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Helpers-at-the-nest in Carrion Crows *Corvus corone corone*

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Accepted 26 January 1989

I report here observations of three cases where a pair of breeding Carrion Crows *Corvus corone corone* was assisted in rearing young. This species was not known before to have helpers at the nest, although the occurrence of third birds in otherwise exclusive territories has been reported earlier (Charles 1972). Some of the third birds in Charles' study were not the offspring of the pair with which they were associated, nor was it shown that the third birds assisted the pair in breeding. Although the present paper is the first description of helpers-at-the-nest in Carrion Crows and in an Old World corvid, this observation is not entirely unexpected. Helping has been observed in other corvids, namely in the Northwestern Crow *C. caurinus* (Verbeek & Butler 1981), in the American Crow *C. brachyrhynchos* (Kilham 1984), and in several species of jay, e.g. Florida Scrub Jay *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984), Mexican Jay *A. ultramarina* (Brown & Brown 1981), Piñon Jay *Gymnorhinus cyanocephalus* (Balda & Balda 1978) and Green Jay *Cyanocorax yncas* (Alvarez 1975). In Northwestern Crows most helpers do not feed the chicks or the incubating female but are involved in territorial defence only. Here I describe the behaviour of the birds and the ecological context in which helping occurred.

The study population

During a study of the breeding and life-history characteristics of individual birds in a rural and in an urban habitat in a Carrion Crow population around Lausanne, Switzerland (Richner 1989a, in press), more than 600 of the birds have been individually marked and measured. Their sex was determined by laparoscopy (Richner 1989b). Juvenile and adult birds were caught in a large cage trap or by the use of a stupefying bait; fledglings were caught in the nest.

The Carrion Crow is a highly territorial species. In the present study, pairs in the rural habitat defended large territories and lived at a density of approximately six pairs per km^2. The breeders in the urban habitat defended much smaller territories, at a density of approximatively 36 pairs per km^2. Areas which were unsuitable for breeding were temporarily used by large flocks of non-breeders. Twenty pairs of

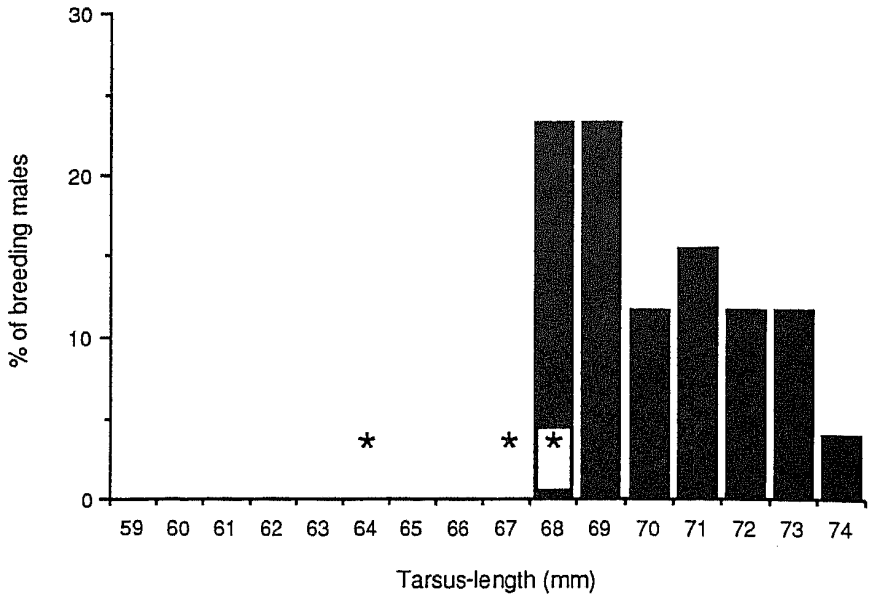

Figure 1. Tarsus-lengths of male Carrion Crow territory holders (■, $n = 28$) and the three male helpers*.

breeders in the rural habitat and 33 pairs in the urban habitat were studied intensively between 1984 and 1988. During the breeding seasons of 1987 and 1988 these pairs were observed closely enough to detect the presence of helpers.

The acquisition of a territory is dependent on body size in both habitats (Richner 1989a). Body size can be represented by tarsus-length since it was shown that the length of tarsus is highly correlated with other body measurements. The empirically determined lower limit for tarsus-size of breeding males was 68 mm in both habitats (Fig. 1), while the mean tarsus-length was found to be 70·2 mm with no difference between the rural and urban habitats. Tarsus-length is fixed at fledging and does not change through an individual's life. Successfully breeding pairs (i.e. pairs which fledge at least one young) in the urban habitat produced on average 1·5 fledglings per year but 76% of these fledglings fell below the critical body size necessary for acquiring a territory and would therefore never have bred. Successful breeders in the rural habitat produced on average 2·7 fledglings per year with only 21% of the fledglings falling below the critical body size. Thus, the breeders in the urban habitat produced a lower number of smaller fledglings than the breeders in rural habitat (Richner 1989a).

The three cases of helping

All three cases of helping occurred in the urban (i.e. high-density) habitat and in two of the three cases the helpers were among the 33 pairs under close observation. In two of the three cases the helpers were sons reared 2 years before in the same territories and in both those cases the adult male territory holders were their fathers. The adult females were not marked, but since Carrion Crows show long-term pair bonds it is very likely that these females were the mothers of the helpers. In the third case the family relationships were not known.

The first case of helping was observed in 1987. The helper had been born in 1985 and had remained in the parental territory since fledging, although it is not known whether he had helped in 1986. This helper fed the chicks on 16 occasions during a total of 13·5 h of observation, while the father fed the chicks on 21 occasions and the

mother on 14 occasions during the same period. Feeding of chicks by the helper lasted on average 3·1 minutes, feeding of chicks by the father on average 2·1 minutes. The length of feeding periods by the mother could not be accurately determined since feeding was often interrupted by variable periods of brooding the chicks. During the 13·5 h of observation, the helper and his parents were involved on three occasions in a violent territorial dispute with the neighbouring pair. The trio raised one female fledgling in 1987 which was comparatively light (310 g) and undersized (tarsus-length of 61 mm) at fledging. Since the helper just reached the critical body size (tarsus-length of 68 mm) necessary for acquiring a breeding territory (Fig. 1), the helper's father was experimentally removed after the breeding season in order to test whether the helper would take over the territory. The helper was present in the territory for a few weeks thereafter but was not seen in the territory later that year, nor in the following breeding season.

The second case was observed in 1988. The helper, marked as a fledgling in 1986, was raised by the pair that he later assisted. His tarsus measured 67 mm (Fig. 1) which is below the critical body size necessary for the acquisition of a breeding territory. It is not known whether he had helped in 1987. In 1988 he was observed on several occasions feeding the female during incubation. He later regularly fed the chicks. All chicks disappeared within 10 days of hatching.

The third case of helping was observed in the breeding season of 1988 but only the helper was individually marked and its relationship to the breeding pair was not known. When first caught in 1987, he was already at least 2 years old. This helper was also below the body size of male territory holders (tarsus-length of 64 mm; Fig. 1), and lived with the pair all year round in the territory. This trio raised one male fledgling in 1988 which was comparatively heavy (440 g) but undersized (tarsus-length of 65 mm).

Discussion

Three types of ecological conditions important in the evolution of cooperative breeding have been recognized by Emlen (1982, 1984), and are comprehensively treated by Brown (1987). The first type of constraint is habitat saturation which entails a shortage of breeding sites or territories relative to the number of birds competing for them. The second type of constraint is the shortage of mates which, in monogamous birds, is the result of a skewed population sex ratio. The third type of constraint is the environmental harshness represented by erratic changes in the carrying capacity of variable and unpredictable environments.

However, a fourth condition, the constraint imposed by body size, could be more important than these three conditions in the evolution of the helping behaviour in the Carrion Crow. It has been shown (Richner 1989a) that territory acquisition in Carrion Crows is dependent on body size (Fig. 1). Two of the three helpers fell below the size limit and consequently would never have become territory owners. The best thing such birds can do is to help their parents in raising chicks, thereby increasing the chance that some of these kin may reach the critical body size necessary for becoming a breeder. Due to the phenotypic constraint, such helpers can increase their overall fitness only through an increase in the indirect component of their inclusive fitness. Thus, in the 'phenotype constraint' model, the evolution of helping behaviour would be entirely explained by kin selection, i.e. through the fitness gain obtained by genetically related helpers which are phenotypically too small for acquiring a critical breeding resource (territory or mate). Acceptance of helpers by the parents would have the highest payoff where the phenotypic size of chicks is most limited by breeding conditions, as occurred in this study among territory-holding

Carrion Crows in the urban habitat. However, due to the small number of observed cases of helping in the Carrion Crow, no firm support is available yet for the phenotype constraint hypothesis. It may be worthwhile to examine this hypothesis in other species where helpers are present but never breed on their own. To my knowledge the only study which explicitly addresses this question is by Brown *et al.* (1982) on the Grey-crowned Babbler *Pomatostomus temporalis*, in which helpers were not detectably smaller in body size than breeders of the same age and sex.

I thank P. Vogel and an anonymous referee for suggestions on the manuscript, and H.-U. Reyer for pointing out a relevant reference. I am grateful to P. Schneiter who was a dedicated field assistant, and to G. Matthey who generously made the necessary funds available from the Conservation de la Faune.

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