

## SYNCHRONIZATION OF BREEDING AND INTRASPECIFIC INTERFERENCE IN THE CARRION CROW

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DARLING (1938) suggested that synchrony of laying in colonial birds is stimulated by interaction between the birds, and the larger the colony, the greater the stimulus. Hence the laying in larger colonies will be more synchronized than that in small ones. In Darling's words, "the degree of breeding synchrony by social stimulation may be density-related" (Darling 1938: 53).

Since then various authors have examined these ideas for different species of birds. Some students found such density correlated onset of laying to occur (Coulson and White 1960 in the Black-legged Kittiwake, *Rissa tridactyla*; Horn 1970 in the Brewer's Blackbird, *Euphagus cyanocephalus*; Nelson 1967 in the Gannet, *Morus bassana*), while others found that they could not confirm the phenomenon in various species of gulls, *Larus* [spp.] (MacRoberts and MacRoberts 1972 in *L. argentatus* and *L. fuscus*; Vermeer 1963 in *L. glaucescens*; Weidmann 1956 in *L. ridibundus*). In addition to these observations, Ashmole (1963), Hailman (1964), and Harris (1970) suggested that "display interaction" or "social stimulation" cause breeding synchrony in some "non-annual breeders" (the Sooty Tern, *Sterna fuscata*, and the Swallow-tailed Gull, *Creagrus furcatus*, respectively).

Darling (1938) suggested that synchronous laying decreased predation, and Brown (1967), Parsons (1971), Patterson (1965), and Kruuk (1964) proved that Herring, Lesser Black-backed, and Black-headed Gulls (*Larus argentatus*, *L. fuscus*, and *L. ridibundus* respectively) that breed at the peak of the breeding season had better breeding success than individuals that breed earlier or later than the peak. Patterson (1965) also showed that Black-headed Gulls that breed outside or on the edge of a colony were more vulnerable to predation and thus less successful than birds in the center. "Edge effect" (i.e. lower breeding success on the edge of a colony) was reported for the Gannet (Nelson 1967) and the kittiwake (Coulson and White 1956). Horn (1968) found that "clumped nesting in Brewer's Blackbird improves foraging efficiency and predation avoidance only when the colony is built in a large expanse of nesting habitat, surrounded by abundant, but patchily distributed, food."

All the species mentioned breed in dense colonies, where the distance between the closest nest is rarely more than a few meters, but there is no reason why territorial species should not synchronize breeding in order to benefit in the way that some colonial birds do. For example,

synchronization of laying was found to be "significantly related to nesting dispersion" for the Starling, *Sturnus vulgaris* (Carrick in Dunnet 1952).

#### THE SPECIES AND STUDY AREA

The Carrion Crow (*Corvus corone*) is a useful species for examining if the "Fraser Darling effect" exists in territorial species. In the study area they bred in different densities, according to the availability of trees. The crows suffer heavily from predation by nonbreeding flock birds as well as by neighboring territorial pairs. Charles (1972), Yom-Tov (1974), Tenovou (1963), and Wittenberg (1968) have shown that cannibalism on eggs and chicks is the major factor causing breeding failure in crows in Scotland, Finland, and Germany. This investigation was carried out during 1972, and some data were kindly given to me by J. K. Charles, who studied part of the same population during 1969-71.

The study area is the surroundings of Newburgh, Aberdeenshire, in northeastern Scotland. It consists of fertile, gently rolling, intensively cultivated farmland, dotted with farms—each with some buildings and trees. Trees are not common and occur only near each farm, in two small plantations, and scattered through Newburgh village and along roads and hedgerows. The mean distance between nesting trees (in an area of about 20 km<sup>2</sup>) was  $498 \pm 277$  m (mean  $\pm$  SD). Most nests were near farmhouses, some on hedgerows, while only 6% were built in plantations. The large standard deviation (55% of the mean) of internest distance was mainly due to the fact that trees are not evenly distributed in this area. While the minimum internest distance was 150 m, in some large fields trees were up to 1 km apart. Charles (1972) demonstrated experimentally that adding a tree in such places (at a distance greater than minimum internest distance) established a new territory between the existing ones, justifying the conclusion that in some regions, trees are in short supply.

Accordingly, the nests in the study area were divided into two categories: "clumped nests," those occurring in places where at least one tree was found between each two existing nesting trees, at a distance greater than minimum internest distance, thus enabling a third pair to settle between the two; and "dispersed nests," where no such trees occur. The study tract contained five areas of each category.

#### RESULTS

If the "Fraser Darling effect" occurs in crows, one would expect that laying dates would be more synchronized in places with an excess of trees than when trees are sparse, as crow populations are denser in the former, i.e. the smaller the internest distance, the better the synchrony of laying. The relationship between largest internest distance of one group and synchrony of laying for each dispersed and clumped group of nests during 1972 is shown in Fig. 1. The measure of laying synchrony employed in this study is  $1/a$  when  $a$  equals the difference in days between earliest and latest laying of first egg in each group of nests. A significant regression ( $F = 15.7$ ;  $n = 10$ ;  $P < 0.001$ ) was found between maximal internest distance and synchrony of laying, indicating that the "Fraser Darling effect" was present in this population of crows.

Further, the Mann-Whitney U-test (Siegel 1956) was used to examine

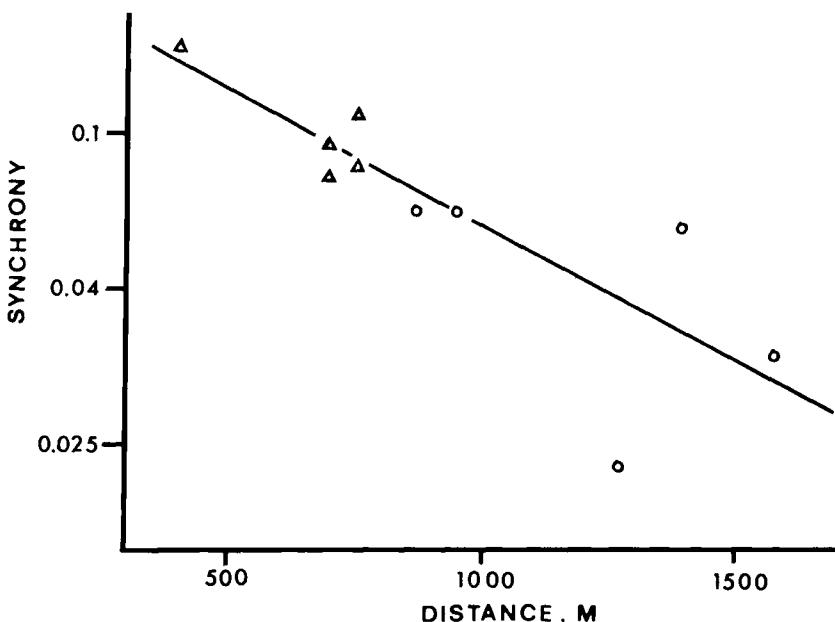


Fig. 1. The relationship between internest distance and synchrony of laying in clumped and dispersed groups of nests. x-axis, the distance between the two most widely spaced nests with one group (meters). y-axis, synchrony, expressed at  $1/a$  when  $a$  is the difference in days between earliest and latest laying dates of laying first egg in each group. Triangles, clumped nests; circles, dispersed nests.  $y = 0.300 - 0.0002x$ ;  $F = 15.7$ ;  $n = 10$ ;  $P < 0.001$ .

the difference in laying synchrony between clumped and dispersed groups of nests (see Table 1), and a significant difference was found ( $n_1 = 5$ ;  $n_2 = 5$ ;  $U = 0$ ;  $P < 0.008$ ). The mean synchrony was 0.172 (range 0.07–0.5, median 0.09) and 0.044 (range 0.02–0.06, median 0.05) in the clumped and dispersed areas respectively (Table 1). Mean laying dates were 20 and 22 April in dispersed and clumped nests respectively, but this difference was not significant and no correlation was found between laying date and synchrony.

To see if the synchrony of laying in clumped areas differed from a random sample, the study area was divided arbitrarily into (a) five areas, from west to east, each with five to six nests; and (b) four areas, northeast, northwest, southeast, and southwest. Both cases revealed a significant difference ( $n_1 = n_2 = 5$ ;  $U = 0.5$ ;  $P < 0.01$  and  $n_1 = 5$ ;  $n_2 = 4$ ;  $U = 0$ ;  $P < 0.08$  respectively) between synchrony of laying in the clumped areas and the arbitrary divisions.

These results (Fig. 1, Table 1) show a significant association between internest distance and synchrony, and this synchrony may be attributed

TABLE 1  
SYNCHRONIZATION OF LAYING IN CLUMPED AND DISPERSED NESTS

Area	Clumped nests			Dispersed nests		
	No. of nests	Mean laying date of first egg <sup>1</sup>	Synchrony <sup>2</sup>	No. of nests	Mean laying date of first egg <sup>1</sup>	Synchrony <sup>2</sup>
1	4	19.5	0.50	5	20.8	0.03
2	4	25.0	0.12	4	16.8	0.06
3	6	18.3	0.09	4	32.8	0.06
4	5	25.8	0.07	4	11.0	0.02
5	5	20.8	0.08	4	16.7	0.05
<b>Mean</b>		<b>22.1</b>	<b>0.172</b>		<b>20.1</b>	<b>0.044</b>

<sup>1</sup> 1 = 1 April.

<sup>2</sup> Synchrony as in Fig. 1.

to social stimulation. An alternative explanation might be that the study area is heterogenous, and some environmental factor such as tree density, leaf emergence, food supply, etc. is responsible. However, such a factor is not likely to operate in the study area, as only 6% of the nests occur in plantations, while the others are where trees are sparse. The main food supply for the crows comes from field crops and farms. Almost all nests, clumped and dispersed alike, occur in or near farms and thus have the same food supply. Laying occurs between 20 April and 10 May, while leaf emergence occurs in mid-May, when all nesting pairs have already laid. Further, no significant difference was found in laying dates between clumped and dispersed nests. Thus, it is difficult to attribute the difference in laying synchrony between clumped and dispersed to any known environmental factor. A final conclusion on this point might be found only by supplying extra food ad libitum to all pairs and then examining breeding success.

Do crows benefit from this synchronization? In Fig. 2 the breeding success of each group expressed as percent of fledglings from eggs laid during 1972 is plotted against synchrony of laying for each of the clumped and dispersed groups. It was found that there was a significant regression ( $F = 40.0$ ;  $n = 5$ ;  $P < 0.005$ ) between laying synchrony and breeding success in clumped nests, while no such correlation was found in dispersed nests. More than 90% of egg and chick losses were caused by cannibalism (Charles 1972, Yom-Tov 1974) and synchronous nests suffer much less from cannibalism than asynchronous ones. The fact that no correlation was found between breeding success and synchrony in dispersed nests might be explained by the large internest distance in these groups being too large for neighboring crows to be effective predators. Thus crows do benefit from synchronizing breeding with their

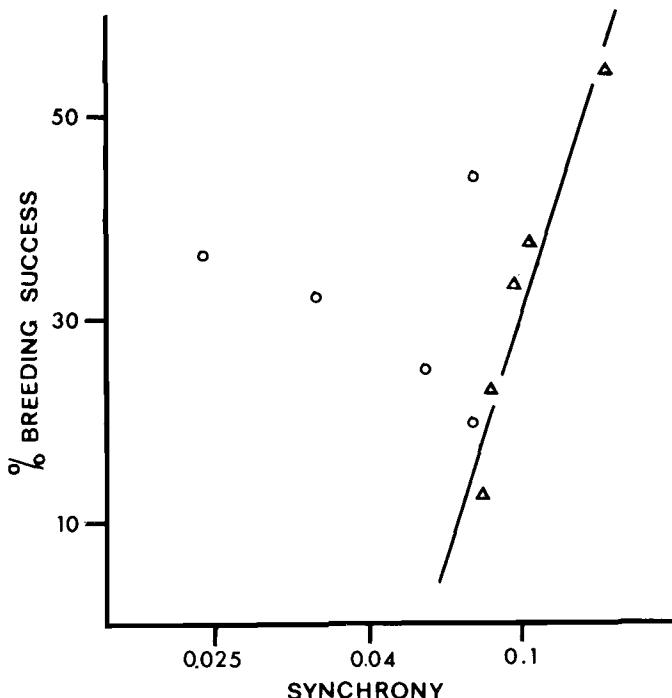


Fig. 2. The relationship between laying synchrony and breeding success in clumped and dispersed nests. Triangles, clumped nests; circles, dispersed nests.  $y = 20.00 + 72.89x$ ;  $F = 40.0$ ;  $n = 5$ ;  $P < 0.005$ . x-axis, synchrony, as in Fig. 1; y-axis, breeding success, percent fledglings from eggs laid in each group.

neighbors, presumably because synchronous crows are busy rearing their young and do not have time to cannibalize other crows' eggs and chicks, and the survival value of synchronous breeding in the crow is to avoid cannibalism.

#### DISCUSSION

Intraspecific interference in breeding is a common phenomenon. It occurs in the three-spined stickleback, *Gasterosteus aculeatus*, where Van Den Assem (1967) found that egg stealing was the major factor causing egg losses and that in a synchronized breeding population, egg losses from stealing did not occur (p. 143). However, in experimental situations where a male had no clutch of eggs in his nest, many more eggs were lost and development was more retarded by interrupted fanning and poor ventilation of the eggs than was the case when all males received eggs (p. 149). Van Den Assem's experiments led Nelson (1967) to suggest that

the nonannual synchronous breeding of the Swallow-tailed Gull is a strategy to avoid intraspecific interference.

In many cases particular colonies synchronize their breeding, but laying does not coincide with external factors such as peaks in food abundance or with the presence of predators. Such cases are found mainly in the tropics, illustrations being the Sooty Tern and other "non-annual breeders" mentioned earlier. However, some also occur in temperate zones, such as the Starling, which in Scotland has a "remarkably synchronous laying" (Dunnet 1955) that cannot be explained as an antipredator device or as an adaptation to food cycles.

Possibly synchronous breeding in such cases is a strategy to avoid intraspecific interference in breeding, which is common and takes various forms—such as cannibalism (many examples are quoted in Wynne-Edwards 1962), savage attack on conspecific chicks as in tropical terns (Ridley and Percy 1958, Ashmole 1963) and various gulls (Brown 1967, Parsons 1971), intraspecific nest parasitism as in ducks (Weller 1959, Grenquist 1963) and the Starling (Yom-Tov et al. 1974), fighting as in Gannets (Nelson 1966), nest destruction as in Rooks, *Corvus frugilegus* (I. J. Patterson pers. comm.), and nest prospecting. A common factor in most (if not all) of these interactions is that they result in lower breeding success for the breeders that were interfered with. It is suggested that at least in some of these cases the survival value of synchronous breeding is to avoid conspecific interference during breeding. If this hypothesis is true, then it might explain other situations where synchronous breeding is not correlated with predation or with food availability.

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#### SUMMARY

Synchronous breeding was found to be present in the Carrion Crow, *Corvus corone*, in northeastern Scotland. Birds breeding close to other pairs synchronized laying better than pairs nesting far apart. Synchronous pairs were more successful in breeding than less synchronous ones because

of decreased cannibalism. It is suggested that the survival value of synchronous breeding here is to avoid cannibalism on eggs and chicks. It is also suggested that in many cases, mostly in the tropics, the function of synchronous breeding is to avoid intraspecific interference in breeding.

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