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Breeding success in relation to parent size and experience in a population of the Hooded Crow

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A population of wing-tagged Hooded Crows *Corvus corone cornix* was studied for five breeding seasons. Pairs that bred in the first year that they occupied a territory laid smaller clutches and bred later than experienced pairs. Some pairs bred for the first time in the second year that they occupied a territory. In this year their breeding success was similar to that of experienced pairs. Pairs with one experienced partner and one that bred for the first time had a breeding success that was similar to that of experienced pairs. A pair's territory increased in area after the first year of occupation. Experienced pairs differed with respect to egg weight, breeding time, and clutch size but not with respect to rate of predation on eggs and nestlings. Large females (measured as bill length plus foot length) and heavy females laid heavy eggs. Heavy females and females in good condition (heavy in relation to their size) bred early.

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1. Introduction

Information on individual performance is important for understanding the population dynamics of a species and the breeding strategy of individuals. The effort that a crow should be prepared to invest in defence of a territory and in other aspects of breeding should depend on expected gain: production of mature offspring. Expected gain is difficult to measure but several breeding parameters may correlate with it: clutch size, risk of predation on eggs and nestlings, breeding time, and egg weight. The first three correlates are rather obvious. Breeding time may influence chick survival if predation rate is high late in the season, which applies to the studied population (Loman 1977). Chicks hatched from large eggs may have better chances to survive than chicks from small eggs, as demonstrated in the Herring Gull (Parsons 1970).

In this paper I will examine the breeding performance of individual Hooded Crows *Corvus corone cornix* in relation to their body measurements and earlier breeding experience and discuss factors that affect clutch size, egg weight, and breeding time.

2. Study area and methods

The study was carried out in parts of the Revinge area in southern Sweden (55°40′ N, 13°30′ E). This is an open area, mainly used for cattle grazing, with numerous small copses and some marsh areas. Breeding Hooded Crows were trapped in their territories in spring and marked with patagial tags for individual recognition. Fledglings were also tagged, and some of these later bred in the study area. The tags could be identified for two or three years before they fell off or became too worn. Some crows were re-tagged and could thus be followed for longer periods. Trapped crows were also given numbered metal rings which permitted identification of all retrapped individuals, regardless of tag condition.

As breeding crows lost weight during the spring, all weights were corrected to pre-breeding weights before

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analysis. For this I used information on 14 crows that were weighed both in the period 29 March to 19 April and in the period 16 May to 10 July. Their mean decrease in weight was 1.1 g d^{-1}, with no significant difference between males and females. I also measured the 'size' of adult crows. For this I used bill length and the length between the tip of the middle toe and that of the hind toe; by simply adding these two measurements I constructed a size index. Body weight divided by the size index was used as an estimate of the bird's condition, a factor likely to vary over relatively short periods in response to e.g. feeding conditions.

A crow was considered as territorial for the first time if it had been seen in a flock during the previous breeding season or if it had a territory that was squeezed in between two previously adjoining territories. A territorial crow was regarded as breeding if eggs were laid in the territory. Some territorial crows built a nest but did not lay eggs, others started building but never finished the nest, and some never built.

Although some pairs contained only one tagged partner, I still assumed that no changes of mate took place. The analysis is not much affected by this assumption as the yearly survival of breeding crows was over 90% and only exceptionally was a change of partner recorded after a territory had been established and never after breeding had started (Loman 1980a). Both partners were tagged in 18 pairs and only one of them in 19. In the study area crows were protected from hunting, but in some instances breeding crows were shot under my supervision to create pairs with one experienced partner (i.e. one that had bred before) and one inexperienced.

Eggs were weighed at different stages of incubation but as the laying date was always known, egg weight could be corrected to pre-incubation weight by adding 0.14 g d^{-1} that they had been brooded (Loman 1980b).

3. Results

3.1. Success of first-time and experienced breeders

If both partners bred for the first time they laid a smaller clutch than in the second year that they bred (Tab. 1). Compared with birds breeding for the first time, experienced birds started laying earlier, laid larger clutches, and had a tendency to suffer less predation (Tab. 2). The net result was that experienced birds produced about twice as many nearly fledged young per breeding attempt as birds breeding for the first time did (Tab. 2). If one of the partners was experienced while the other was breeding for the first time, success was similar to that of experienced pairs (Tab. 2).

Clutch size was smaller in those pairs that bred in the first year that they occupied a territory than in those

Tab. 1. Breeding data for pairs of Hooded Crows in their first and second breeding seasons.

	First season		Second season		p‡
Clutch size	3.33±1.0	(9)	4.33±0.87	(9)	<0.05
Egg weight	19.6 ±2.2	(9)	18.9 ±2.2	(9)	>0.10
Breeding time*	7.0 ±8.2	(9)	3.5 ±3.7	(9)	>0.10
Number of fledged young	0.9 ±1.20	(10)	1.4 ±1.26	(10)	>0.10

* Measured as number of days after each year's median date. The median date was calculated on the basis of all breedings in the area, also those of untagged pairs.
‡ Computed from a two-tailed t-test for correlated means.

Tab. 2. Breeding performance of Hooded Crows breeding for the first time and of experienced and semi-experienced birds, respectively. Semi-experienced birds are pairs where one bird bred for the first time while the other had bred before. In constructing this table (in contrast to Tab. 1) I used all known breedings of the three categories of birds. For experienced birds I used the mean of all known breedings of each pair, and the table gives the means of these values; N thus refers to the number of pairs. The entries in the upper half of the table give means ±SD and, in parentheses, N.

	Pairs breeding for the first time	Experienced pairs	p‡	Semi-experienced pairs
Clutch size	3.15±0.99 (13)	4.33±0.68 (27)	<0.001	4.60±0.77 (7)
Egg weight (g)	19.7±1.9 (12)	19.4±2.2 (24)	>0.10	19.2±2.1 (5)
Breeding time*	8.8±6.6 (12)	2.1±4.8 (27)	<0.01	0.7±5.2 (6)
No. of fledged young	0.69±1.1 (13)	1.56±1.23 (30)	<0.05	1.63±2.20 (8)
Successful breeding attempts	4	45		5
			<0.10	
Breeding attempts failing due to predation	8	25		3

* In relation to each year's median date, as in Tab. 1.
‡ Computed from t-test for independent means (upper half of Tab.) and from χ^2-test (lower half of Tab.).

Tab. 3. Breeding performance of Hooded Crows that bred for the first time in their first year in a territory and of crows that did not breed until the year after territory establishment. Values given are means ± SD and, in parentheses, N.

	Breeding in the year of territory occupation	Breeding in the year after territory occupation	p‡
Clutch size	2.62±0.74 (8)	4.00±0.71 (5)	<0.10
Egg weight (g)	19.5±1.64 (8)	19.8±2.66 (4)	>0.10
Breeding time*	9.8±5.1 (8)	7.0±9.5 (4)	>0.10
No. of fledged young	1.0±1.20 (8)	0.5±1.0 (4)	>0.10
Successful breeding attempts	4	1	>0.10
Breeding attempts failing due to predation	4	3	

* In relation to each year's median date, as in Tab. 1.
‡ Computed from two-tailed t-test for independent means (upper half of Tab.) and from Fisher's exact probability test (lower half of Tab.).

that postponed breeding until their second year in the territory (Tab. 3). No difference was found between these two categories with respect to egg weight, breeding time, predation rate, or number of nearly fledged young (Tab. 3).

Crows that start breeding late lay smaller clutches than do early ones (Loman 1977). However, if only birds breeding for the first time are considered, no such correlation was found ($r = 0.04$, d.f. = 12), whereas a significant negative correlation existed for experienced pairs ($r = 0.46$, d.f. = 58, $p < 0.001$).

Five pairs had both mates tagged during both their first and their second breeding season. The size of their territories was calculated according to the convex polygon method and corrected for different number of observations following Jennrich and Turner (1976). In all five cases the territory was larger in the second year than in the first (binomial test, $p < 0.05$), the mean area being 9.6 ha in the first and 18.0 ha in the second year.

3.2. Consistency of breeding performance

There was a significant difference in egg weight between different females ($F = 10.5$, d.f. = 18:33, $P < 0.001$). Excluding their first breeding season, pairs differed significantly in clutch size ($F = 3.04$, d.f. = 21:46, $p < 0.001$) and breeding time ($F = 3.91$, d.f. = 20:45, $P < 0.001$). No significant difference between pairs with respect to susceptibility to predation was found (Kruskal-Wallis one-way analysis of variance; $\chi^2 = 19.7$, d.f. = 18, $0.5 > P > 0.3$).

When a female's clutch increased by one egg from one year to the next, the weight of the eggs increased in two cases and decreased in two, and when clutch size decreased by one egg, egg weight increased in five cases and decreased in five. Thus, there was no suggestion that females adjusted egg weight to clutch size.

3.3. Body measurements and breeding success

There was only a weak and insignificant correlation between the size and condition of females ($r = 0.24$, d.f. = $P > 0.10$). On the other hand, size and condition were both significantly correlated with female weight ($r = 0.70$, d.f. = 23, $P < 0.001$ and $r = 0.86$, d.f. = 23, $P < 0.001$).

Heavy females laid larger eggs, bred earlier, and had a tendency to lay larger clutches than light ones did

Tab. 4. Correlation coefficients for the relationship between body measurements and reproductive success in Hooded Crows. Size = foot length + bill length. Condition = body weight/size.

	Females			Males		
Variables compared	N	r	P	N	r	P
Size – egg weight	23	0.51	<0.01	22	0.24	n.s.
Size – breeding time	23	−0.28	n.s.	22	−0.07	n.s.
Size – clutch size	22	0.20	n.s.	21	0.16	n.s.
Body weight – egg weight	24	0.49	<0.05	25	0.27	n.s.
Body weight – breeding time	24	−0.51	<0.01	25	0.20	n.s.
Body weight – clutch size	24	0.38	<0.10	24	0.04	n.s.
Condition – egg weight	23	0.30	n.s.	22	0.22	n.s.
Condition – breeding time	23	−0.51	<0.05	22	−0.24	n.s.
Condition – clutch size	22	0.36	<0.10	21	−0.06	n.s.

(Tab. 4). Egg weight, but neither clutch size nor breeding time, was correlated with female size. On the other hand, egg weight was not correlated with female condition, whereas breeding time was. There was also a tendency for clutch size to correlate with female condition (Tab. 4). There was no correlation between either of the three female measurements and susceptibility to nest predation, nor was any correlation found between these measurements in males and their performance.

4. Discussion

4.1. The influence of experience on reproductive success

The reproductive output of pairs breeding for the first time was low, at least if the pair bred in the first year that it occupied a territory. Pairs that postponed breeding until their second season as territorials probably did so because their reproductive output would have been even lower than for pairs that attempted breeding in the first year. The tendency to refrain from breeding in the first year as a territorial was also pronounced in the Magpie *Pica pica* (Högstedt 1980). The fact that only some crows bred in the first year that they were territorial could, among other things, be related to differences in territory quality or to differences in the time that the territory had been held before the first potential breeding season.

One reason for the higher success of experienced pairs probably was that they had been able to enlarge their territory after their first breeding season. It is possible that the observed increase in territory size after the first breeding season and the higher reproductive output had a common cause, e.g. increased experience resulting both in better fighting and food finding ability. However, if this was the case, it remains to explain why the pair took the trouble to increase the territory. It is more probable that the territory was increased in order to benefit reproduction through an increased food supply.

The good breeding success of pairs where only one partner was experienced (usually the male) was probably due to two factors. First, these pairs were usually formed at the end of the previous breeding season (shortly after the death of the old female; Loman 1980a, Göransson and Loman 1982). This means that the new female had been associated with the territory for nearly one year and knew it well. Second, the male occupied the territory continuously and its size remained unchanged. Thus, even a female breeding for the first time is capable of laying a large clutch, and to do so early in the season, if she has access to a large territory and/or has some experience of the territory.

It is intriguing that no inverse correlation was found between breeding time and clutch size in birds breeding for the first time as this was found in older crows. This suggests that partly different facators determine the breeding success of these two categories. In first time breeders it is possible that the mates' familiarity with each other and with their territory is particularly important.

An increase in clutch size with age (at least during the first years) has also been found in e.g. the Great Tit *Parus major* (Perrins 1979, Hildén 1981, Källander 1983) and the Rook *Corvus frugilegus* (Røskaft et al. 1983).

4.2. Female body size and egg weight

There was a tendency for females that laid heavy eggs to do so also in succeeding years. Jones (1974), van Noordwijk et al. (1980), and van Noordwijk et al. (1981a) showed that egg weight in the Great Tit to a large extent is genetically controlled and I assume that the same is true for the Hooded Crow. The fact that egg weight is correlated with female size, which possibly is also inherited, strengthens this assumption. Size has indeed been shown to be an inherited character in some bird species. Garnett (1981) showed this for tarsus length in Great Tits and Smith and Zach (1979) for bill and tarsus measurements in Song Sparrows *Melospiza melodia.*

4.3. Female condition, clutch size, and breeding time

Breeding time and, probably clutch size were influenced by the condition of the female. Also, females that bred early or laid a large clutch in one year tended to do so also in the following year. This could be due either to characteristics of the female or of the territory that she occupied (the latter was never changed between two breeding seasons). I have previously shown that pairs breeding in very dry territories lay small clutches (Loman 1977). This could be because first-time breeders settle in these territories, but this explanation can be rejected as only one first year territorial out of 13 settled in this habitat. The result is therefore best interpreted as demonstrating the influence of territory quality on clutch size. Territory quality could well affect both female condition and breeding parameters, resulting in the correlation between female condition and breeding time and, possibly, clutch size. If territory quality alone were responsible, however, a similar correlation between male condition (indicating a good territory) and breeding time and clutch size should be present. This was not found, suggesting that female condition per se was partly responsible for breeding time and clutch size. In addition, these breeding variables could be genetically influenced as shown for clutch size and breeding time in Great Tits (Perrins & Jones 1974, van Noordwijk et al. 1981b, van Noordwijk et al. 1981c).

4.4. The influence of female weight on breeding time

Heavy females bred early. This, of course, is related to the fact that females in good condition breed early, as discussed above. For comparative purposes I will discuss weight rather than condition in this section alth-

ough I do not think that the conclusions are dependent on which of these measurements one choses. In contrast to my findings for the Hooded Crow, Jones (1973) found that light Great Tits bred early. I think that this difference can be understood if we consider that the total clutch of a crow is about 20% of the female's body weight, while the corresponding figure for the Great Tit is about 80%. Jones (1973) suggested that the female Great Tit cannot store resources in her body and therefore postpones breeding until her daily food intake is sufficient for her own maintainance plus the production of one egg (on egg is laid per day in both species). If light tits can gather food as efficient as heavy ones can but require less for themselves, they can start producing eggs earlier than can large ones. In contrast, female crows can probably store a substantial fraction of the resources necessary for egg production. Heavy females are likely to be those least dependent on a high daily food intake and are thus in the best position to start breeding early. The inverse correlation between weight and early breeding in Great Tits has not invariably been observed. However, nobody has demonstrated a direct correlation, like I have for the crows, so the difference between the species seems indisputable.

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