Reproduction in a population of the hooded crow Corvus cornix

Jon Loman

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Nest density was stable during the 8-year study period. The mean clutch size was 4.3, and the production of fledglings was 2.0 per pair. Incubation started, on average, when there were still two eggs to be laid and lasted for 18 days. Few eggs were lost but 23% of all broods of nestlings were lost to predators. Single nestlings in a brood were not lost to predators but often starved to death, this applied to 25% of all nestlings. A large proportion of the nestlings were probably infected by *Syngamus tracheae*, and some of these succumbed during the first weeks after fledging. A comparison with other studies of crow populations shows that the major causes of breeding failure are different in different populations. The causes of variation in breeding success between populations are discussed, especially considering the role of nonbreeding crows.

J. Loman, Dept of Animal Ecology, Univ. of Lund, Ecology Building, S-223 62 Lund, Sweden.

1. Introduction

This paper presents a descriptive study of the reproduction of the hooded crow. The data were collected as basis for an analysis of a crow population in South Sweden. A discussion of the relation between different breeding parameters in this population has been presented elsewhere (Loman 1977). Similar studies have been made on other populations and a comparison with these is concluded in the paper. The studies are of populations from Norway (Olstad 1935), Finland (Tenovuo 1963), West Germany (Wittenberg 1968), Scotland (Yom-Tov 1974, Picozzi 1975), Switzerland (Tompa 1975, Böhmer 1976b) and central Sweden (Sondell 1976).

2. Study area

The study area involved part of the Revinge area (22 km^2) and adjacent farmland (2 km^2) in South Sweden ($55^{\circ}40'\text{N}$, $13^{\circ}30'\text{E}$). Since 1967, the Revinge area has been used for military training, having been converted from mixed farmland to permanent grazing. Military training is carried out there for about five weeks each year. During the rest of the time about half of the area is

grazed by cattle. Numerous groves (up to 15 ha in area) and rows of trees are scattered over the area. There are several ungrazed marshes, which make up about 3 km² of the area. Adjacent to the study area is an eutrophic lake that covers 3 km². I have previously reported on the distribution of crows' nests in this area (Loman 1975). Flocks of nonbreeding crows are mainly concentrated to areas adjacent to the study area. The area is rich in other vertebrates.

3. Material and methods

Nest counts were made 1971–1978. Complete data, from egg laying up to fledging or failure were obtained for about 250 nests during 1973–1978. Some further nests were found when breeding had progressed for some time and could not be used in all tabulations. In 1976–1978 a total of 50 nests were used for experiments where nestlings were transferred. Data influenced by these experiments were omitted. Care was always taken to avoid bias when utilizing data from nests with partly known history.

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Tab. 1. Number of nests in the census area of 21 km^2 . In 1971 and 1972 the number of nests destroyed by man is unknown. As the hunting effort was similar to that in 1973 the destroyed number could be estimated. The number observed in 1971–1973 is given in parentheses.

	1971	1972	1973	1974	1975	1976	1977	1978
Number of nests	about 50(41)	about 50(37)	51(41)	39	39	52	48	40

From 1974, the nesting crows were protected in most of the study area. All those shot by local hunters were probably reported to me. They were also reported in 1973 when 10 nests were destroyed before I had found them. Some nests might have been overlooked but to judge by the number of times that others reported nests with old nestlings or that I observed untagged fledglings in the study area, this applies to, at most, five nests a year.

The number of eggs in a nest was checked twice to ensure that the egg counts referred to complete clutches. If a clutch was lost before the second check, the count was omitted from the clutch size tabulations. In some cases, predation could have decreased a clutch before the first count. The rate of predation was low (see below) and this bias was disregarded. The eggs were weighed (1974 to 1978) and in some cases individually marked and re-weighed. This informed on weight loss rate. Some clutches were counted both during the first half and the latter half of the incubation period. This informed on the rate at which single eggs were lost to predators. The number of hatched eggs was determined when the nestlings were at most three days old. In 1973 and 1974, the nestlings were weighed at the nest with a spring balance about every three days up to about age 12 d, when they were ringed. The young nestlings were individually identified by paint on the feet (filt-tip pen). In all years the nestlings were weighed at least at about age 24 d. Nestlings at this age are in the following referred to as old nestlings. These were also individually marked with patagial tags (Picozzi 1971). If all nestlings had disappeared between two checks, the loss was considered to have been caused by predation. Information on the survival of juvenile crows was obtained by monitoring the study area throughout the year.

4. Results

4.1. Nest density and fate of nestings

The nest density fluctuated between 1.9 and 2.5 nests per km^2 during the years 1971 to 1978 (Tab. 1).

Excluding nests destroyed by humans, 61% (N = 97) of the nests produced old nestlings (Tab. 2). At least 24% (N = 42) of the clutches that failed during the incubation stage were relaid. Destruction by humans sometimes included the shooting of the female crow; if

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these failures are excluded the re-laying rate was 34% (N = 29). Of the re-layings, 50% (N = 10) produced old nestlings. Predation was the most common cause of nesting failure. In all, 23% (N = 83) of nests with nestlings were lost to predators. This figure was 38% (N = 8) for relayings. The losses due to desertions were probably partly due to my visits at the nests, at least those that occurred before and during the laying period. Also in one case, a nest with newly-hatched nestlings was deserted immediately after a visit.

4.2. Number of eggs, hatchlings and old nestlings per nest

The number of eggs was similar for first clutches and re-layings (Tab. 3). But there were indications that the number of old nestlings produced was much less for re-layings (t = 1.20 P > 0.05). Only the number of eggs differed significantly between the years (F = 2.91, N = 249 : 5). Comparing the different years, there was an inverse correlation between the mean number of eggs and the mean date of laying (r = 0.75, p < 0.05) (Fig. 1).

Tab. 2. Fate of regularly checked nests. Re-layings are excluded. Nests were considered deserted when the eggs were found cold or the nestlings were dead in the nest. Nests found empty and without sign of human activities were considered victims of predation. Data from 1976 to 1978 are excluded, as the experiments performed introduced some bias.

		n n n n n n n n_		Total
	1973	1974	1975	number 1973–75
Started nestings	40	37	38	115
Egg losses: Deserted Human predation Other predation (Re-laid of the lost clutches)	1 6 4 1	3 1 2 3	3 1 1 2	7 8 7 6
Nestings with hatched eggs	29	31	33	93
Nestling losses: Deserted Human predation Other predation	2 4 6	2 1 2	0 5 11	4 10 19
Nestings with nestlings ≥ 20 days old	17	26	17	60

Tab. 3	. Rep	productive out	put. The	values for	1973-1978	are pooled.	Nests destro	yed b	y humans a	are omitted
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	First layings				Re-layings		
	X	S.D.	IN	X	5.D.	IN	
Number of eggs laid	4.3	0.97	255	4.1	0.74	10	
Number of eggs hatched (all nests)	3.4	1.6	238	2.4	1.5	10	
one egg hatched are included)	3.8	1.2	213	3.0	0.93	8	
Number of large nestlings (all nests) ¹	2.0	1.7	89	0.7	0.82	10	
one nestling reaching 20 days of age are included)	2.8	1.2	118	1.4	0.55	5	

1. Nests from 1976-1978 are omitted as an experiment introduced bias in this value.



Fig. 1. Relation between mean clutch size and mean date for the hatching of the first nestling in the different years. The figures give the sample sizes (number of clutches; number of hatching dates). Data from 1972–1978.

4.3. Fate of the eggs

At least 75% (N = 617) of all eggs (not destroyed by humans) hatched. This figure is perhaps too low as I have omitted a few cases when the first count of nestlings was lower than the last count of eggs. This may have represented cases when a hatchling died at an early age. Eight percent (N = 617) of the eggs were addled. Twelve of those that could be checked contained partly developed embryos and 6 showed no sign of embryonic development. Three nestlings died during hatching because the head-end pole of their eggs was covered by the empty half-shell of a previously hatched egg. After making a small hole in their own shell, the nestlings were apparently unable to penetrate the other shell.

4.4. Egg weight change

The eggs decreased in weight at a rate of 0.14 g d^{-1} . This is based on 104 eggs observed over a period of 880 d.

4.5. Egg loss rate

During the incubation stage repeated observations were made to calculate the rate at which single eggs were lost. The calculations were based on intervals starting with an egg count after the last egg had been laid and terminating with count before the first one had hatched. The total time of all such intervals was 911 d. During this time, ten eggs were lost, probably to predators. The egg loss rate was thus 0.011 eggs per day or 0.20 eggs per nest, the incubation time being about 18 d. The first count of clutch size was done on an average 10 d after the start of incubation. This clutch size value is given in Tab. 3, but because of the disappearences of single eggs before the first count, these values are probably 0.10 too low.

4.6. Hatching date, start of incubation and incubation time

The median date for the hatching of the first young in the first clutches varied from 29 April to 9 May (Fig. 1). Though some first clutches were quite late, the mean and median dates never differed by more than one day in one year (Fig. 2).

Regarding the start of incubation, two opposing hypotheses can be formulated: Incubation begins (1) when a fixed number of eggs are laid or (2) when a fixed number of eggs are still to be laid. "Fixed" in this context means a number characteristic of the population, regardless of clutch size. Fig. 3 was prepared to test these hypotheses. The second hypothesis is more prob-

 g_{1}^{g} g_{2}^{g} g_{2

Fig. 2. Hatching of first egg in the clutches in relation to the median date of the respective years. Data from 1972 to 1978. Re-layings are shaded.



Fig. 3. Comparison between the incubation time in clutches of different size and for two different hypotheses concerning the start of incubation. A gives the predicted relation under the assumption that incubation started with the laying of the third egg and lasts for 18 d. B gives the predicted relation under the assumption that incubation started with the laying of the third last egg and lasts for 18 d.

able. Presuming an incubation time of 18 d, incubation probably begins with the laying of the third to last egg. Individual variation is likely, but for those crows that conform to this pattern, the result is that all except two eggs hatch on approximately the same day, and the last two do so on the next and the second nest day. This conforms fairly well to the observed pattern in the field.

When the eggs were found and counted before the last egg in the clutch had been laid, I could estimate the laying date for the last egg by adding one day for each egg still to be laid. When the last nestling to hatch was found on its hatching day (body weight less than 18 g), the incubation time for this egg could be estimated. In 7 out of 11 cases, it was 18 d, in 3 it was 19 and in one it was 20.

4.7. Growth of the nestlings

The nestlings spent 30 to 35 d in the nest.

The growth curve of nestlings was fitted, according to the method of Ricklefs (1967). This was done separately for the years 1973 and 1974 (in 1975–1978 most measurements were made only in the beginning and the end of the growth period). The curves represent all nestlings that did not starve to death in the nests. The sigmoid growth curve was taken as model, and the relation between age (t) in days and weight (W) in grammes can be expressed:



Fig. 4. Growth curves for the crow nestlings 1973 (upper curve) and 1974. The curves have been calculated according to Ricklefs (1967) and assuming that a sigmoid curve gives the best fit. Only nestlings that survived 20 d or more were used when calculating the curve.



Fig. 5. Relation between weight and growth rate of old nestlings. Growth intervals beginning after 20 d of age and of 4 to 15 d duration are included. The upper half of the striped area covers those values that refer to nestlings which at the beginning of the growth interval were lighter than the mean nestling but after 10 d were or would have been heavier if their rate of increase in weight continued. The lower part of the striped area covers those values that refer to heavy nestlings that would have been light ten days later, i.e. around fledging time, if the growth trend continued.

$$W_{1973} = \frac{430}{1 + e^{-0.316} (t - 10.1)}$$
$$W_{1974} = \frac{430}{1 + e^{-0.295} (5 - 10.1)}$$

Growth levelled off after 20 d (Fig. 4); therefore, in calculating the asymptote, the mean of all measurements made after day 20 were used. If a nestling had been weighed more than once after day 20, the measurement nearest to day 25 was used. The time required to grow from 10% to 90% of the asymptotic weight was 14.5 d in both years.

In some cases, nestlings were weighed after day 20 and again 4 to 15 d later. During this time, small nestlings continued to increase in weight whereas large ones decreased (Fig. 5). This indicates that light nestlings age 20-25 d were light not only because of a low individual asymptotic weight but also because they reached their asymptotic weight later than larger ones. However, most "light" nestlings were still light at the time of fledging (Fig. 5). This means that the weight at 20-25 d of age provides an adequate basis for a fledging weight classification. In all, 31 nestlings lost weight and 18 gained it after reaching age 20 to 25 d. Fig. 6 shows a growth model, based on these conclusions.



age

Fig. 6. A model for the weight development of a light and a heavy nestling during the last ten days in the nest. The maximum weight of the light nestlings is reached later and decreases at a slower rate than the heavy ones.

4.8. Age and size of lost nestlings

Single nestlings disappeared from the nest more often before than after age 12 d (Tab. 4). All nestlings that disappeared were underweight (Tab. 5). In exceptional cases, nestlings as light as half the expected weight (according to the growth curve given above) could survive, but usually those less than 70% of the expected weight were lost. I therefore conclude that starvation rather than predation was the cause when single nestlings disappeared. As light nestlings seemed to be more easily stimulated to beg, at least by other agents than their parents (see below), it is possible that they are more vulnerable to predation than are their heavier siblings. However, as literally all lost nestlings were light and in many broods other nestlings than the lightest begged, it is improbable that more than a few, if any, of these had fallen victim to predation.

In the few cases when the exact hatching order of a clutch was known, the nestlings that disappeared were the last (four cases) or the next to last (one case) to hatch.

4.9. Behaviour of disturbed nestlings

When the nests were visited, or even when the nest tree was knocked on, some nestlings begged, i.e. stretched

Tab. 4. Losses of nestlings at different ages. Data from 1973 and 1974.

Age (days)	06	7–12	13–24
Number of nestlings entering the age interval	201	168	141
Proportion disappearing during the age interval	9%	8%	7%
Proportion disappearing per day	1.6%	1.4%	0.6%

Tab. 5. Relative weight of disappearing nestlings at last check. Weights are given in relation to the standard growth curve that was determined for surviving nestlings. Data from 1973 and 1974.

Relative weight	Number of disappearing nestlings	Number of nestlings surviving this minimum weight
0.21_0.30	2	0
0.21-0.50	2	õ
0.41_0.50	$\frac{2}{2}$	õ
0.51_0.60	5	3
0.61-0.70	9	7
0.71-0.80	7	12
0.81-0.90	2	15
0.91–1.00	4	24
1.01–1.10	11	15

1. This nestling had possibly fallen from the nest as this was tilted.



Fig. 7. Proportion of the nests at different stages that were brooded. The values are running five-day means. The number of observations on different days are given below the figure. Visits were not made during rain.

their necks, gaped, and chirped. There was a tendency for this to be done by the lightest nestling in a brood more often than by any of the others (60% out of 40 versus 41% out of 94, $\chi^2 = 3.52$, twotailed test, 0.1 > P> 0.05). It is possible that the same difference applies when the parents feed at the nest, but it is also possible that the begging behaviour, driven by hunger, is relatively more important than fear for small nestlings than for others.

4.10. Brooding period

If a crow left the region of the nest in the nest tree when I approached, I considered that it had been brooding. At least 80% of the nests with eggs were brooded at day time (Fig. 7). Continuous observations at some nests showed that the eggs usually (possibly always) were brooded by the female and she left the nest for periods of 1 to 5 min at 10 to 20 times a day. This explains partly the 20% of the nests which were not brooded when inspected. In some cases the brooding crow might have left the nest without my noticing. The nestlings were brooded for at least 70% of the daytime until the oldest nestling was about one week old. Brooding decreases to about 25% at a nestling age of about two weeks. After three weeks, brooding ceased, at least during daytime. During rainfall, even four week old nestlings were brooded.

4.11. Syngamus-infection

"Snoring" nestlings were considered to have been infected by the parasitic nematode Syngamus tracheae (Hilbrich 1967) in the trachea. Only 11% of the nestlings snored, but the proportion of infected birds was probably much higher as all seven young found killed by cars in June were infected by parasite (12–20 parasites per crow). Snoring nestlings were only insignificantly lighter than those not snoring ($\chi^2 = 1.22$, P > 0.10). There was, however, a tendency that snorers, and thus probably early (heavily) infected ones, were less often observed in July and later, suggesting heavier mortality

Tab. 6. Size distribution and survival for *Syngamus* infected and normal nestlings. The nestlings were considered infected if they snored at an age of about 24 d. Light nestlings were those that did not exceed the mean weight of old nestlings (the mean weight was calculated separately for the years 1973–1976).

	Light	Heavy	N	Observed alive 1 July or later N		
infected	61%	39%	23	22%	23	
infected	46%	54%	186	45%	186	

for these birds ($\chi^2 = 3.68$, one-tailed test, P < 0.05) (Tab. 6).

5. Discussion

5.1. Causes of reproductive failure in different crow populations

Tab. 7 summarizes reproductive data from different crow populations studied.

Several authors (Olstad 1935, Wittenberg 1968, Yom-Tov 1974, Tompa 1975) ascribe much of the predation on eggs and young nestlings to the activities of other crows, especially nonbreeding ones. There are indications that this applies also to the present study area. Shells of eggs that had probably been opened by birds were found close to two preyed crow nests and in two cases eggs were lost following what might have been fights between crows in the vicinity of nests. In Wittenberg's (1968) study most predation on nestlings affected young ones (less than 12 d old) and was considered by him to be caused by other crows. Also Yom-Tov (1975) considered other crows the most important predator on nestlings (apart from man). In my study also older nestlings were lost to predators (this refers to the loss of complete clutches; single nestlings were probably never preyed on). For six broods, the approximate time for predation could be determined. It occurred in the time intervals (age of the lost nestlings): 11-19, 5-10, 0-2, 12-19, 10-20, and about 20 d. As it is unlikely that crows prey on nestlings that are more than 12 d old (Wittenberg 1968), this cause is probably unimportant. Possible predators in my study area are feral cat Felis catus L., goshawk Accipiter gentilis (L), and common buzzard Buteo buteo (L). I consider the last-mentioned to be the most likely, especially as the goshawk is uncommon in the study area during spring.

The over-all reproductive success differs between the populations studied in detail. The independent factors that can influence the reproductive characteristics are abundance of food and other predators. There is an interplay between the reproductive characteristics and the social structure. All investigated crow populations exhibited a relatively high stability in breeding density and probably also reproductive output (Tab. 8). This Tab. 7. Summary of reproductive data in different crow populations. Some of the data are taken directly from the authority cited; in other cases, I have deduced them from other information in the published accounts. NE = Nest with eggs, NN = Nests with nestlings, NHE = Nests with hatched eggs, NON = Nests with old nestlings. Notes: 1. Refers to first clutches. 2. This attempts to consider the effect on total production from the fact that some pairs hold territories but do not breed and/or the effect of re-layings. 3. 45 nests in the mountains and 19 in the lowland. 4. Two nests in which the nestlings were killed by man are excluded. 5. Mainly predation. 6. No sample size is given as the figure is calculated indirectly from other data. 7. Refers to nestlings at least

	South Norway Mountains Olstad (1935)	South Norway Lowland Olstad (1935)	Southwest Finland Archipelago Tenovuo (1963)	Southwest Northern Finland DDR Mainland Abshagen Tenovuo (1963) (1963)	Northe BRD Wittenb (1968	east) berg 3)
% territories with NE of all territo % deserted NE of all NE % completely depredated NE of a % completely depredated NN of a % deserted NN of all NHE % addled eggs of all eggs in NHE	ories 82 6 11 NE 6 11 NHE 7 0 12	(64 ³) (52) (52) (46 ⁴) (46) (140)	$\left. \begin{array}{c} 62 & (26) \\ 8 & (63) \end{array} \right.$		53 23 ¹⁵	(250^{14}) (125^{14}) (207)
% depredated eggs of all eggs in NHE % starved (to death) nestlings of all in NON % depredated nestlings of all nestlings in NON	1	(140) 5 (114)	$ \begin{array}{c} 3 (63) \\ 36^8 (440) \end{array} $	} 24 ⁸ (480)	°"fe 27 0 ¹⁶	(207) ew" (128)
% relaid clutches of all deserted or depredated NE % relaid clutches of all deserted or depredated NHE eggs/NE ¹	4.3 (24)	4.9 (10)	37 ⁹ (16) 0 4.6 (56)	4.7 (142)	78 40 4.5	(65) (10) (74)
hatched eggs/NHE Old nestlings/pair ² Old nestlings/NE	3.9 1.7 2.0	6 (31) (36)			1.2 ^{6,7} 0.9 ^{6,7}	
Old nestlings/NON % NON of NE % NON of all pairs ²	2.8 81	⁷ (26) (52 ⁴)	2.7 ¹⁰ (108)	3.1 ¹⁰ (138)	3.0 ⁷ 30 ⁷ 41	(47) (158)
Hatching time of the first egg in the clutches ¹ Weight of old nestlings Nests/km ²	16/5 (24) 480	29/4 (13)) (14)	24/5 (13) $0.9-1.3^{11,12}$ (11)	$23/4 (110) \\ 490 (0.075)^{13}$	12/4 4–5	(82) (3.5)

indicates that each population is balanced at a certain breeding density. It seems that this balance is mediated by social mechanisms in a territorial system (e.g. Charles 1972, Tompa 1975). The density level might ultimately be set by the availability of food resources in the nesting area.

The number of old nestlings or fledglings per pair (disregarding cases where the whole clutch or brood was lost) in the different studied populations is similar, i.e. 2.7. to 3.1. The figure 2.2 (Böhmer 1976) is an exception but this value is based on a count of fledged and observed young, and the author himself considered this number a minimum. On the other hand, there is a considerable variation in the proportion of completely destroyed nestings. No relation between nest density and reproductive success could be found (Fig. 8). This is hardly to be expected, as differences in food abundance and distribution (and thus distribution of non-breeding crows) must influence the result. In the most successful

Tab. 8. Stability of breeding populations in different study areas.

Minimum number of pairs	Maximum number of pairs	Number of years	Author
31	34	3	Tenovuo (1963)
32	35	5	Wittenberg (1968)
19	23	4	Picozzi (1975)
36	36	2	Tompa (1975)
9	43	10	Sondell (1976)
39	52	8	this study

three weeks old. 8. Mainly starvation. 9. Minimum figure. 10. Refers to nestlings at least two weeks old. 11. Refers to the larger islands. Density per land area is larger if smaller island are included. 12. The span between different years is given. 13. This refers to a colony of nests in a small wood. There were no nests in the proximity of the colony. 14. 23 nests destroyed by man are excluded. 15. Mainly small nestlings, 16. or very few. 17. Three nests destroyed by man are excluded. 18. Refers to fledged young. 19. Most losses were due to destruction by man. 20. Cases where nests were destroyed by man are excluded as most nests were protected. 21. Data from all years of the study. Nests biased by experiments are excluded. 22. Estimated. No definite figure available.

Scotland Yom-Tov (1974)		Scotla Picoz (197	Scotland Picozzi (1975)		Scotland Picozzi (1975)		land ated a pa 5)	Switzerl Hilla Tomp (1975	land a ba 5)	Central Sweden Sondell (1976)		Switzerl Cultiva area Böhm (1970	and ted er 5)	South Sweden This study ^{20,21}	
		95	(78)									90–95 ²²			
22 22	(23) (23)	}15	(71 ¹⁷)									5 6	(238) (238)		
}17 ⁵	(12)	}13	(60)									23 4	(83) (180)		
)15	(150)									9	(552)		
	few"	} ¹⁵	(150)									4	(552)		
305	(36)	118	(99)									25	(256)		
J	(00)	J	()									016	(256)		
												34	(129)		
4.1	(28)	4.1	(49)	4.1	(9)			4.3	(192)			0 ¹⁶ 4.3	(41) (255)		
3.7	(12)											3.8	(213)		
1.27	(22)	1.6 1.7 ⁶	(84)			2.4 ⁶		2.6	(200)	1.418	(7)	2.07	(89)		
2.6 ⁷ 45	(10) (22)	2.9 60	(47) (78)	2.8 ¹⁸ 20 ¹⁹	(6) (36)	2.8 ¹⁸ 87	(24)	3.0 86	(174) (229)	2.2 ¹⁸ 76	(18) (24)	2.8 ⁷ 61	(118) (98)		
490 2.3	(31)	1.0–1.2	2 (23)	3.0	(12)	3.7	(7)	0.3-1.3 ¹²	(33)	9	(2)	5/5 440 1.9–2.5	(258) (280) (21)		

populations in Norway (Olstad 1935), central Sweden (Sondell 1976), and Swiss hill-land (Tompa 1976) 81 to 86% of the nestings produced fledglings. The density of the Norwegian population is not reported, but as most nests were from the mountain zone, the density was probably low. The central Swedish population increased from 0.3 to 1.3 pairs km⁻² during the ten-year study. This increase was thought to be associated with the cessation of alkyl-Hg preparation of seed grains in agriculture. However, even the highest level, 1.3 pairs km⁻² is low. The population in the Swiss hill-land was comparatively dense. A possibly important factor was the lack of nonbreeding crows in the nesting area. The slowest reproducing populations were those from West Germany (Wittenberg 1968), Scotland (Yom-Tov 1974) and a Swiss cultivated area (Tompa 1975) with

20–45% of the pairs producing fledglings. In all these populations nonbreeding crows were considered an important cause of breeding failures. In the Swiss population, many nests were also destroyed by man. The breeding density in these populations was high or fairly high, 2.3–5 pairs km⁻². The very high rate of predation on egg clutches in the West German population was partly compensated by the high re-laying rate: 78%. The Swiss population studied by Böhmer was dense, 9 pairs km⁻² and had a high breeding success, 76% of the pairs producing fledglings. This is especially noteworthy as the breeding area was close to a flock area with about 40 nonbreeding crows. In this study breeding success was moderately high (61% of the nests producing fledglings) and the density average.

In conclusion: the breeding success might benefit



Fig. 8. Relation between nest density and production of fledglings in some studied crow populations. References: 1: Wittenberg (1968), 2: Yom-Tov (1974), 3: Picozzi (1975), 4: Tompa (1975), 5: Sondell (1976), 6: Böhmer (1976), 7: This study, 8: Olstad (1935) (no density value is given in this study but I assume it to be low).

from a low breeding (and presumably crow) density, lack of suitable open areas for nonbreeding birds (Tompa 1975), or a situation where the nonbreeding crows for some other reason (possibly a suitable flock area with superabundant food), do not interfere with the breeding crows. The latter might apply to my study, where the nonbreeding crows usually occupied rather well-defined areas adjacent to the study area. It is also possible that it applied, to some extent, to Böhmer's study area. Thus the nonbreeding crows might or might not (possibly depending on the food distribution) have a significant effect on the breeding success of the territorial pairs. This is somewhat at variance with the hypothesis that the importance of the intraspecific predation is to disturb the breeding crows and thus making them give up their territories (Charles 1972). Either this is not very important or possibly a very dense breeding population, supported by abundant food, with small territories renders nest defence easier as the adult crows are never very far away. Charles's (1972) observations show, however that if a group of nonbreeding birds make a conserted attack on a nest, the parents are unable to defend it.

The population reported on by Abshagen (1963) is quite exceptional (as the author himself states) in that the crows have adopted a colonial breeding structure. It supports Böhmer's (1976a: 131) model for the social structure in *Corvus*, where colonial breeding is considered an evolution from solitary breeding in conditions of food abundance, permitting a high breeding density. From an evolutionary point of view, especially of behavioural adaptations, it is important to note that different causes of failure are important in populations having a low reproductive success. The important causes are predation on eggs in the populations studied by Wittenberg (1968) and Yom-Tov (1974); on broods of young nestlings in the study by Wittenberg (1968); on broods of old nestlings in the population reported here, and on single nestlings in the population studied by Yom-Tov. Starvation of single nestlings is important in the present population and in those studied by Tenovuo (1963). Destruction by man in the study by Tompa (1975) is also important. It had probably been important in my study area unless the crows were protected.

5.2. Reproductive success and population equilibrium

Several authors (Tompa 1975, Böhmer 1976) have commented that published figures on the reproductive rate of crows are not high enough to sustain a crow population if the figures on survival rate calculated from ringing data are true. Available results give an adult survival of 50–70% (Holyoak 1971, Kalchreuter 1971 and Loman unpubl.). Possibly, survival is higher than ringing data suggest because of loss of rings or because crows have mainly been ringed in areas with a dense human population and thus a high hunting pressure. It is also possible that the survival of breeding crows is considerably higher than the average for all adult crows; also that most breeding studies have been made in areas with a low reproductive success. This seems quite likely as a breeding study is more easily undertaken in an open landscape where the nests are easily found. These are suitable areas for the flocking of nonbreeding crows and have a comparatively high density of humans. Nests are also easily found by hunters in these areas. This explanation is put forward by Tompa (1975) for his study area, and because the likelihood of study site bias it might be generally applicable. Most likely, a combination of these explanations would resolve the contradiction.

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