

Factors affecting clutch and brood size in the crow, *Corvus cornix*

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Positive correlations were found between large clutch size, low predation, and early breeding in a south Swedish population of the hooded crow, *Corvus cornix* L. Clutches in very dry habitat were smaller than others. Nestlings of above average weight one week before fledging suffered less mortality before independence than did light ones. The probability that a nestling will starve to death is independent of the clutch size. Starvation was most common during the first week of the nestling's life. Body weight one week before fledging was independent of the number of brood mates at that age. There was some evidence that pairs maintained approximately the same clutch size from year to year and it is speculated that the clutch size is in some way correlated to the number of nestlings each pair can expect to raise. It is also speculated that the early starvation of nestlings is a mechanism for late adjustment of the brood to an optimal size.

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Найдены положительные корреляции между большой численностью выводка, низкой смертностью и ранними сроками размножения в популяции *Corvus cornix* L. в южной Швеции. Выводки в очень сухих местообитаниях были меньше, чем в других участках. У птенцов выше среднего веса за неделю до достижения самостоятельности смертность ниже, чем у более легких особей. Возможность гибели от голодания у птенцов не зависит от величины выводка. Голодание обычно наблюдается у птенцов в течение первой недели их жизни. Вес тела за неделю до окрыления не зависит от числа особей того же выводка. Имеется доказательство, что пары поддерживают примерно одинаковую величину выводка от года к году; предполагается, что величина выводка в определенной степени скоррелирована с количеством птенцов, выращиваемых каждой парой. Предполагается также, что раннее голодание птенцов представляет собой последний механизм для регулирования оптимальных размеров потомства.

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1. Introduction

In this paper I analyse the factors that influence the clutch-size and final reproductive success in a hooded crow (*Corvus cornix* L.) population. The conclusions are based on correlations between different data related to the reproduction (phenology, clutch-size, predation, starvation, number and weight of old nestlings). Similar correlations have been examined in other studies on the reproduction of the species (Sondell 1976) and its closer relative, often considered conspecific, the carrion crow (*Corvus corone* L.) (Wittenberg 1968). Experimental studies on the importance of nest-site and food for the reproductive success in these species have been made by Charles (1972) and Yom-Tov (1974).

2. Study area and methods

The study was conducted on parts of the Revinge area (22 km²) and adjacent farmland (2 km²) in south Sweden (55° 40'N, 13° 30'E). The density of breeding crows varied between 1.9 and 2.5 pairs km⁻² during the different years of study, 1973–1976. The fate of 140 nests in the study area was followed from the incubation stage to destruction or successful fledging of the nestlings. Some further nests were found later and provided information that could partly be used in the study. If all eggs or nestlings had disappeared between two checks of a nest, the loss was considered due to predation. When single nestlings had disappeared, the loss was considered to be the result of starvation and death of the nestling. This is motivated by the fact that in all instances when a single nestling disappeared, it was lighter than the mean for its age. This aspect is treated in more detail in another paper that also gives more information on the methods employed along with basic data on breeding time, clutch size, growth and number of nestlings (Loman unpubl.). Before fledging the nestlings were tagged with wing tags (Picozzi 1971) that could later be identified from a distance.

3. Results

3.1. The importance of habitat

The territories were classified according to the proportion dry and moist habitat within 250 m of the nest. This corresponds to the approximate territory size in the study area. I do not know for sure what habitat is most advantageous for the breeding crows but if differences in breeding performance are found with this classification they should be due to the habitat difference. The number of eggs per clutch was less in nests in very dry habitats than in others ($t = 3.47$, two-tailed test, $P < 0.001$) (Tab.1). There were strong indications, but not significant, that this difference still existed with respect to the number of old nestlings per brood with nestlings (old nestlings are about 24 d old) (comparing the two drier habitats with the two moister ones, $t = 1.93$, two-

Tab. 1. The relation between habitat and other reproductive parameters. A: Very dry habitat, B: Less than 25% of the area within 250 m of the nest covered by marsh habitat but, subjectively not as dry as A, C: 25%–75% of this area covered by marsh habitat, D: More than 75% of this area consists of marsh habitat.

| | A | B | C | D |
|---|------|------|------|------|
| Egg number | | | | |
| Mean number per clutch | 3.4 | 4.7 | 4.2 | 4.6 |
| Clutches | 14 | 51 | 40 | 11 |
| Predation | | | | |
| Completely depredated nests . | 4 | 11 | 14 | 3 |
| Not completely depredated nests | 9 | 31 | 24 | 6 |
| Old nestlings | | | | |
| Old nestlings, if any, per brood | 2.3 | 2.7 | 3.1 | 3.5 |
| Number of broods with old nestlings | 8 | 25 | 22 | 6 |
| Post-fledgling success | | | | |
| Number of young per brood that were seen after 1 July | 0.50 | 0.70 | 0.80 | 0.60 |
| Broods | 11 | 43 | 39 | 10 |

tailed test, $P = 0.06$). The size of the broods after independence (estimated on the basis of the number of juveniles observed after 1 July) hardly differed. This was partly because of a higher, but not significantly higher, predation rate on clutches in moist habitat. The counts of independent young are moreover less conclusive as several surviving juveniles may not have been observed. There were no strong indications of differences in breeding time, egg weight, probability of starvation, predation rate or mean weight of old nestlings between nests from different habitat categories.

3.2. Breeding success in relation to breeding time

Late clutches contained fewer eggs than early ones (Tab. 2). More nestlings per brood starved to death in late than in early broods but this was not significant. Predation was heavier on late clutches than on early ones. Considerably more juveniles per early than per late brood were observed after 1 July, indicating a higher production of independent young. The total success per individual egg was also higher for those from early than for those from late clutches; of the former 28% were observed as juveniles after 1 July but only 7.5% of the latter.

3.3. Breeding success in relation to egg weight

There was no tendency for clutches with light eggs to contain a higher proportion of added eggs than those with heavy eggs. Of those with a mean egg weight of 19 g

Tab. 2. Relation between breeding time and other factors. The breeding time has been divided into three periods: I, to the median breeding date of the respective year, II, the median date and the four following days, III, five days or more after the median date. Re-layings are excluded. The t-tests are two-tailed. N = number of clutches or broods.

| | I | II | III | t | Compared periods | P |
|---|------|------|------|-----------------|------------------|--------|
| Egg weight (g)..... | 19.5 | 20.0 | 19.0 | | | |
| N | 32 | 36 | 18 | | | |
| Number of eggs per clutch | 4.5 | 4.4 | 4.0 | 2.43 | I, II vs III | 0.016 |
| N | 47 | 43 | 29 | | | |
| Number of starving nestlings per clutch | 0.90 | 0.93 | 1.50 | 1.59 | I, II vs III | 0.12 |
| N | 32 | 29 | 12 | | | |
| Proportion of clutches depredated during the egg stage ... | 2 % | 8 % | 6 % | $\chi^2 = 37.0$ | I, II vs III | <0.001 |
| During the nestling stage | 10 % | 16 % | 56 % | | | |
| N | 49 | 49 | 34 | | | |
| Mean weight of nestlings in the clutch (g) | 448 | 421 | 439 | | | |
| N | 29 | 30 | 11 | | | |
| Mean number of young per clutch observed after 1 July | 1.26 | 0.54 | 0.30 | 3.67 | I vs II, III | <0.001 |
| N | 39 | 37 | 27 | | | |

or less, 34% (N = 43) contained added eggs while the proportion was 28% (N = 39) for those with a mean egg weight of 20 g or more ($\chi^2 = 0.27$, two-tailed test, P > 0.50). There was no tendency for clutches with light eggs to give rise to nestlings that starved more frequently than there was for clutches with heavy eggs. If clutches in which all eggs or all except one hatched are considered, 60% (N = 15) of those with a mean egg weight of 19 g or less contain a nestling that starved to death while the corresponding proportion for heavy clutches was 65% (N = 26). On the other hand, there was a weak tendency for clutches with heavy eggs to give rise to heavier old nestlings than there was for those with light eggs. If clutches in which all eggs or all except

one gave rise to old nestlings are considered, the mean weight for the nestlings from clutches with light eggs was 427 g (N = 11) and that for those from heavy eggs was 470 g (N = 11) (t = 2.08, two-tailed test, P = 0.05).

3.4. Breeding success in relation to clutch size

Clutches of 2-4 eggs were more often preyed on (during the egg nestling stage) than were larger clutches ($\chi^2 = 13.5$, two-tailed test, P < 0.001) (Tab. 3). The large clutches also contained more old nestlings per brood, and more juveniles per brood from these clutches were observed after 1 July, indicating a higher production of independent young. No difference was found in egg size

Tab. 3. Relation between the clutch size and other breeding parameters.

| | 2 | 3 | 4 | 5 | 6 |
|--|------|------|------|------|------|
| Weight of the eggs | 19.6 | 19.0 | 19.8 | 19.8 | 20.4 |
| N (nests)..... | 7 | 15 | 29 | 38 | 5 |
| Proportion of nests that are depredated | 67% | 54% | 43% | 15% | 17% |
| N (nests)..... | 6 | 13 | 35 | 41 | 12 |
| Number of old nestlings per nest | 0.67 | 0.81 | 1.4 | 2.7 | 2.8 |
| N (nests)..... | 6 | 16 | 35 | 39 | 11 |
| Number of young/nest observed after 1 July | 0.33 | 0.50 | 0.71 | 0.84 | 1.08 |
| N (nests)..... | 6 | 12 | 31 | 37 | 12 |
| Weight of old young (mean of clutch means) | 515 | 440 | 428 | 443 | 437 |
| N (nests)..... | 2 | 7 | 19 | 29 | 9 |

Tab. 4. Relation between clutch size and the probability that the individual egg or chick will reach different ages or be lost.

| Clutch size | 2 | 3 | 4 | 5 | 6 | 7 |
|---|------|------|------|------|------|----|
| Proportion of eggs that are added or infertile | 0% | 13% | 10% | 7% | 3% | 0% |
| N (eggs) | 12 | 54 | 112 | 225 | 36 | 7 |
| Proportion of eggs giving rise to old nestlings (all clutches) | 0.33 | 0.27 | 0.26 | 0.54 | 0.47 | |
| N (eggs) | 12 | 48 | 140 | 195 | 66 | |
| Proportion of eggs giving rise to old nestlings (nest with at least one old nestling) | 1.0 | 0.72 | 0.51 | 0.66 | 0.57 | |
| N (eggs) | 4 | 18 | 72 | 160 | 54 | |

Tab. 5. The probability of starvation for nestlings in clutches of different size.

| Clutch size | 2 | 3 | 4 | 5 | 6 | | | | | |
|--|---|-----|------|-------|------|------|------|------|------|------|
| Number of hatched eggs | 1 | 2 | 2 | 3 | 3 | 4 | 4 | 5 | 5 | 6 |
| Probability of starvation for a nestling | | 0.0 | 0.13 | 0.083 | 0.33 | 0.30 | 0.23 | 0.26 | 0.20 | 0.33 |
| N (nestlings) | 0 | 8 | 8 | 12 | 30 | 24 | 52 | 80 | 30 | 36 |

or weight of old nestlings between clutches of different size.

There is an insignificant tendency for eggs from small clutches (2–4 eggs) to be added or infertile more often than for those from large clutches ($\chi^2 = 2.07$, two-tailed test, $P = 0.10-0.20$) (Tab. 4). The probability of giving rise to an old nestling is larger for eggs from large (5–6 eggs) than for eggs from small clutches ($\chi^2 = 22.1$, two-tailed test, $P < 0.001$). If deserted and depredated clutches are excluded, the difference is insignificant ($\chi^2 = 1.04$, two-tailed test, $P = 0.50-0.20$). The probability of starvation did not differ between nestlings from clutches with many or few eggs (Tab. 5). Nor did the probability decrease if one of the eggs failed to hatch.

3.5. Growth rate in relation to brood size

The number of nestlings was sometimes reduced from the egg stage because one or more eggs were added or because one or more nestlings starved to death at an early age. When this happened there was a tendency for the relative growth rate of the remaining nestlings to be above average. (The method of calculating the relative growth rate is explained in Fig. 1). The improvement only occurred if the number of siblings was reduced by two (Tab. 6). The difference between these cases and those in broods reduced by one nestling or not at all is significant (one-tailed t-test, $P = 0.012$).

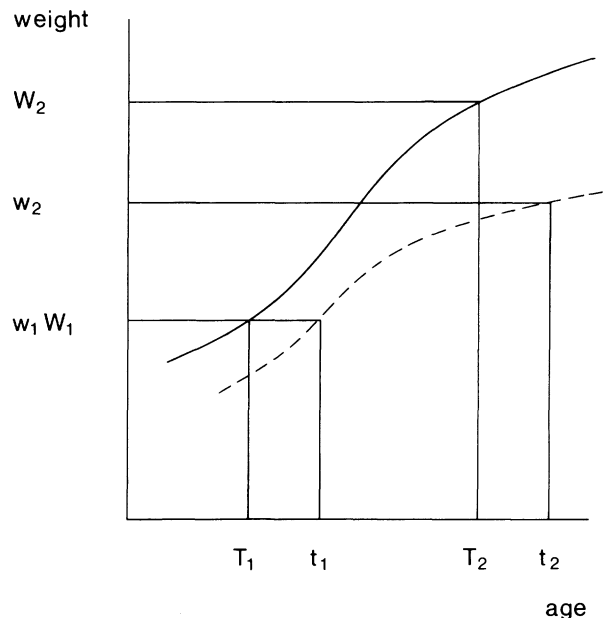


Fig. 1. Method of calculating the relative growth of a nestling. The broken line and the lower case letters refer to the nestling under consideration, while the unbroken line and the upper case letters refer to the mean growth for all nestlings that survived to at least 20 days of age. t_1 , t_2 are the limits of a known growth interval and w_1 , w_2 the nestling's weight at these ages. W_1 is defined by $W_1 = w_1$. T_1 is the age at which the standard nestling has the weight W_1 . T_2 is defined by $T_2 = T_1 + (t_2 - t_1)$. W_2 is the expected weight of the standard nestling at age T_2 . The relative growth of the nestling under consideration is $(w_2 - w_1)/(W_2 - W_1)$.

Tab. 6. Mean growth of nestlings in complete and reduced broods. Broods originating from clutches of four or five eggs are considered. The relative growth (see Fig. 1) has been calculated for nestlings weighed twice between an age of 4–15 d if the second weight was measured 4–7 d after the first and the number of brood-mates remained constant during this interval. Nestlings that later starved to death are not included. N: number of clutches, \bar{x} : mean and S.D.: standard deviation. Cases with a reduction of more than two were scarce and are not included in the analysis.

| | \bar{x} | S.D. | N |
|--|-----------|------|----|
| Complete clutch | 1.01 | 0.31 | 29 |
| One nestling less than original clutchsize | 0.90 | 0.22 | 39 |
| Two nestlings less than original clutch size | 1.09 | 0.16 | 21 |

3.6. Post fledging survival in relation to fledging weight

Forty-nine % (N = 91) of all old nestlings (about one week before fledging) that were heavier than the mean weight of the nestlings of the same year were observed in July or later the year of hatching. This was the case with only 24% (N = 71) of those that were lighter ($\chi^2 = 10.6$, two-tailed test, $P < 0.001$). It is thus likely that light nestlings suffered a higher mortality during the first weeks out of nest than did the heavy ones.

3.7. Evidence for individual characteristics in breeding performance

The hypothesis to be tested is that a female crow tends to lay the same, or nearly the same, number of eggs each

year. It is assumed that she uses the same nest site year after year. Current work shows this to be a realistic assumption (pers. obs.). Considering nests from consecutive years and within 100 m from each other, the distribution of all differences in clutch size (0–5 eggs) between all such pairs was determined. To calculate the expected distribution of differences I used all 118 known clutch sizes (1973–1975) and found all possible 118×117 differences. If a new female used a nest site, her clutch size would, according to the hypothesis, differ more from that recorded at the nest site the previous year than would the clutch size of the old female. Also, as the mean clutch size differed somewhat between the years, the virtual random difference is somewhat greater than that calculated here. Both these biases will work in a conservative direction. However, the difference in clutch size between nests from the same site was significantly less than expected ($\chi^2 = 6.83$, one-tailed test, d.f. = 2, $P < 0.025$) (Tab. 7). Apart from individual characteristics, this difference could be due to differences in territory quality, as discussed below.

I also tested the hypothesis that nests at certain sites, and presumably of the same pair, are more likely to be depredated than others and that certain pairs tend to breed early and others late. The same technique was used, i.e. I compared the distribution of successive results on the same nest site in consecutive years with all theoretically possible permutations regardless of nest site. In these two cases no adherence could be demonstrated.

The adherence to a particular clutch size but not to a particular breeding time does not conflict with the tendency for late clutches to be smaller than the early ones.

Tab. 7. Expected and observed differences between breeding performance and time of the same pair (approximated as "same nest site") in successive years.

| Number of eggs Difference | 0 | 1 | 2 | 3 | 4 | 5 |
|----------------------------|------|------|------|-----|-----|-----|
| Expected proportion, | 29 % | 43 % | 19 % | 7 % | 2 % | 0 % |
| Cases found | 18 | 21 | 2 | 1 | 0 | 0 |
| Cases expected | 12 | 18 | 8 | 3 | 1 | 0 |

((For the statistical test the differences of 2 and more were combined))

| Predation | Fledged young both years | Predation and fledged young one year each | Nest depredated in both years |
|----------------------------|--------------------------|---|-------------------------------|
| Expected proportion, | 49 % | 42 % | 9 % |
| Cases found | 15 | 13 | 2 |
| Cases expected | 15.9 | 12.6 | 1.5 |

| Breeding time | 0–4 | 5–9 | 10–14 | 15– |
|--|------|------|-------|-----|
| Difference between the deviation from mean hatching date for the first young | | | | |
| Expected proportion, | 50 % | 33 % | 13 % | 4 % |
| Cases found | 14 | 7 | 2 | 0 |
| Cases expected | 11.5 | 7.5 | 3.0 | 0.9 |

It could hypothetically be that certain pairs lay small clutches, say 3 or 4 eggs. If they in one year breed early they lay 4 eggs but if they in another year breed late, they might lay 3 eggs. The corresponding situation goes for pairs that lay large clutches, say 5 or 6 eggs. It could also be that there really is a tendency for some pairs to be late and others to be early but that my material and method have not been sufficient to reveal this.

4. Discussion

4.1. Factors affecting the reproductive success of crow pairs

There are positive correlations between the following characteristics of a clutch: many eggs, low depredation and early breeding. Starvation and the fledging weight does not differ for nestlings from large and small clutches. Clutches with these three traits thus produce more independent youngs. Some youngs are seen independently from their parents from the middle of July and probably most could live independently by this time. The number of young per brood that is observed in July or later is thus an index of independent young. This number is highest for large clutches. Many eggs (if everything else is unaffected) and low predation rate are adaptive traits and this may also apply to early breeding as it increases the possibility of re-laying if the first clutch is lost (Wittenberg 1968). It is also possible that early breeding directly contributes to a low predation rate but these characteristics may have a common cause (e.g. old and experienced parents or a territory with abundant food). Some of the breeding pairs thus possess a set of favourable reproductive characteristics and others a set of unfavourable ones. Fifty-five % of the young seen in July or later belonged to the 13% most successful parents. (Tab. 8).

For each of the above-mentioned favourable characteristics one can ask to what extent they are due to:

(1) Inherited properties such as laying many eggs, breeding early, defending the nest more fiercely and persistently and collecting food efficiently.

(2) Inherited ability to identify and defend a territory that is favourable for the raising of many independent young, e.g. because it offers a rich food supply, predators are sparse or concealed nest sites are available.

(3) Random distribution of pairs or individuals on

territories that have attributes that are more or less favourable for the raising of many young. As crows usually stay in the same territory year after year (Charles 1972, Loman unpubl.) a limited number of territories become available in a given year and random events may affect the distribution of crows on different territories (3) above. If it can be demonstrated that crows move from bad to good territories or several territories may simultaneously be "free" within the range of crow establishing territory for the first time, (2) above is of some importance. Carrick (1963) has shown that territorial black-backed magpies (*Gymnorhina tibicen*) strive to move to better territories.

Clutches in very dry territories contained fewer eggs than others, and nests in some territories contained, year after year, more eggs than those in others. Without experiments, however, it is not possible to decide whether this is due to differences in quality between territories ((2) or (3) above) or between individuals ((1) or (2) above). It is possible that crows which for some reason lay few eggs also tend to settle in inferior territories. They could, for example, be first breeders. This would increase the apparent effect of habitat.

Data from studies elsewhere provide more clues, although sometimes contradictory ones, as to what factors may determine breeding success.

In Wittenberg's (1968) study area in West Germany, there were considerable differences in territory size. Smaller territories, moreover, were situated in the inferior habitat (forest). Wittenberg found indications that crows breeding in the more favourable territories laid more eggs and were less subject to predation of whole clutches and to starvation of single nestlings. This supports alternatives (2) and (3) above. Sondell (1976) also found a tendency for nests in open terrain to contain more eggs (but not more nestlings) than did those in wooded habitat. Yom-Tov (1974) improved territories by supplying extra food, starting three months before breeding. This, however, failed to affect clutch size convincingly, indicating that this is genetically restricted ((1) above). On the other hand, extra food supply while the parents had eggs and nestlings, decreased predation on single nestlings. However, since the extra food was offered very close to the nest, a situation may have been created that was more favourable for the

Tab. 8. Distribution of reproductive success.

| | The whole clutch depredated or deserted before day 20 | At least one young more than 20 days old Number of young seen in July or later the year of hatching | | | | | |
|---------------------------------|---|---|-----------|-----------|-----------|---------|---------|
| | | 0 | 1 | 2 | 3 | 4 | 5 |
| Clutches | 52 37% | 42 30% | 19 13% | 12 8% | 15 11% | 1 1% | 1 1% |
| Young in this category | | 0 | 19 20% | 24 25% | 45 46% | 4 4% | 5 5% |

defence of the nest than is ever likely to occur in natural circumstances.

All in all, there seems to exist some correlation between territory quality and clutch-size. This is consistent with Yom-Tov's results, especially if the following assumptions are made: (1) That some territories are more favourable because more food is available for the nestlings in them; (2) that the nests in these territories are easier to defend (this could be due to the better food availability that makes it possible for the parents to stay close to the nest), and (3) that these territories are occupied by pairs whose female partner has an inherited trait to produce many eggs per clutch. Conceivably, this trait may not be inherited but acquired at an early age.

4.2. Brood reduction and evaluation

Mortality due to starvation is higher among nestlings during the first week of life than later (Loman unpubl.). This was also found by Tenovuo (1963), Wittenberg (1968) and Picozzi (1975). Early starvation may be due to the fact that during the first week the male almost alone feeds the clutch whereas later on the pair cooperates. According to Yom-Tov (1974) the total energy requirement for a brood of five at an age of six days is half that for a brood of four (which is the number of nestlings an original clutch of five eggs can be expected to have yielded at this stage) at an age of 15 days. However, reduced feeding intensity during the first days may, as was hinted at by Wittenberg (1968), be an adaptive strategy leading to the early death of the weakest nestlings in a food situation where it is anyhow doomed to starvation, thus reducing the parents' total amount of feeding effort. This strategy has been termed brood reduction by Ricklefs (1965).

Nestlings in large clutches do not suffer greater starvation than those in smaller clutches (Tab. 5) and larger clutches are not subject to a higher rate of predation than smaller ones (Tab. 3). Large clutches thus produce more old nestlings and more independent young than do smaller ones (Tab. 3). If the number of "old nestlings" is regarded as the best index of reproductive success, since it is probably subject to less random variation than is "number of young observed after 1 July", the gain going from clutches of five to clutches of six is small; 2.7 to 2.8 old nestlings. This gain may be offset by the increased stress on the parent crows and there may thus be a constant selection for the commonest clutch size, which is five. Smaller and larger clutches may be the result of (for this area) unfavourable gene combinations that, at least on a short-term basis, are selected against. It is also possible that the clutch size is in some way correlated to the pair's ability to feed and defend a large brood. This seems more plausible to me, since clutch size was correlated with other favourable characteristics such as, early breeding and small losses due to predation. No causal relation is obvious between these variables and it is more likely that they all depend on

Tab. 9. Relation between the number of old nestlings in a nest and their weight.

| Number of nestlings per nest | 1 | 2 | 3 | 4 | 5 |
|------------------------------|-----|-----|-----|-----|-----|
| Mean weight, g | 438 | 450 | 436 | 425 | 438 |
| Number of nests | 11 | 14 | 27 | 11 | 7 |

something else such as the parents' social status, size and/or age. This may seem to be contradicted by Tenovuo's finding that clutch size was equal in two areas, viz. archipelago and mainland though nestling mortality differed, being higher in the archipelago. However, if nestling mortality in the archipelago was largely due to catastrophies (involving an unpredictable decrease in resource availability) such as bad weather, it would be best for the crows to lay the clutch they would be able to raise in the absence of catastrophies. If the female adjusts her clutch size according to her and her mate's ability and the quality of the territory, this is the strategy termed "evaluation" by Ricklefs (1965). The crows probably use this means to compensate for individual differences in their ability to raise nestlings. The strategy is successful to the extent that those pairs that are presumably least competent do not lose a higher proportion of their nestlings because of starvation than do those that are otherwise more successful (Tab. 5). Variation in weather and in territorial quality that are "unforeseen" at an early stage of breeding are compensated for through brood reduction. This strategy is successful to the extent that there is no difference in the weight of old nestlings from large and small broods (Tab. 9). The fact that eggs from small clutches have a smaller probability of producing old nestlings is mainly due to the fact that these are more liable to be depredated than the larger clutches. If it is assumed that the parents, regardless of the number of nestlings, feed them at a maximum rate, the probability of predation cannot be influenced by this strategy as no special time is set off for guarding the nest. This is not necessarily the case, but it is possible that the time used solely for guarding the nest is independent of the feeding intensity. A reduction in feeding rate (made possible by laying fewer eggs, or the early starvation of more nestlings) could reduce the probability of predation if proportionally more time could be spent guarding the nest, but it is possible that even a slight decrease, say by 10%, in predation rate (due to guarding), would require a large decrease in feeding effort, say by 50%. In this case it would not pay to take predation into account when "deciding" the optimal brood size.

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