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BROOD SIZE OPTIMIZATION AND ADAPTION AMONG HOODED CROWS *CORVUS CORONE*

In this study, two problems have been investigated by brood size manipulation. First, would it pay a pair of birds to lay more eggs than they actually do? Lack (1954) believed brood size to be optimal in that those broods of the commonest size resulted in the greatest number of fledglings. Assuming that the birds are maximizing their fitness, clutch size might differ from the most productive brood size for three reasons:

1. More young may fledge from a larger than normal brood but, because of the extra stress imposed on the parents, the raising of such a brood might decrease the parents' life-time fitness (Charnov & Krebs 1974). In this case, the most productive broods could be expected to be larger than the average brood.

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2. A clutch larger than the most productive brood size may be laid in order to compensate for possible egg-loss. If all eggs hatch, adjustment could then be made by starving one nestling to death immediately after hatching.
3. If conditions during the nestling period are difficult to predict, extra eggs could be laid to allow for adjustment, by starvation, to the number of hatchlings that conditions make it possible to raise (Ricklefs 1965).

The second problem concerns the relationship of clutchsize to resources (territory quality, age, experience, etc.) of each pair: is a pair that lays many eggs also able to raise more young than the pair that lays fewer eggs? In early experiments with brood size manipulation, it was apparently accepted that no such difference existed, since results from artificial and natural broods were pooled (e.g., Perrins 1965). However, several authors have suggested recently that clutch size is adapted to the different abilities of individual pairs (e.g., Perrins & Moss 1975). I have previously suggested that this is true for the Hooded Crow *Corvus corone* (Loman 1977).

The experiments reported here were designed firstly to compare the production from broods where all eggs hatched, with that of broods where all eggs hatched and additional hatchlings were supplied, and secondly, to compare the production from manipulated broods with that of non-manipulated ones, both having the same number of hatchlings but different numbers of eggs.

The study was conducted in the Revinge area in south Sweden (55°40'N, 13°30'E). This is an area of open country with numerous copses and marshes; it is a military training ground but for most of the year the fields are grazed by cattle. The breeding density of Hooded Crows is 2·5 pairs/km^2 (Loman 1977).

Information obtained from 1973 to 1978, on 128 broods has been utilized. Twenty-four broods were enlarged in experiments performed between 1976 and 1978. Most manipulations were done at the peak of the breeding season when donor and recipient pairs were most easily matched. To prevent bias caused by late clutches being less successful than others (Loman 1977), only nestlings that had hatched within four days of the median hatching date for each year were considered. Transfer of nestlings was always done before the oldest in the recipient brood was six days old (average age: 2·8 days). Transferred nestlings were never the lightest ones in their original broods (in order to reduce the risk that they were already starving), but were chosen to be lighter or only slightly heavier than the heaviest in the recipient brood. The time from removal to arrival in the new nest was about half an hour. Number and weight of nestlings were checked in all nests when they were 20–25 days old. These nestlings are referred to as 'old nestlings'.

TABLE 1

Survival and weight (g) of transferred and original Hooded Crow nestlings. Data from 1976

	Percentage surviving to become 'old nestlings'	*n* (hatchlings)	Av. weight of 'old nestlings'	*n*
Transferred nestlings	72	18	423	13
Original nestlings	60	30	383	18

RESULTS

The transferred nestlings did not suffer higher mortality than their new nest mates (Table 1) indicating that the transfer was not a stressful process and that their foster-parents did not reject them. There were small and statistically non-significant differences between the years as regards clutch size, nestling survival and weight of old nestlings (Table 2), therefore, results from all years are combined. The following statistical analysis is based on the assumption that, if all eggs hatch, there are no differences in individual nestling survival nor in the weight of 'old nestlings' between small and large clutches. This was indeed approximately the case and, for all brood sizes, an average of 72% nestlings survived to become 'old' (Table 3).

TABLE 2

Annual variation in clutch size, nestling survival and weight (g) of 'old' Hooded Crow nestlings. Only nestlings hatched within four days of the median hatching date for each year are included

	Av. clutch size[1]	n (clutches)	Percentage of hatchlings that survived to become 'old nestlings'[2]	n (hatchlings)	Av. weight of nestlings[3]	n (broods)
1973	4·8	25	87	15	447	6
1974	4·6	29	69	51	430	18
1975	4·1	22	70	46	445	19
1976	4·2	33	74	35	440	11
1977	4·4	40	70	54	456	14
1978	4·2	31	57	28	424	10

Notes: [1] This test and those below refer to the significance of the annual variation. $F = 1·84$, df 174:5 $P = 0·108$.
[2] Only clutches where all eggs hatched are included. $\chi_5^2 = 4·53$ $P > 0·1$.
[3] Computed as an average of average brood weight. Only clutches where all or all but one egg hatched are included. F-tests were made separately for these two categories; $F = 0·92$ and 0·76, df = 40:5 and 27:5, $P = 0·48$ and 0·59.

TABLE 3

Relation between the number of eggs per clutch and the survival and weight (g) of 'old' Hooded Crow nestlings. Only broods where all eggs hatched, there was no predation and no transfers are considered

Number of eggs laid and hatched	Percentage of nestlings surviving to become 'old'[1]	n (original nestlings)	Av. weight of nestlings calculated from the average brood weight[2]	n (broods)	Number of 'old nestlings' per brood if 72% survive
2	85	6	468	3	1·44
3	76	21	460	6	2·16
4	72	36	435	9	2·88
5	72	125	438	23	3·59
6	69	36	439	3	4·31

Notes: [1] Comparing broods of 2–3 eggs with those of 4–6 eggs: $\chi^2 = 0·20$ $P > 0·10$.
[2] $F = 1·35$, df = 41:4, $P = 0·27$.

For each clutch size, the production of 'old nestlings' was directly related to the number of nestlings present immediately after hatching (Table 4). Reproductive success was thus higher for those pairs which received extra hatchlings [Mann-Whitney U-test, $U = 350·5$, $n_1 = 22$, $n_2 = 49$, $P < 0·01$ (Table 5)]. This suggests that more fledglings would have been produced by the crows had they laid more eggs. Members of enlarged broods were not significantly lighter than those of unaltered broods (Mann-Whitney U-test, $U = 436·5$, $n_1 = 21$, $n_2 = 47$, $P = 0·23$) nor was the probability of total failure, due to predation, higher for enlarged broods (Table 6).

TABLE 4

Average number of 'old nestlings' produced by pairs of Hooded Crows with different number of eggs and different number of hatchlings. Broods suffering total loss are not included. n = *the number of broods, and is given in parentheses*

Number of eggs	Number of hatchlings[1]					
	1	2	3	4	5	6
2	1·0 (1)	1·7 (3)				
3		1·8 (4)	2·3 (7)		3·0 (4)	
4	1·0 (2)	1·6 (5)	2·0 (5)	2·9 (9)	3·6 (7)	3·8 (5)
5		2·0 (1)	2·9 (9)	3·2 (12)	3·6 (25)	4·0 (6)
6					5·0 (1)	4·2 (6)

Note: [1] The number of hatchlings includes those transferred from other broods. When the number of hatchlings is less than the number of eggs laid, either eggs were addled or lost to predators, or some hatchlings were removed for transfer to other nests.

TABLE 5

Relative performance of Hooded Crow broods with transferred nestlings

	Score[1]	*n* (broods)	s.d.
No extra hatchlings	1·00	49	0·28
One extra hatchling	1·18	13	0·47
Two extra hatchlings	1·35	9	0·43

Note: [1] The following score is used: 1·00 if the number of 'old nestlings' produced was that expected from the original clutch unless it had been enlarged. The score is higher than one in proportion to any deviation from the expected success rate, i.e., 72% of the unmanipulated clutch size. For example, if all three eggs in a clutch hatch, two nestlings are added and four 'old nestlings' are produced, a score of 4/(3 × 0·72) = 1·85 is obtained.

TABLE 6

Weight of 'old nestlings' (g) and proportion of Hooded Crow broods completely predated among broods in which all eggs hatched and some hatchlings were added

	Av. weight of nestlings	*n* (broods)	s.d.	Percentage of broods predated	*n* (broods)
No extra hatchlings	440	47	48·1	14	57
One extra hatchling	446	12	34·5	14	15
Two extra hatchlings	395	9	84·0	0	9

For each number of hatchlings (after manipulations, if any), those pairs that laid the largest clutches on average reared the largest number of nestlings (Table 4). To allow statistical comparisons, a measure of relative reproductive success was used to compare decreased, normal and increased broods. Table 7 shows that success was higher for broods that started with most eggs (Spearmann rank, $r_s = 0{\cdot}36$, df = 105, $P < 0{\cdot}001$). This is also suggested by the fact that a higher proportion of nestlings survived from broods where the number of hatchlings was fewer than the number of eggs laid, than from broods where there were more hatchlings than eggs (Table 8). This means, for example, that a brood with three eggs and three hatchlings had a nestling survival of 72% (Table 3) but one starting with five eggs but only three hatchlings to rear had a survival rate of 92% (Table 8). No correction for different brood sizes is necessary since the survival rate was the same for nestlings from non-manipulated broods of all sizes (Table 3).

Table 7

Production of 'old nestlings' by pairs of Hooded Crows with reduced or enlarged broods compared with production from broods having the same number of nestlings which were not manipulated and did not suffer egg losses

Number of hatchlings in relation to original clutch size	Score[1]	*n* (broods)	s.d.
−3	1·39	2	0·0
−2	1·26	14	0·27
−1	1·13	23	0·29
equal	1·00	49	0·28
+1	0·96	13	0·38
+2	0·86	9	0·28

Note: [1] The following score was used: 1·0 if 72% of the nestlings (including experimentally added ones) in a brood survived. For example, if all three eggs in a clutch hatch, two nestlings are added and four 'old nestlings' are produced, a score of $4/(5 \times 0{\cdot}72)$ is obtained. If only two out of three eggs hatch, and both nestlings become old this gives a score of $2/(2 \times 0{\cdot}72)$.

Table 8

Reproductive success (survival per nestlıng) in Hooded Crow broods with reduced, unaltered or enlarged number of nestlings in relation to eggs laid

Number of hatchlings in relation to original clutch size	Percentage of hatchlings that become 'old nestlings'	*n* (hatchlings)
−3	100	2
−2	92	71
−1	79	138
equal	72	224
+1	69	71
+2	57	56

DISCUSSION

The two problems raised in the introduction may overlap but can be kept separate. If clutch size is optimal and it is accepted that there are differences in the ability of different pairs to raise young, it follows that pairs laying many eggs are also those most able to raise many young. The reverse does not follow: those able to raise a large number of young may lay more eggs than those able to raise less young, although both categories may lay more or fewer eggs than optimal.

It is clear that the number of eggs laid by the Hooded Crows studied is suboptimal with respect to the number of fledglings that can be produced in any one year. If the suggestion that Crows practice brood reduction (*sensu* Ricklefs 1965, Loman 1977) is correct, then this seems to reduce the output of fledglings, as the experiments described here show that most pairs could have successfully reared the nestling that is usually starved to death shortly after hatching. It is possible that the observed clutch size is optimal if the stress caused by raising young is taken into account. That this parental stress is important has been verified for the Pied Flycatcher *Ficedula hypoleuca* by Askemo (1977, and in press).

Another mechanism determining clutch size is also suggested. If the number of eggs laid is dependent on the energy the female is able to store before egg-laying (Murton & Isaacson 1962), selection will tend to lengthen the pre-laying period. If the survival of the young is higher the earlier they hatch (Perrins 1965), another selection pressure will tend to shorten it at the cost of the number of eggs laid. Breeding time and clutch size will be determined by a balance between these two forces.

This mechanism allows for super-abundant food during the nestling period and is thus an alternative explanation (to the 'parental-stress' hypothesis) for the fact that additional nestlings can be successfully reared.

It was also found that those pairs laying many eggs were able to raise most young. A random mortality process would also produce an individual nestling survival that was independent of clutch size but in this case survival would not have been affected by the addition or removal of hatchlings. This suggests that each pair lays a specific number of eggs according to the resources available.

Females in productive (pre-laying) environments and experienced females will probably be able to store more energy during the pre-laying period, whatever its length, and thus lay more eggs than females with fewer resources. If the productivity of an environment during the pre-laying period is correlated to that during the nestling period, both mechanisms suggested above will cause pairs with the highest number of eggs laid to have the highest relative reproductive success, and any effects cannot be separated on the basis of the experiments described here. It could even be argued that pairs use resources during the pre-laying period as a clue to those during the coming nestling period.

The hypotheses examined have been tested previously by similar experiments on other birds. Marine birds that lay only one egg usually do not increase their productivity if another egg is added. This was so in the Laysan Albatross *Diomedea immutabilis* (Rice & Kenyon 1962), Manx Shearwater *P. puffinus* (Harris 1966) and Short-tailed Shearwater *Puffinus tenuiristris* (Norman & Gottisch 1969). However, more young were produced from experimental clutches of two nestlings in the Gannet *Sula bassana* (Nelson 1964). Several species of gull that usually lay three eggs have also been studied. In one population of Glaucous-winged Gull *Larus glaucescens* (Ward 1973, cited by Haymes & Morris 1977), the addition of juveniles probably decreased breeding success. In four other populations [Glaucous-winged Gull (Vermeer 1963, Ward 1973), Lesser Black-backed Gull *L. fuscus* (Harris & Plumb 1965) and Herring Gull *L. argentatus* (Haymes & Morris 1977)], the naturally occurring clutch size was suboptimal if only the quality and number of fledglings is considered.

In passerines, Askemo (1977) found that pairs of Pied Flycatcher *Ficedula hypoleuca* provided with extra hatchlings were less productive than those feeding only nestlings from their original clutch. Schifferli (1978) increased the number of fledglings produced by pairs of House Sparrow *Passer domesticus* by supplying them with extra hatchlings. Fledglings from the increased broods were, however, lighter than those from natural ones, and production of adult offspring was probably decreased by the experiment. Bryant (1975), as in the present study, probably increased the production of fledgling House Martins *Delichon urbica* by providing the parents with extra hatchlings. In summary, Lack's (1954) model seems, in most cases, to give a satisfactory explanation of the evolution of clutch size in birds, at least when considered at population, in contrast to individual, level. However, the effect of rearing a large brood on adult survival must also be considered. Clutch size has been found to be adapted to a pair's individual resources in the Great Tit *Parus major* (Perrins & Moss 1975), in the Herring Gull (Haymes & Morris 1977), in the Pied Flycatcher (Askemo 1977) and in the present study of the Hooded Crow.

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GREGARIOUS BEHAVIOUR AMONG MIGRATING HONEY BUZZARDS *PERNIS APIVORUS*

Although colonial breeding and communal roosting have received much attention, the gregariousness which many birds display while on migration has hitherto been largely neglected. It has been suggested that the gregarious behaviour displayed by some breeding and wintering birds increases the efficiency of food-finding. This behaviour has also been

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