \quad (15)$$

The difference between \hat{e} and \hat{E} is the number of eggs by which a female can be expected to reduce her clutch after the addition of one egg;

$$\hat{e} - \hat{E} = \frac{1}{2} + \frac{1 - 2d}{4b + 4ab} \quad (16)$$

The optimum choice is thus dependent on the parameter values a , b , and d .

3 The Clutch Manipulation Experiment

3.1 Methods

The experiment was conducted in the Revinge area in South Sweden (55°40' N, 13°30' E). In 1978, seventeen clutches of hooded crows were reduced by one egg each. The eggs were removed when the nest held two or three eggs. In 1979, seventeen clutches were increased by one egg each. Before the additions, the nest held one or two eggs. In both years, the number of eggs in the nests was counted six or seven days after the manipulations. The clutch size was also determined for other nests in the study area. In both years, the experimental and the control clutches were begun at approximately the same date (Table 1).

Table 1. Number of eggs in complete clutches (after manipulations of the experimental clutches) and the timing of experimental and control clutches

	Mean number of eggs	S.D.	N	Mean date for the laying of the first egg
1978 (one egg removed from experimental clutches)				
Experimental clutches	2.9	0.97	17	April 17
Control clutches	4.2	0.81	47	April 17
1979 (one egg added to experimental clutches)				
Experimental clutches	5.6	0.87	17	April 19
Control clutches	4.4	0.98	18	April 20

3.2 Results

In neither case did crows with manipulated clutches compensate for the loss or gain of one egg (Table 1). On the contrary, those that lost one egg produced even fewer than did the control females and those that received an extra egg produced slightly more. However, these small differences were not significant ($t=1.14$, $P>0.10$ and $t=0.64$, $P>0.10$, respectively).

4 Discussion

4.1 Linearity of the Basic Functions

It can be asked how realistic is the model. Even if one accepts the hypothesis as put forward in the introduction, the

linear functions (1) and (2) might be unrealistic. But there is one argument in support of these functions. Only few days are important during which the equations must be good approximations; and for short intervals linear functions are usually good approximations. In Fig. 1, I suggest an imaginary example and how it should be modelled. Eighty-seven per cent of all pairs in the studied population of hooded crows started breeding during a 12-day period, if inter-year differences in median date are compensated for (Loman 1980).

4.2 The Parameter Values a , b , and d

In this section, I treat information from hooded crows, in particular the same population as that on which the experiment (Sect. 3) was performed.

4.2.1 The Rate at which Energy for Egg Formation (a) is Stored

The values of the parameters are difficult to determine as they are specific for each female. I will make an "educated guess" of the range of likely a -values, utilizing information on the relative amount of the daily energy requirement necessary for the formation of an egg. This approach assumes that energy is the limiting factor for egg production. Some other, e.g., calcium, is also possible. The mean weight of a crow's egg is 20 grammes (Loman 1980), its energy content is 19 kcal and the amount required for the processing is 30% of the energy content (Kendeigh et al. 1977). A crow thus needs 25 kcal metabolized energy to form one egg. The existence metabolism of a 500 g crow at +10°C is about 120 kcal/24 h. Flying requires another 34 kcal/h (Kendeigh et al. 1977). From telemetric studies, I know that a crow in April spends about 0.5 h flying per day. Thus, the formation of an egg requires approximately 18% of the daily maintenance energy. I think it is fairly safe to guess that the true a -value lies between 0.2 and 2.0.

4.2.2 Decrease in Breeding Success with Time (b)

There is the same difficulty with the determination of b as with a . However, this value probably differs less between different females than does the a -value. Eq. 1 have not found any difference in predation rate between first-time breeders and others (unpubl.). I will thus utilize information on the breeding success for all females to determine a common b -value (Table 2). A further difficulty lies in deciding what "survival" (s in Eq. (1)) should represent. One alternative is the survival from egg to fledged young. The data in Table 2 yields

Table 2. Survival of eggs to young aged about 24 days old (nearly fledged) for clutches started at different parts of the breeding season

Time of breeding start (mean and span) in relation to the median (M) of the year	-3.4	1.5	9.3
	($M-11$ to $M-1$)	(M to $M+$)	($M+5$ to $M+21$)
Proportion of offspring not predated	88%	76%	38%
Proportion of young starved to death	20%	21%	38%
Total survival	70%	60%	24%
N	47	43	29

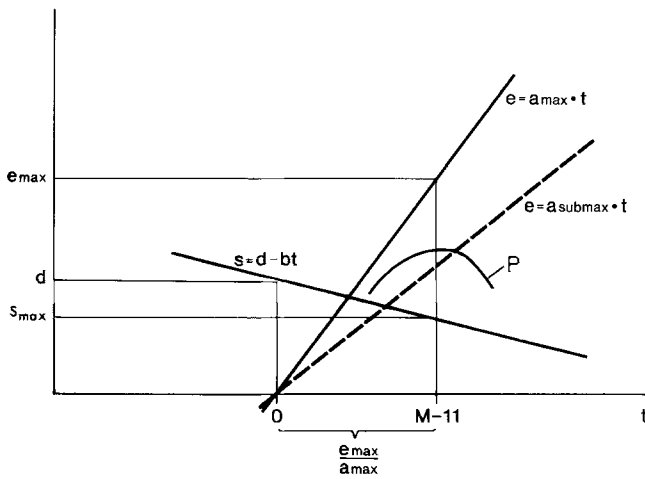


Fig. 2. A graphic model that shows how the auxiliary parameter d can be computed from information on egg-production and survival of off-spring from early-breeding females. The egg number - time graph of a later breeding female (with the same d -value) is also given with a hatched line

$$s = 0.61 - 0.036t_m \tag{17}$$

where t_m is the number of days before or after the median breeding date of the year. However, it seems more realistic to consider the survival to mature birds, say one year old, (which actually may be too young for a crow to be mature, although at that age it certainly is independent of its parents). As newly fledged crows from early and late broods do not differ much in weight, it is reasonable to presume the same survival for all categories, say 37% (Busse 1969). Equation (17) corresponds to this supposition.

$$s = 0.23 - 0.013t_m \tag{17'}$$

0.013 is the sought-for b -value. If the model holds, late crows are those that have a low a -value, (i.e. are slow to gather resources), and it seems probable that there is a correlation between these and those that have difficulties in warding off nest predators. If this is true, the b -value found by pooling all crows is too high as the slope in Eq.(17) falls more steeply than it would if the hypothetical probability of predation for one brood at different times had been considered. I discuss this further below.

4.2.3 The Auxiliary Constant d

To determine d from available data, I assume that all females start gathering resources at the same time (have a common d) but differ in the rate (have different a :s). For convenience, I now consider those females that are earliest to breed. They do so, according to field data, eleven days before the median date of the year, have a clutch size of 5.1 ($=e_{max}$) (unpubl.), and a survival of s_{max} . This value, s_{max} , is 1.0 or 0.33 depending on whether Eq.(17) or (17') is used.

From Fig. 2, it is clear that we have

$$d = s_{max} + \frac{b \times e_{max}}{a_{max}} \tag{18}$$

Note: the utilization of the b -value does not presume that Eq.(2) is a good approximation of the real survival-function in the region of $t = -K$ (Fig. 2); it is only the slope (b) around t that is used.

Table 3. Values of the auxiliary parameter d and the resultant prediction of the number of eggs produced for different presumptions of the a -value and the parameters of the survival function. The latter parameters are the slope (b) and survival of early broods (s_{max}). The d -values are computed from Eq.(18) and the e_{max} -values (eggs produced by early breeding females) from Eq. (6))

a_{max}	$s_{max}=0.33$		$s_{max}=0.33$		$s_{max}=1.00$	
	$b=0.008$		$b=0.012$		$b=0.036$	
	d	e_{max}	d	e_{max}	d	e_{max}
0.2	0.53	5.5	0.66	4.6	1.9	4.4
0.5	0.41	8.5	0.45	6.3	1.4	6.3
0.7	0.39	10	0.42	7.2	1.3	7.2
1.0	0.37	12	0.39	8.1	1.2	8.2
2.0	0.35	15	0.36	10	1.1	10

Given the range of a - and b -values considered in the previous sections, possible d -values are listed in Table 3.

4.3 Predictions and Facts

4.3.1 Predicted Clutch Size

The model gives reasonable predictions for the clutch size of crows (Table 1) only if a small a -value is presumed. This prediction is fairly resistant to changes in b (Table 3). This fact can lead to two conclusions. First; the model is not definitely wrong, as reasonable parameter values give "correct" predictions. Alternatively, if we presume the model to be correct, the value of the parameter a is, for the crow population under study, in the region of 0.2. I think this makes intuitive sense. My most severe criticism of the hypothesis is that egg-production does not seem to be very demanding for a crow, at least, not in terms of energy; thus the energy available for the female before breeding should not be a factor likely to limit egg-production. This agrees with the finding that, for a -values above 0.5, the model is clearly contradicted (Table 3).

4.3.2 Correlation Between Size and Timing of Clutches

The model predicts that those females that breed early should also be those that have the largest clutches. Such a correlation has been found for several species of birds (Klomp 1970), (Loman 1977).

4.3.3 Predictions on the Out-Come of the Experiment

If one egg is removed, the model predicts that this should be replaced by, on average, 0.5 eggs. No tendency to replacement was observed. It can be argued that it is not possible to lay 0.5 egg. But the originally "planned" clutch-size (e) is a compromise between integers, and I would, therefore, expect every second female to replace the lost egg with one and every other not to do so. It could also be argued that it may be physiologically impossible to produce an extra egg when egg-laying is already well under way. This is quite probable, but again there are counter-arguments. The loss of single eggs to predators is not an improbable event, at least not in the population under study, and if it were profitable to replace it, one would not be surprised if such a mechanism had evolved. Furthermore, some passerines, among them the closely related jackdaw (*Corvus monedula*) (Stieve 1919), have been recorded as indeterminate layers (i.e. the number of eggs laid

Table 4. Predicted compensation ($\hat{e}-\hat{E}$) by the female after the addition of an egg to the clutch during the laying period. Different a - and b -values are presumed within the range of reasonable values, provided that the production of one-year old offspring is maximized

b	$a=0.2$	$a=0.5$	$a=0.7$	$a=1.0$	$a=2.0$
0.005	3.6	8.1	8.1	7.4	5.6
0.010	-3.3	2.6	3.2	3.4	2.8
0.015	-5.5	0.8	1.6	1.0	1.9

is affected by manipulation during the laying period (Cole 1917).

If one egg is added during the laying period, the prediction is unfortunately very sensitive to the values of a , b , and s_{\max} . If we assume that what counts in terms of survival is the production of one-year-old off-spring and thus s_{\max} is about 0.37 and b in the region of 0.005–0.015, (Sect. 4.2.2) the model predicts compensation for most a -values, for some values even by several eggs (Table 4). This does not really make sense, but for large a -values, there are anyhow (see above) reasons to suppose that the model does not hold. Only for small a -values (i.e. $a=0.4$, $b=0.015$ or $a=0.2$ and $b=0.007$) the prediction agrees with the obtained result of the experiment, i.e. there was no compensation.

If, alternatively, we presume that what counts is the number of fledged young, a similar computation of $\hat{e}-\hat{E}$ yields, for $0.2 \geq \hat{a} \geq 2.0$ and all $0.03 \geq \hat{b} \geq 0.09$, values below -0.9 . This means that if one egg is added, the female can be expected to lay not only the originally "planned" number of eggs but also additional eggs. I think it interesting to note that the outcome of clutch size manipulation experiments, i.e. the determination of whether or not a species (or a population) consists of determinate layers, might depend on subtle changes in environmental parameters (a and b). It is thus not surprising to find differences between related species or even between different populations of one species in this property.

4.3.4 Further Evidence

There is another field experiment that positively strengthens the first part of the hypothesis. Yom-Tov (1974) supplied crows (*Corvus corone* × *cornix*) with extra food during winter and spring up to the time of egg-laying. These crows bred earlier and had larger clutches than control pairs, thus suggesting that prelaying resources are a limiting factor for the number of eggs produced. If his feeding introduced a positive f -value (Eq. (9)), the results obtained are precisely those predicted from the model (Sect. 2.2).

4.3.5 An Alternative Hypothesis and Conclusions

Another hypothesis concerning the determination of clutch-size states that the number of eggs laid is adjusted to correspond to the maximum number of nestlings that can be successfully reared with those resources expected to be available during the nestling period (or rather, while the brood is dependent on the parents for feeding) (Lack 1954). If this hypothesis is correct, one would expect the females to compensate for the loss or gain of eggs during the laying period, contrary to the outcome of the experiment (Sect. 3.2). It could (as already considered in Sect. 4.3.3) be that, for physiological reasons, it is too late to make compensations in number of eggs laid when egg-laying is already begun. If this is so, my experiment does not invalidate this alternative hypothesis.

Yom-Tov's (1974) experiment could also be interpreted in a way that favours this hypothesis. It may be that, for a given territory, there usually is a correlation between pre-laying resources and nestling time resources and that the females use the prelaying resources as a clue to the latter. This would explain at least the increased clutch-size after her artificial winter feeding. Why breeding should start earlier than for the control females in Yom-Tov's experiment is not obvious under this hypothesis.

In another field experiment, I studied the effect on the production of fledged young if additional hatchlings are introduced in crows' nests (Loman unpubl.). This increased the production, which is consistent with the lastmentioned hypothesis only if this larger production depended on a very large effort by the parents, decreasing the probability of survival to the following breeding season and thus decreasing their long-time fitness.

In conclusion, I think that the hypothesis presented in the introduction can only with hesitation be accepted for the studied crow population. A critical variable can not be measured sufficiently accurately; only if it is true that egg production is comparatively demanding on the resources of the female crow can the hypothesis be accepted. "comparatively demanding" means that a is in the region of 0.2 in the language of the model. An alternative hypothesis (presented in the beginning of this section) is supported if it can be shown likely that the raising of a large brood is demanding not only on the breeding pair's short-term resources, but also on its longterm survival. Some support is given the model by the fact that it correctly predicts the correlation between early breeding and large clutches that has been observed for several species of birds. I suggest, as a hypothesis, that the model is particularly relevant to birds for which the production of eggs is a demanding process.

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