SOCIAL ORGANIZATION AND REPRODUCTIVE ECOLOGY IN A POPULATION OF THE HOODED CROW, *CORVUS CORNIX*

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1. Introduction.

The thesis is based on the following papers:

A. Nest distribution in a population of the hooded crow Corvus cornix. Ornis Scand. 6:169 - 178. 1975.
B. Factors affecting clutch and brood size in the crow, Corvus cornix. Oikos 29:294 - 301. 1977.
C. A model of population dynamics in territorial animals. Anser supp. 3:163 - 166. 1978.
D. Nest tree selection and vulnerability to predation among hooded crows Corvus corone cornix. Ibis 121:204 - 207.
E. Reproduction in a population of the hooded crow Corvus cornix. Holarct. Ecol. 3:26 - 35.
F. Brood size optimization and adaption among hooded crows. Manuscript.
G. A model of clutch size determination in birds. Manuscript.
H. Breeding success in relation to parent size and experience in a population of the hooded crow. Manuscript.
J. Social organization in a population of the hooded crow. Manuscript.

They will henceforth be referred to by their respective letters.

All papers except C and most of G treat data obtained from a study of the crow population in the Revinge area, 20 km east of Lund in south Sweden. The study started in 1971 and during the first years most work concerned a description of the breeding biology and nest distribution. Attempts were also made to tag crows for individual identification at a distance. From the breeding season in 1975 and onwards a sufficiant number of crows were tagged to permit analysis of their individual breeding success and social structure. In 1976 to 1979 field experiments involving breeding crows were made (F, G). The field study was terminated in 1979. Papers C and G present theoretical work that was stimulated by information obtained from the field studies of the crow.

This thesis is not a complete and balanced summary of the papers that form its basis. I have chosen to discuss briefly some of the problems that arise from the findings in several of the papers. In section 2 - 4 I limit the discussion to results presented in papers A - J while in section 5 information that has not been treated elsewhere is presented and used to elucidate an aspect that I have previously only hinted at (C, E).

2. Clutch size.

I will consider two hypotheses of the determination of clutch size that could have relevance to the crow.

1. The number of laid eggs corresponds to the maximum number of well-nourished nestlings that can be expected to be brought up in the parents' territory.
2. The number of laid eggs is limited by the female's condition at the time of egg-laying.

These two hypotheses are difficult to separate as there probably is often a correlation between the female's condition during laying and the quality of the territory when the nestlings are raised. Results that strengthen the first hypothesis by conforming to predictions made under it are:

a. Crows that were nesting in territories without moist areas (territories that probably had comparatively little food) had small clutches (B). This is predicted under the first hypothesis as crows fed exclusively in their territories during the nestling period (J). It gives less support for the second hypothesis as many territorial crows fed outside their territory before feeding.

b. Experiments where some pairs were given extra hatchlings showed that parents having large clutches were more able to raise many nestlings than those that had smaller ones (F).

c. The probability of a nestling starving to death was the same in small and large broods and there was no difference between fledgling weight in small and large broods (B).

The second hypothesis was strengthened by these results that conformed to predictions made under it:

d. Thre was a correlation between large clutches and early breeding (B). This is predicted by a model that is based on the second hypothesis, extended with the assumption that late clutches are more likely to be preyed on than early ones (G).

e. This model predicts clutch-sizes that are similar to those observed (E). However, this prediction only applied under the condition that the production of eggs is a relatively demanding process.

The first hypothesis was contradicted, and the second thus strengthened, by the following result:

f. Females in good condition laid large clutches, as predicted under the second hypothesis but is also quite possible under the first because of the correlation mentioned above. However, there was no correlation between male condition and clutch size (H), as expected under the first hypothesis because both parents feed the nestlings.

No definite choice between the two hypothesis is possible. For a definite test, advantage should be taken of taken of field situations where some territories in an area regularly are subject to a drastic change in the food situation during the brooding period while others are not.

3. Number of fledglings.

Apart from clutch size, which is discussed above, the number of fledglings is affected by starvation and predation. Starvation was more common in the dry habitat than in any other (B). This could be due to the fact that clutches laid in dry habitat were small. On the other hand, late clutches lost a higher proportion of the nestlings through starvation than early ones, despite the fact that late clutches were smaller (B). This could be related to the fact that inexperienced breeders bred later than experienced ones, but there was probably no difference between experienced and inexperienced breeders with respect to their tendency to breed in dry habitat (H). Assuming that there is an adjustment of clutch size to territory quality, inexperienced breeders might be less good than experienced ones in making this adjustment.

To some extent predation was a random event as there was no significantdifference between pairs in the probability of predation on eggs and nestlings (H). There was a weak tendency for inexperienced pairs to run a higher risk of losing their clutches or broods (H) but considering the fact that late clutches were more often preyed upon than early ones (B) this tendency was less than expected. The higher rate of predation on late clutches was thus not associated with some individual pairs that were late breeding and prone to lose their clutches, I rather suggest that this was a characteristic of the predators life cycle. The most important predator probably was the common buzzard (E). Predation was also affected by the kind of nest tree; nestlings in conifers were less often preyed on than those in decidous trees, probably due to lack of cover in the latter before leafing (D).

4. Distribution of nests.
A characteristic feature of the crow´s social system is the presence of non-breeding individuals during spring (J). These were mainly found in the vicinity of places with a particularily good food supply. In these areas nests were less common than expected, at least if one considers the good availability of food. This was probably due to competition from the non-breeding crows, they also constitute a threat to the breeding crows´ eggs and nestlings. This last aspect was not as important in my study area as it has been found to be in others (E).

Nests were overdispersed but only moderately so. I interpret this as a consequence of territoriality modified by the distribution of nest trees (A). However, there was no tendency to avoid nesting in certain areas because of the kinds of trees present. Only if a certain nest-site permitted a choice between different kinds of trees were conifers preferred (D).

5. Population dynamics.
Previously published data on the survival rate of crows (Busse 1969, Holyoak 1971, and Kalchreuter 1971) and their production of fledged young (references in E) suggest that no studied population is in equilibrium; rather, they are rapidly declining. As this obviously is not true, according to the published accounts, some bias must be involved. It has been suggested that nestling mortality is high in most studied po-

pulations (Tompa 1975) and that survival rates based on ringing recoveries are unreliable because old rings may fall off (Seber 1973) or because young crows are more liable to be shot than older ones (Böhmer 1976). It is also possible that the calculated survival rates are too low to be generally applicable because most recoveries are from heavily hunted areas where survival is low (E). These populations could be sustained by an influx of other , non-ringed, crows from areas less accessable to hunters and ringers.

Tompa (1975) obtained exceptionally high figures for the production of fledglings in an area that was not affected by hunters and where non-breeding crows were uncommon. Charles (1972) and I found high values for the survival of crows when basing our calculations on observations of individually tagged crows. In the rest of this section I will use my data on survival (J) and production of fledglings (E) to calculate the expected equilibrium density of the population, employing a mathematical model which is presented in paper C. I have recently read a paper by Brown (1969) where a similar idea is presented, the formulation in C is however more convenient for the present purpose.

The survival rates for individually tagged crows in my study area was 92 % for breeding, territorial crows, 73 % for non-breeding crows, and 26 % for juveniles, from fledging to the start of the next breeding season (J). The last two values may be too low as dispersal was included in the losses. With these survival rates, a minimum production of 0.61 fledglings per pair per year is required for equilibrium if breeding can start at one year of age. If only two-year old crows and older are able to breed, the population is in equilibrium if 0.84 fledglings are produced (C). In my study areathere there were 2.3 territories per km^2 and each territory produced 2.0 fledglings per year (E). With these values, the model predicts a density of 7.7 crows per km^2 immediately before the breeding season (C).

As a test of the model, this value can be compared to the density actually calculated for the study area in April. This is at the beginning of the breeding season and after the departure of all winter migrants from north. The density was calculated according to the Petersen method from the formula $N = Mn/m$, where N is the population size to be calculated and M the total number of tagged crows in the study area in April. I estimated this to be equal to all tagged crows that were observed at least once in the period March to May. m is the total number of observations of tagged crows and n the total number of tagged and of positively untagged crows. For the determination of n and m a standard census was carried out four times per month. All observed crows were counted while driving a car along a fixed route in the study area.

The mean population size during three years was 430 with a 95 % confidence interval of 290 - 560 (Table 1). The study area was 20 km^2 but a larger influence area must be taken into account. Considering information on territory sizes and home-ranges of non-territorial crows in April (1) a total influence area of 30 km^2 is reasonable. This gives a mean density of 14.0 crows per km^2 (9.7 - 18.8)[1/].

Table 1.
Size of the crow population in the study area. The abbreviations are explained in the text.

Year	N	95 % confidence interval	M	n	m
1976	380	250 - 510	55	166	24
1977	490	330 - 660	90	126	23
1978	410	290 - 520	94	138	32

[1/]This value is higher than those given for different habitats in the study area during winter (Loman 1980). This appears contradictory as more crows were present during winter when winter migrants frequented the area. However, data given in that paper does not include places where concentrations of food brought together large flocks of crows.

The density calculated with this method differs from that predicted from the model. However, observations of survival of tagged crows were biased as dispersal could not be separated from mortality. Considering the information on dispersal-like movements in the study area (J), it is reasonable to guess a survival of 80 % and 35 % for non-breeders and juveniles, respectively. With this modification, the model predicts a density of 10.8 crows per km^2. This is only 23 % less and within the confidence interval of the density calculated with the Petersen method.

I draw two conclusions from this. Firstly, survival of crows is probably much higher than computed from ringing recoveries. This could be due to any of the biases suggested above. Secondly the model of population dynamics presented in paper C fits data from the studied crow population reasonably well.

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