

History, environment and social behaviour: experimentally induced cooperative breeding in the carrion crow

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Kin-based cooperative breeding, where grown offspring delay natal dispersal and help their parents to rear new young, has a long history in some avian lineages. Family formation and helping behaviour in extant populations may therefore simply represent the retention of ancestral features, tolerated under current conditions, rather than a current adaptive process driven by environmental factors. Separating these two possibilities challenges evolutionary biologists because of the tight coupling that normally exists between phylogeny and the environmental distribution of species and populations. The carrion crow *Corvus corone corone*, which exhibits extreme interpopulational variation in the extent of cooperative breeding, with populations showing no delayed dispersal and helping at all, provides a unique opportunity for an experimental approach. Here we show that offspring of non-cooperative carrion crows from Switzerland will remain on the natal territory and express helping behaviour when raised in a cooperative population in Spain. When we transferred carrion crow eggs from Switzerland to Spain, five out of six transplanted juveniles delayed dispersal, and two of those became helpers in the following breeding season. Our results provide compelling experimental evidence of the causal relationship between current environmental conditions and expression of cooperative behaviour.

Keywords: cooperative breeding; delayed dispersal; phylogenetic history; carrion crow

1. INTRODUCTION

Most cooperative societies arise through family formation, when young remain on the natal territory and help their parents to rear new offspring (Emlen 1995). In such systems, delayed dispersal is a necessary precondition for cooperation. The idea that social behaviour responds to current environmental conditions has been challenged by increasing evidence that cooperative breeding is not randomly distributed among avian taxa and represents the ancestral state in some lineages (Edwards & Naem 1993; Cockburn 1996; Arnold & Owens 1998). Since ‘yesterday’s adaptation may be today’s constraint’ (Ligon 1993), cooperative breeding in extant species or populations might merely represent the retention of ancestral features, tolerated under current conditions (Gould & Lewontin 1979; McKittrick 1993; Gittleman *et al.* 1996) rather than a current adaptive process driven by environmental factors. Separating these two possibilities is difficult because of the tight coupling that normally exists between phylogeny and the environmental distribution of species and populations, and because experiments that prove a causal link between current environmental conditions and the expression of social behaviour are difficult to carry out. A phylogenetic bias does not exclude the possibility that a trait arose as an adaptation in the past, and therefore phylogenetic constraints should not be invoked as the

ultimate explanation of any trait (McKittrick 1993). Nevertheless, the truth about history cannot ever be known, while strong evidence of adaptation can be provided by uncovering current processes and by showing the causal link between environment and behavioural traits (Martins 2000). Phylogenetically based comparative methods are widely used to assess to what extent social behaviour is constrained or responds to current environmental factors (Brooks & McLennan 1991; Harvey & Pagel 1991; Martins 2000). However, these methods are correlative and provide weak tests of evolutionary hypothesis. An experimental approach would be far more powerful. The carrion crow (family Corvidae) provides a unique opportunity to test experimentally if the occurrence of a cooperative organization responds to current environmental conditions. The carrion crow has been almost invariably reported as a socially monogamous species that breeds as unassisted pairs (Richner 1990), but the recent finding of a cooperative population in northern Spain in which 73% of territories are held by cohesive groups of up to nine individuals demonstrates that cooperative breeding varies among populations (Baglione *et al.* 2002). In the Spanish population 28% of the offspring remain on the natal territory for at least 1 year and 71% of those act as helpers, contributing to nest building, nestling care and territorial defence. Both sexes help, and social groups live year-round in all-purpose territories. By contrast, rural carrion crow populations in Switzerland are representative of the most common social organization of this species in Europe (Richner 1990), with juveniles abandoning the natal terri-

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tory before the end of their first winter and by their lack of helping at the nest. This study was based on a transfer of carrion crow eggs from a Swiss non-cooperative population to the Spanish cooperative one in order to rear Swiss chicks in Spanish foster nests. We were conservative by choosing to transfer eggs from the non-cooperative population to the cooperative one. Helping requires a sequence of behaviours from delayed dispersal to delayed reproduction and alloparenting. We transferred eggs from Switzerland to Spain because the positive result, induction of helping in offspring originating in a non-cooperative population, is a compelling test of the hypothesis that helping responds to environment. It requires the occurrence of all three steps in the sequence leading to helping, whereas absence of helping in offspring transferred from Spain to Switzerland could result from failure at any of the three steps.

2. METHODS

A previous study of the social system of the Swiss population of carrion crows showed absence of offspring retention and cooperative breeding (M. Griesser, unpublished data) as in other rural areas of Switzerland (Richner 1990). In April 2000 we transferred 39 eggs from 17 carrion crow nests in a rural area near Zurich, Switzerland (47° N, 8° E) to foster nests in La Sobarrriba, León, northern Spain (42° N, 5° W). We removed two or three eggs from each donor pair leaving a minimum of two eggs in the nests. The eggs were marked, transferred to an incubator and moved to northern Spain within 10 h. There the eggs were kept in an incubator until the first signs of hatching were visible, when all eggs from the same donor nest were transferred to a foster nest. Brood size was kept constant in the foster nest by removing an equivalent number of eggs. The foster nests were visited every day after egg transplantation until the nestlings were 12 days old. This procedure allowed us to identify and mark the chicks hatched from transplanted eggs. At day 12, each nestling received a unique code of coloured rings. All the surviving nestlings in the foster nests in Spain (seven transplanted and three native) were fitted with a radio transmitter when they were close to fledging. The surviving nestlings ($n = 21$) in the donor nests in Switzerland were also banded with a unique combination of colour rings and a bleaching of the tertiary feathers. Such bleaching, obtained from a product for human hair, is durable in the crows (at least 1 year) and highly visible from long distances (up to 500 m) using binoculars and spotting scopes. We collected 50–200 μ l of blood from each juvenile banded carrion crow. These birds were sexed by using the P2/P8 molecular sexing method (Griffiths *et al.* 1998). (For details on DNA extraction and sex identification in crows see Baglione *et al.* (2002).)

We located the transplanted fledglings in Spain at least once a month. Simultaneously an intensive search of juvenile banded crows in Switzerland was carried out in August, October, December 2000 and April 2001, surveying the natal territories and the surrounding landscape. Fledgling resightings in Switzerland were defined as 'within the territory' if the distance from the natal nest was equal to or shorter than an average territory radius (average radius calculated on 32 Swiss territory-year; methods described in Baglione *et al.* (2002) and M. Griesser *et al.*, unpublished data). In Spain, where the shape and extension of the territories were known (see Baglione *et al.* (2002) for details on territory size assessment), resightings were classified

according to the observed territory boundaries. However, all resightings classified 'outside the territory' occurred several territories away from the natal nest. This fact contributed to an unequivocal classification of all the observations.

During the breeding season 2001 in Spain, we surveyed the four territories where transplanted birds were still present to record any evidence of helping behaviour, defined as cooperation in nest building, nest or territory defence and food provisioning to the nestlings or the incubating female. At each territory we carried out a minimum of three observation bouts (3 h each) per week from favourable spots using binoculars and a 20 \times 60 zoom spotting scope. One video camera was placed close to the only nest where food delivery could not be observed from a distance.

We applied conservative criteria to analyse the effect of the area where juveniles were reared (Spain or Switzerland) on natal dispersal. All the juveniles of unknown fate ($n = 15$, all of them in Switzerland) and a transplanted bird that died after fledging were excluded from the analysis. A forward stepwise logistic regression was carried out. Removal testing was based on the probability of the likelihood-ratio statistic based on the maximum-likelihood estimates (Norusis 1990). The effect of sex and body condition at fledging (residuals from the regression of body mass on tarsus length) was controlled for in the analysis, as both factors can affect dispersal in birds (Belthoff & Dufty 1998; Baglione *et al.* 2002). The final dataset included 12 individuals from nine different broods. Because siblings are not independent genotypes and the territory where they were reared could also affect their dispersal decision, some data were not truly independent. We therefore repeated the analysis excluding at random one individual from each of the three pairs of siblings. The results did not change qualitatively.

3. RESULTS

Seven juveniles fledged from eggs transferred to five nests in Spain (three males and four females, 'transplanted juveniles' hereafter), but one died on its territory 56 days after fledging. The rest of the Spanish experimental nests ($n = 12$) failed. In Switzerland, 21 juveniles (13 males and eight females) fledged from nine donor nests. The difference in nestling survival between the two areas was expected according to the very low reproductive success of the Spanish population in comparison with other European populations (J. M. Marcos and V. Baglione, unpublished data). The rearing environment (Spain or Switzerland) had a highly significant effect on delayed dispersal, the first step towards kin-based helping behaviour (table 1). As expected, fledglings from the nests in Switzerland showed dispersal patterns typical of the non-cooperative population. In August only six juveniles were resighted, four of which had already joined the big flocks of floaters on communal feeding grounds, showing no connection with the natal territory (figure 1a). Two birds still moved to and from the natal territory in August, but by October they were only observed outside the territory (figure 1b). In Switzerland, no banded juveniles were found on their natal territories in the next breeding season. Conversely, in Spain, all but one of the six surviving transplanted juveniles remained on their natal territories through their first year of life (figure 1). The exception was a juvenile that abandoned the natal territory at the end of its first summer.

At the beginning of the breeding season of 2001, five

Table 1. Factors affecting delayed natal dispersal of Swiss juvenile carrion crows. (Dispersal data refer to the situation in spring 2001.)

	retained juveniles	dispersed juveniles	variable	d.f.	p^a	included in the model
Spain	5	1	area	1	0.001 (0.007)	yes
Switzerland	0	6	sex	1	0.439 (0.576)	no
			body condition	1	0.124 (0.174)	no

^a The p -values obtained excluding at random one individual from each pair of siblings are shown in brackets.

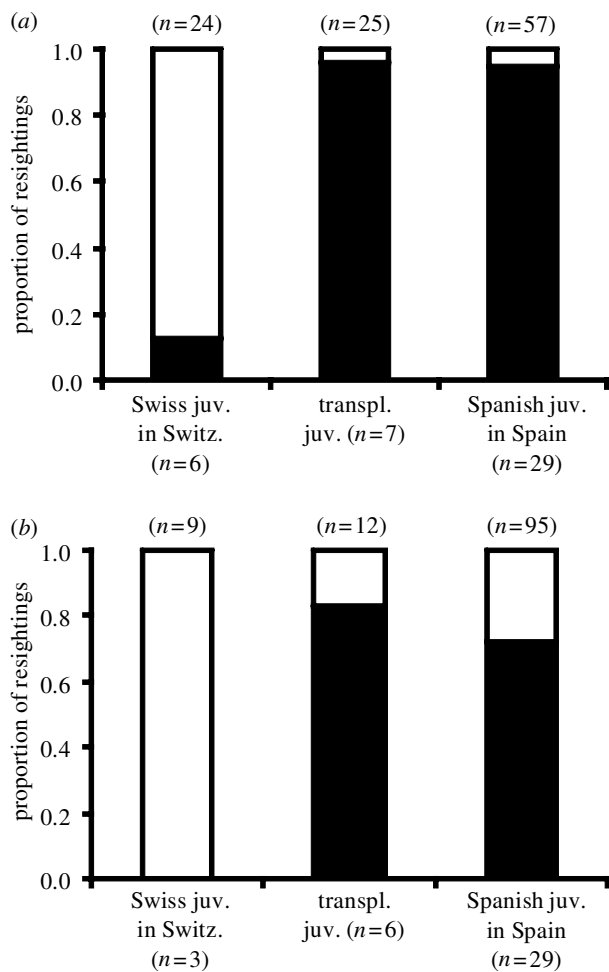


Figure 1. Natal dispersal of juvenile banded crows in Spain and Switzerland. Each datum corresponds to a bird resighting. Filled bars correspond to resightings inside the natal territory, open bars to resightings outside. Resightings of the same birds at the same place (i.e. inside or outside the territory) within a day were considered only once. Numbers of resightings (above the bars) and numbers of juveniles retrieved (on the x-axes) are shown. (a) Resightings from the end of the four weeks post-fledgling dependence period (Cramp & Perrins 1994) until the end of August. Resightings of Spanish juvenile carrion crows (Baglione *et al.* 2002) are also shown (third column). (b) Resightings in the two months following August.

transplanted juveniles still remained on their natal territories, cohesively associated with the resident birds (table 2; see the legend for the explanation of individual identity code). One juvenile female, A26, visited the nest in her territory only occasionally during incubation, but, 7 days

after the eggs hatched, she began to provide food to the nestlings at a relatively high rate (figure 2) and continued to do so until the nestlings fledged. This bird also contributed actively to territory/nest defence (44% of 80 recorded events). A second juvenile female, B5, contributed to nest-building and participated in five of 11 events of territory/nest defence (45%). The nest failed during egg laying. This bird remained on the territory for another 43 days but eventually dispersed. A third female, C11, dispersed after early nest failure, but returned to the territory 10 days before the lone chick reared in the replacement nest fledged. C11 again formed a cohesive group with the resident birds, but refrained from visiting the nest. During laying and thereafter, two juvenile males, d1 and e1, had been attacked by the alpha-male and they confined their activities to the periphery of the territory for the rest of the spring. Similar behaviours had been observed before in the study area among native birds (J. M. Marcos and V. Baglione, unpublished data).

4. DISCUSSION

The response to the transfer shows that non-cooperative carrion crows of Swiss ancestry can express delayed natal dispersal and helping behaviour when reared in a cooperatively breeding population of the same species in Spain. This result is bolstered by our concurrent observations of the nests from which the transplanted chicks were derived. These nests showed the typical patterns of offspring dispersal and an absence of helping behaviour previously described for the Swiss populations. By showing that helping responds to the rearing environment and that lack of cooperative breeding in the Swiss population is explained by plasticity rather than by phylogenetic constraints, we provided compelling evidence of the causal relationship between current environmental conditions and expression of cooperative behaviour. Our data therefore support the general argument that environment has a role in the evolution of social behaviour. Such a role has been indicated by recent studies that incorporate phylogenies into the analysis of comparative data (Edwards & Naem 1993; Arnold & Owens 1999). Comparative methods represent a useful tool to infer the evolution of behaviour (Harvey & Purvis 1991), but only a combination of comparative studies and experimental manipulations would ideally solve the problem of correlation versus causation (Martins 2000). Our experimental results are consistent with the prediction of Arnold & Owens (1999) that, within avian lineages predisposed to cooperative breeding (e.g. corvids), the current environment determines exactly

Table 2. Helping behaviour of transplanted juvenile carrion crows.

individual ^a	nest building	territory defence	nestling care
A25	not observed	yes	yes
B5	yes	yes	nest failure before egg hatching
C11	not observed	yes, but only one event recorded in this territory	no
d1	not observed	no ^b	no ^b
e1	not observed	no ^b	no ^b

^a Letters identify individuals (capital and small letters symbolize female and male respectively). Numbers indicate the territory where the juveniles were reared and retained.

^b Attacked by the alpha-male of its group, the bird confined its activity to the periphery of the territory during the whole breeding period.

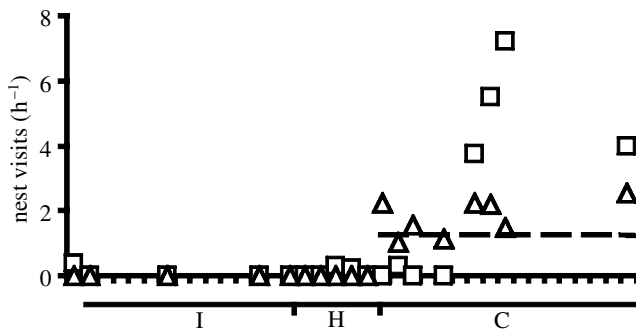


Figure 2. Contribution to nest food provisioning of a transplanted carrion crow A26 (squares) and its foster Spanish sibling (triangles) through the breeding period. The x-axis is based on a daily scale. (I, eggs in incubation; H, eggs hatching; C, chicks in the nest.) The broken line indicates the average nestlings feeding rate of retained offspring that act as helpers in the Spanish population.

which species or populations will adopt cooperative behaviour.

The search for the ecological correlates of cooperative behaviour in birds has attracted the attention of behavioural ecologists for decades, but it has proved difficult to identify the key factors that lead to cooperative breeding (Koenig *et al.* 1992; Arnold & Owens 1998; Hatchwell & Komdeur 2000; Kokko & Lundberg 2001). Comparative analysis identified year-round territoriality as one of the key ecological predictors of the occurrence of cooperative breeding (Edwards & Naeem 1993; Arnold & Owens 1999). The proximate mechanism suggested to explain this correlation is that year-round territoriality limits the opportunity for independent breeding by decreasing territory turnover (Arnold & Owens 1999; Hatchwell & Komdeur 2000), forcing juveniles to delay dispersal until a vacancy arises. Interestingly, a peculiar feature of the Spanish cooperative carrion crow population is the year-round residency of the social groups in exclusive all-purpose territories (Baglione *et al.* 2002). Nevertheless, this population does not seem to be more constrained than other non-cooperative populations in Europe in terms of breeding opportunities. Some of the non-cooperative populations of carrion crows, including the Swiss one (Richner 1991), live at a very high density and up to 75% of the birds do not breed (Picozzi 1975; Loman 1985). The proportion of non-breeding carrion crows in the Spanish cooperative population is much lower (34.4%) and naturally occurring vacancies are not always immedi-

ately filled (Baglione *et al.* 2002). In our experiment, the Swiss crows that delayed dispersal were those that, after the transfer, found themselves in a less competitive environment in terms of access to territory vacancies (Spain). The importance of constrained suitable breeding vacancies in determining offspring retention (Emlen 1994) has received support from some single-population studies (Woolfenden & Fitzpatrick 1984; Komdeur 1992) but has also been severely questioned by theoretical models (Koenig *et al.* 1992; Kokko & Lundberg 2001), and the constraints model is challenged here by our experimental results.

The ecology of cooperative breeding is still far from being understood (Cockburn 1998). The environment-determined inter-population variability of the social system in the carrion crow represents a promising model to test current hypothesis, but more data are needed to identify the specific factors that drive the expression of helping behaviour in this species.

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