

Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow?

Running headline: Baglione et al. Natal dispersal in carrion crow

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Abstract

1) The ecological factors that promote delayed dispersal of offspring in cooperatively breeding bird species are poorly understood. While single population studies have supported the view that natal dispersal is delayed as a consequence of lack of suitable breeding vacancies (ecological constraints hypothesis), recent theoretical models claim that habitat saturation cannot be the main factor leading to kin sociality.

2) The carrion crow (*Corvus corone ssp*) is an ideal model to investigate the ecology of delayed dispersal. The occurrence of kin sociality is highly variable among European populations, and it is known to be determined by environmental rather than genetic factors. Here we compare juvenile dispersal, territory turnover, habitat saturation (number of competitors per breeding vacancy), variability of territory quality and territoriality of two crow populations that differ in social organization (extensive kin sociality in Spain vs social monogamy in Italy).

3) We found that philopatry occurred in the less competitive and less variable environment. A review of the information available in literature on other crow populations qualitatively supports this result.

4) In crows, juvenile philopatry seemed to be associated with breeders' year round residency in territories. This association is widespread among birds and it has been previously explained through an ecological constraints perspective, with residency slowing territory turnover and therefore augmenting saturation. Our data do not support this explanation.

5) We suggest that year round residency might play a direct role in determining kin sociality in crows. In Spain, adults occupy and defend the territory year-round, providing the offspring with a place where they enjoy a preferential access to resources that may represent an incentive to stay. Conversely in Italy, where adults

often abandon their territories after breeding, the natal site does not have any special value for the offspring that hence disperse.

Key-words: Benefits of philopatry ecological constraints, *Corvus corone*, social behaviour

Introduction

Kin societies in birds form when offspring delay natal dispersal and prolong their association with the parents. In most species living in kin groups, non-dispersing offspring forgo reproduction and usually help their parents to rear new young. Therefore, delayed dispersal is a precondition for kin-based cooperative breeding to arise.

Although the ecological factors that promote delayed dispersal have been discussed for decades (for an historical perspective of the dispute between the Habitat Saturation Hypothesis and the Benefits of Philopatry Hypothesis see Emlen 1982 and 1991, Stacey and Ligon 1991, Koenig et al. 1992, Cockburn 1996, Hatchwell and Komdeur 2000) the actual factors that drive the formation of families are still unclear. Most single-population studies on cooperative species, including elegant experiments, have detected severe constraints on independent breeding (e.g. Woolfenden and Fitzpatrick 1984, Emlen and Wrege 1989, Pruett-Jones and Lewis 1990, Komdeur 1992, Walters, Copeyon & Carter 1992) providing empirical support for the Ecological Constraints Model. This model predicts that offspring will “stay at home” when suitable opportunities for independent breeding are scarce either because of lack of vacant territories (habitat saturation) or because the variability in habitat quality is so high, that it pays to wait for a good territory instead of attempting to breed on a low

quality vacancy (saturation of high quality territories). However, the model lacks of predictive power as many non cooperative species are as constrained as the cooperative ones in term of breeding opportunities (Ekman et al. 2001), suggesting that habitat saturation might not be a key factor in determining the expression of cooperative breeding (Koenig et al. 1992, Cockburn 1996). Furthermore, the model cannot explain why, under conditions of intense competition for breeding, philopatry should be preferred to a floating strategy, where roving individuals could sample many territories and detect vacancies more efficiently (Ekman et al. 2001).

In recent years, the search for the ecological correlates of delayed dispersal and helping behaviour has moved from the generalization of single-species studies to the application of comparative analyses and mathematical modeling. Some comparative analyses seemed to confirm the essential role of habitat saturation in the expression of delayed dispersal. Arnold and Owens (1998 and 1999) showed that cooperative breeding in birds is associated with low annual mortality (but see criticism in Cockburn 2003) and year-round residency. These factors would slow population turnover, leading to an overcrowded environment that facilitates the expression of cooperative breeding (Arnold and Owens 1999; but see Hatchwell and Komdeur 2000).

Recent theoretical models suggest instead that delayed dispersal might be disjoined from the saturation of the habitat. Kokko and Lundberg (2001) showed how habitat saturation can arise either when survival of year round resident breeders is high (i.e. slow territory turnover) or when the survival of disperser increases, but the effects of these two traits in selecting the dispersal strategy are opposite. When a population saturates the habitat as a consequence of high dispersers' survival, delayed dispersal is selected against and cooperative breeding is unlikely to evolve.

While theory has developed fast in recent years, providing many new insights and fueling the debate, few empirical studies have attempted to test the new ideas. The carrion crow (*Corvus corone* L.) exhibits extreme inter-populations variation in the extent of natal philopatry and cooperative breeding. In northern Spain, crows breed cooperatively in about 75% of the territories, whereas elsewhere in Europe helpers at the nest are either rare (e. g. 6% of the territories in an urban population in Switzerland, Richner 1990) or totally absent (Baglione, Marcos & Canestrari 2002a). Despite the phylogenetic predisposition to cooperative breeding in some bird taxa, corvids in particular (Cockburn 1996), in the carrion crow it has been shown experimentally that current environmental conditions determine the expression of cooperative behaviour (Baglione et al. 2002b). This species therefore represents a good model species to further investigate the ecology of cooperative breeding. In this study we compare two populations of crows that differ in social organization and in patterns of natal dispersal and we review the information available on other well studied European populations. The aim is to test whether the observed between-populations variability is consistent with the ecological constraints model, which would predict higher habitat saturation and/or higher variability in the territory quality in the cooperative population. Subsequently, we examine the hypothesis put forward by comparative analyses and theoretical models that year round residency is, compared to habitat saturation, a better predictor of the occurrence of delayed dispersal than is habitat saturation (Arnold and Owens 1998 and 1999, Kokko and Lundberg 2001).

Methods

Study areas

We studied two different crow populations, one in northern Italy (1989-1991 and 2001, 2002) and one in northern Spain (1995-2003). In Italy we studied non cooperative crows at two different agricultural sites, 10 km apart (45°N, 9°E). The two areas (10 km² each) were similar, with a flat landscape dominated by rice fields, maize and, to less extent, meadows. Agriculture was intensive, with fields irrigated regularly and natural vegetation confined to the shores of irrigation canals. Crows nested in poplar tree (*Populus sp* L.) plantations or in small patches of relict oak (*Quercus robur* L.) forest, with similar breeding densities at the two sites (6.3 and 6.2 pairs /km²). Crows in Italy are socially monogamous, and non breeders live year-round in non territorial flocks. Occasional observations (n = 2, 6% of observed territories) of a “third bird” in a territory have been reported (Baglione et al. 2002a, Baglione V. unpublished data), but the helping role of those crows could not be confirmed.

The habitat in rural northern Spain (42°N, 5°W) was markedly different, with low intensity agricultural use (no irrigation) and a mosaic of crops (mainly wheat and oat), meadows, uncultivated land for grazing of sheep and cattle, and oak (*Quercus pyrenaica* Willdenow) forest patches. Here 75% of crow territories are held by cooperative groups of up to nine individuals (mode 3 birds). Extra birds are either non-dispersing offspring that stay with their parents on the natal territories or immigrants that form coalitions with resident territorial birds. Groups may have up to three helpers involved in feeding the nestlings (for details on the Spanish crow society see Baglione et al. 2002a).

Dispersal

Nestlings were banded with wing tags and coloured rings when they were about to leave the nest (28-32 days old). The banded juveniles ($n = 79$ in Italy, $n = 188$ in Spain) were followed within the study areas and the surrounding landscape. We visited the territories at least once a week during the first 5 weeks after offspring had fledged, when they still depend on their parents (Cramp and Perrins 1994), and thereafter at least once a month until the following breeding season. We concentrated the search for dispersing young on communal feeding grounds and communal roosts. To determine whether the behavior of the parents played a role in provoking offspring dispersal in Italy, we surveyed 5 crow families until the offspring dispersed in 2002. We observed families for 30-60 min at least once a week for five weeks after fledging in order to document any evidence of parental aggression towards offspring.

Habitat saturation

We measured habitat saturation in Italy and Spain as number of competitors per breeding vacancy arisen in a year time span (Kokko and Lundberg 2001). To do so in the two populations, we collected data on the number of individuals competing for territory vacancies and the proportion of breeding vacancies available for each year of study.

Both in Italy and Spain, we searched all new nests at the beginning of the breeding season. Afterwards, regular surveys allowed the detections of any late nesting attempts. We used different methods to estimate the number of non territorial crows of the two populations. In 1989, 2001 and 2002 we counted crows in the Italian study areas at least three times throughout the breeding season, following a standard itinerary with a car. The extreme structural simplicity of the landscape allowed a very

accurate bird census. We also surveyed the surroundings of the study sites, where we commonly observed other stable flocks of floaters. As same-year bird counts within the study plots gave almost identical results (variation between 1 and 3%), we believe that we assessed the actual number of birds settled within the study sites and that our censuses were not inflated by individuals occasionally coming from elsewhere. We therefore regarded the maximum number of crows observed during the censuses as the number of crows living on the study areas. The number of potential competitors for territories was obtained by subtracting $2 \times$ number of active nests from the total number of individuals.

In Spain, floaters were a negligible component of the studied population during the breeding season (Baglione et al. 2002a). Small flocks of floaters were observed only twice within the study area in five years (9 and 13 individuals respectively). Almost all individuals that do not own a territory either lived on their natal territory or immigrated to a new territory, where they associated with the resident birds. The total number of potential competitors for territory vacancies was therefore obtained by counting the extra-birds in the territories. To do so, we have recorded the group size of every territory since the beginning of our study. For 64-79% of territories we assessed group size every year by observing the territories from a favorable spot for at least three hours (for details see Baglione et al. 2002a). In the remaining territories we obtained group size when we visited them for routine data collection (eggs laying sequence, nestlings' growth, fledgling dispersal). Since group members usually form a cohesive group, those short visits to the territories (15 - 30 minutes) provided reliable information on group size.

Population's sex ratio was known both in Spain (Baglione et al. 2002a) and in Italy, where it was derived from a large sample of adult crows ($n= 121$) that had been

caught as part of provincial administration's pest management programs (see Acquarone, Cucco & Malacarne 2001). The sex ratio of non-breeders was derived from the population sex ratio, allowing assessing habitat saturation for each sex separately in both populations (Tab. 1).

To measure the proportion of breeding vacancies available each year, we caught free-flying crows in 1999 and 2000 in Spain ($n = 61$), and in 2001 and 2002 in Italy ($n = 41$; see Baglione et al. 2002a for details on trapping system). Crows were banded with wing tags and an individual code of coloured rings and blood samples were collected. P2/P8 DNA-based identification (Griffiths et al. 1998) provided the sex of the carrion crows (for details on blood samples storage and DNA extraction see Baglione et al. 2002a and 2002c).

In Italy, in the first days after banding, we observed crows with binoculars and spotting scopes until we saw them providing food to the nestlings. We therefore regarded them as breeders of that particular territory. In Spain, captured crows were more easily assigned to a specific territory, due to the virtual lack of floaters and to the scattered distribution of the territories (Marcos and Baglione 2003), and breeding status was assigned according to a parentage analysis based on 8 polymorphic microsatellite loci (see Baglione et al 2002c for details). In both populations we considered that a breeding vacancy arose when a breeder disappeared from a territory before the commencement of the breeding season. In Spain, in groups where reproduction was shared, we considered that a vacancy arose when the alpha-breeder disappeared. As almost all vacancies were later occupied by new territorial crows in both sites (100% in Italy, $n=15$; 87% in Spain, $n=15$), the proportion of breeding vacancies approximated the actual turnover of individuals in the breeding territories. Therefore for simplicity, we'll refer to this datum as "territory turnover" hereafter.

The fate of the breeders that disappeared from the territories was unknown in most cases. Two individuals, one in Italy and one in Spain, were found dead. One Spanish male immigrated to another territory, probably after usurpation of his own territory, and one breeding female in Italy joined the non-breeding flock after her mate had disappeared. The lack of resightings during our regular surveys of the study areas, roosts, and communal feeding grounds suggests that most of the missing individuals had died.

Variability of territory quality

We defined the variability of habitat quality as among-territories coefficient of variation (CV) of the number of fledglings produced in a number of territories over the study period (according to Stacey and Ligon 1991). We measured the productivity of 19 territories in Italy and 20 territories in Spain over three (1988, 1989, 1991) and five years (1995-1999) respectively, considering only those territories that could be recognized unequivocally throughout the study period (Baglione et al. 2002c). The difference between the CVs was tested according to Sokal and Braumann (1980). To ensure that the result was not influenced by the different duration of the sampling periods at the two study sites, we also calculated the Spanish CV on the productivity of territories in periods of three consecutive years (1995-1997, 1996-1998 and 1997-1999) and compared the results.

When helpers have a positive effect on reproductive success, the CV of productivity of the territories can be a biased index of the variation of habitat quality because the difference between territories might be overestimated. Better territories produce more young that will become helpers, which will further enhance the productivity and therefore also the difference with less successful territories. This

potential bias may inflate the calculation of the CV only in Spain, where crows are cooperative, but this is conservative with respect to the conclusions of this paper (see discussion).

Territoriality

We used two different methods to determine the shape and the overlap of the breeding territories in the two populations. Method A: we assessed territory shape by following crows' feedings trips to the nest and mapping the location where they landed to resume foraging activity. Since crows attend only one nest, this method guaranteed that we always followed the crows belonging to the territory we were interested in, even when such birds were unbanded. Observations were collected for at least 9 hours in three different bouts (three hours each) for each territory. Such a sampling effort guarantees an accurate measurement of territory size (Spray 1978) in crows. In this way, we sampled 22 territories in Spain (from 1995 to 1998) and 12 territories in Italy (1989). Method B: in territories where adult crows were banded, we mapped their position each time we visited the territory. We selected for analysis only those territories where we collected a number of locations corresponding at least to the minimum number of locations per territory taken with method A ($n = 27$), i.e. 19 territories in Spain, sampled in 1999 and 2000, and 11 in Italy in 2000 and 2001.

Territories were defined as the minimum convex polygons among 95% localizations of territory holders (Kenward 1987). Within areas, territory size did not significantly differ between years (Spanish territories, Kruskal-Wallis non parametric ANOVA, $H = 6.64$, $df = 5$, $p = 0.25$; Italian territories, Kruskal-Wallis non parametric ANOVA, $H = 1.0$, $df = 2$, $p = 0.32$) nor between sampling methods (Spanish territory, Kruskal-Wallis non parametric ANOVA, $H = 3.42$, $df = 1$, $p = 0.06$; Italian

territories, $H = 1.00$, $df = 1$, $p = 0.32$). For each pair of adjacent territories (a and b for example) we calculated the overlap as: surface shared / (surface a + surface b). We used this value as measure of territory overlap, because we could not always assess for each territory the actual surface shared with all the neighbors (some of which had not been sample in most cases). Since some territories contributed to more than one datum, we based the statistical analysis of territory overlap on a randomization (Manly 1991). We randomized the samples 1000 times, resampling the data without replacement, and calculated the t -statistic at each step, using Pop Tools 2.6 (available on the internet www.cse.csiro.au/poptools). The proportion of times the randomized t -values exceeded the actual t -value represents the p value of this test.

Thirty territories sampled in Spain were surveyed year-round to assess the degree of residency of territory holders and the rate of intrusion of conspecifics. We visited the territories at least twice a week during the breeding period (15th of March – 15th of July) and once a month outside the breeding season, recording the presence of territory holders and intruders. Group size was known for all those territories, and all the groups contained at least one banded individual (one or more retained offspring in 22 territories, adults and retained offspring in 8 territories). Since crows in Spain form cohesive and stable groups and retained offspring always associate with their parents on their natal territory (Baglione et al. 2002a), the consistency of group size and the presence of retained offspring reliably indicated the presence of the territory holders on the territory. This made possible to survey also territories where some group members were unbanded (22 territories). Conversely in Italy, reliable information on year round residency of territory holders and rate of intrusion could be collected only on territories where at least one of the breeders was banded (11 territories).

Results

Juvenile dispersal

During the five weeks after fledgling, a conspicuous proportion of banded fledglings (40% and 45% in Spain and Italy respectively) was not resighted on their natal territories, with no significant difference between the two populations (Fig. 1). At this stage, crow fledglings still depend on their parents (Cramp and Perrins, 1994; Baglione, Pieri and Bogliani 1994), suggesting that those that were not resighted had probably died. By the age of 81 – 90 days and thereafter, the proportion of fledglings remaining on their natal territories was significantly higher in Spain than in Italy. In Spain, this proportion declined steadily until the next breeding season, when 28% of the banded fledglings were still “at home”, acting as helpers in most cases (on average 71% of non dispersing yearlings help at the nest, Canestrari unpublished data). Conversely in Italy, already at the end of their first summer, no fledglings were longer associated to their natal territory. Dispersal was confirmed for 11 Italian juveniles, which were observed joining large flocks of non-breeders and foraging on communal feeding sites within the study area after dispersal. None of them returned to the natal territory thereafter.

Our observations did not suggest parental aggression as a mechanism of offspring dispersal in Italy. In the five territories surveyed in 2002 (828 min in 31 bouts distributed among 45 days, covering a range of ages of the offspring between 30 and 77 days), the parents never showed any aggressiveness toward their offspring. After the first 4 weeks they ceased feeding them and thereafter merely ignored their begging. It must be noted that detecting offspring eviction in the field might be difficult. However, our data are supported by previous less standardized observations carried out in 1989-1991 (Baglione and Bogliani, unpublished data), which also

suggested that parental aggressiveness is negligible in determining the dispersal decision of the offspring in the Italian population.

Habitat saturation and variability in territory quality

In Spain the percentage of individuals potentially competing for territory vacancies averaged 39.8% between 2000 and 2002 (range 38.5 - 41.4%, Tab. 1). In 1999, such a percentage was 31.9. In Italy 55.8% and 58.4% of the total population of the study area did not own a territory in 2000 and 2001 respectively (in 1989 the percentage was 65.9). Even though Spanish males seemed to be less likely to disappear from their territories than Italian males (Tab. 1), the turnover of breeders did not significantly differ between the two populations (Fisher exact test; males, $p = 0.5$; females, $p = 0.76$; both sexes, $p = 0.27$). The number of competitors per breeding vacancy (habitat saturation) was consistently higher in Italy than in Spain for both sexes (Tab.1), with the exception of females in 2002.

The two study sites did not differ significantly in term of variability of territory quality. The coefficients of variation of fledglings' productivity of territories in Spain (76.1; $n = 20$) was lower than in Italy (98.4; $n = 19$), but the difference was not significant ($F_{19,18} = 1.54$; $p=0.18$). The result did not change qualitatively when we equated the sampling periods of the two sites. The CVs obtained for three periods of three consecutive years in Spain (72.6 in 1995-1997; 78.7 in 1996-1998 and 105.1 in 1997-1999) did not significantly differ from the Italian CV.

A review of crow's studies carried out in Europe supports the view that high saturation might be disjoint from the occurrence of delayed dispersal and cooperative breeding. Table 2 shows how other non cooperative crow populations in Europe are characterized by a high proportion of non breeding individuals, which are comparable

to that of the Italian population. Despite estimates of H in terms of competitors per breeding vacancies are not available for those populations, such high numbers of non breeders suggest that co-occurrence of strong saturation and lack of cooperative breeding is widespread among European crows. Tab. 2 also suggests that the expression of delayed dispersal is not restricted to the subspecies *Corvus corone corone*. Offspring retained in the natal territory beyond the first winter have been described to occur occasionally in the Swedish *C. c. cornix* population (Loman 1985). Furthermore, *C. c. cornix* shows variability in the timing of dispersal comparable to that of non cooperative populations of *C. c. corone* (typically from a few weeks after fledglings to the end of the first winter; see Cramp and Perrins 1994 for a review). This indicates that *C. c. cornix* also possesses the capacity to adjust dispersal to current conditions and that our results are not biased by considering both subspecies.

Territoriality

Crows' mean territory size differed between the two study sites (Mann-Whitney U test, $U = 234$, $p = 0.001$), being larger in Spain (average \pm SE = 0.13 ± 0.01 km², $n = 41$) than in Italy (0.08 ± 0.01 km², $n = 23$). Adjacent breeding territories only marginally overlapped in Spain (average proportion of overlap \pm SE = 0.01 ± 0.01 , $n = 14$), while in Italy the proportion of surface that two neighbours share (0.1 ± 0.03) was significantly higher (randomisation test, $p = 0.001$). By considering all the neighbours, where possible, we found that a pair in Italy could share up to 70% of its territory with other pairs.

Crows in Spain showed a significantly higher rate of year round territory occupancy (i.e., for each territory sampled, the number of times that the territory owners were found "at home" divided by the total number of surveys; Mann-Whitney

test, $U = 21$, $p < 0.01$; Fig. 2a), which did not correlate significantly with the size of the group that held the territory (Spearman $R = 0.16$, $n = 30$, $p = 0.42$). Conspecific intrusion rate (measured, for each territory, as the number of times that at least one crow intruder was found foraging on that territory divided by the total number of surveys) was lower in Spain than in Italy, both in the breeding and non breeding period (Mann-Whitney test, breeding $U = 38$, $p < 0.01$; non breeding $U = 12$, $p < 0.01$; Fig. 2b). In Spain, we found a marginally non-significant positive correlation between group size and intrusion rate in the breeding season (Spearman $R = 0.3$, $n = 40$, $p = 0.06$) but not in the non breeding period (Spearman $R = 0.18$, $n = 30$, $p = 0.36$).

Discussion

Although the role of ecology in the expression of cooperative breeding has been a central issue in behavioral ecology for decades, it still represents an unresolved puzzle. The widespread acceptance of the “ecological constraints model” (Emlen 1994) has been attributed more to its broad and unspecific definition of constraints (Hatchwell and Komdeur 2000, Kokko and Ekman 2002), rather than to its actual predictive power, which is in fact very low (Cockburn 1996). The model identifies habitat saturation, lack of potential mates, costs of dispersal and lack of high quality territory as factors that prevent natal dispersal. As most avian species face one or more of these “constraints”, easy *post hoc* explanations that apply to almost any cooperative society have created the illusion of a high explanatory power of the model. In this paper we restricted the definition of constraints to habitat saturation, which is thought to be the most widespread cause of kin sociality among birds, and is certainly the most debated. Hereafter, the term “constraints” will refer to habitat saturation only.

Habitat saturation, variability of territory quality and geographic patterns of natal dispersal in crows

Recent theoretical models have proposed that delayed dispersal is disjoint from habitat saturation and that cooperative breeding can evolve in absence of such a constraint (e.g. Kokko et al. 2001, Perrin and Lehmann 2001, Kokko and Lundberg 2001), but only a few studies, reporting on species living in apparently unsaturated habitats, seem to support this view (Caffrey 1992, Macedo and Bianchi 1997, Williams, Lawton & Lawton 1994). However, as the suitability for breeding of unfilled vacancies is difficult to prove, such data offer only a weak support to the new theory. On the other hand, most studies on the relationship between habitat saturation and delayed dispersal have failed to show causation (Hatchwell and Komdeur 2000), and experimental evidence is restricted to single population studies, which leave uncertainty about the role of constraints in determining differences across species or populations. In this respect, the environmentally determined geographic variation of the social behaviour of the carrion crow represents an ideal model to assess the actual role of habitat saturation in shaping avian social systems.

Our findings contradict the expectation of the ecological constraints model (Table 3). The habitat turned out to be consistently more saturated in Italy, where crows are not cooperative, than in Spain, especially for crow males, which are more likely to help at the nest (Baglione et al. 2002a). It might be argued that a comparison of only two populations might be randomly biased and that therefore represents an inconclusive test of the model. However, the review of data published on other European crow populations supports our conclusions by showing qualitatively a widespread lack of association between high saturation and occurrence of cooperative breeding.

The ecological constraints model predicts lack of delayed dispersal in homogeneous environments, regardless of the saturation of the habitat. When territories do not differ in quality, “staying at home” does not offer any advantage to the offspring in terms of future reproduction (i.e. by queuing a juvenile does not get a better territory) or can also be detrimental, if philopatric individuals miss a vacancy elsewhere (Stacey and Ligon 1991, Emlen 1994). A relative higher homogeneity of the habitat in Italy (i.e. lower CV, see methods) might have therefore reconciled our results with the ecological constraints model. Nevertheless, our data again showed the opposite pattern, namely the quality of territories was more variable, although not significantly, in Italy than in Spain (Tab. 3). Furthermore, our data cannot be reconciled with the interpretation of ecological constraints suggested by Arnold and Owens (1998), where a slow turnover of breeders (high survival) represents the permissive factor to cooperation to arise, as it leads to the saturation of the habitat. In crows, the slowest territory turnover is associated with the lowest saturation, showing that the relationship between the two factors is not as straightforward as previously thought.

Kokko and Lundberg (2001) showed theoretically how the alternative demographic routes that lead to saturation, i.e. high survival of resident individuals or high survival of migrants/dispersers, have contrasting effects on the expression of delayed dispersal (the former favouring it, the latter selecting against). In crows, average residents' survival seems to be higher in Spain than in Italy, especially in males (males: 80.6 vs 72.7% respectively; females: 66.7 vs 64; both sexes: 75% vs 68%; derived from Tab. 1), although the difference was not statistically significant. More data are needed to assess how saturation is achieved in Italy and in Spain, and in particular to estimate survival of dispersers in the two populations. However, to the

extent we could explore it, the crow system seems to fit into Kokko and Lundberg's theoretical framework.

The role of year round territoriality

In 1987, Brown already noted that cooperative breeding in birds is especially common among year-round territorial species. More recent comparative analyses have shown that year round territoriality is correlated with the expression of delayed dispersal and cooperative breeding (Arnold and Owens 1998 and 1999). Such a link seems to exist in the crow as well. The Spanish cooperative crows showed a significantly higher degree of year round residency in the territories than Italian non cooperative crows. Furthermore, unlike in Italy, territories in Spain are used exclusively by their owners both during the breeding and non breeding season. Information on territorial behaviour of other European populations (Tab. 2) is not fully comparable to that presented in our study, as data were collected in different ways. However, at least qualitatively, the review presented in Tab. 2 suggests that year round residency is peculiar of cooperative populations.

Arnold and Owens (1999) interpreted the correlation between year-round territoriality and the occurrence of delayed dispersal under an ecological constraints perspective. Year-round territoriality would act by slowing territory turnover, which in turn would limit further the opportunities for independent breeding (saturation) eventually leading to natal dispersal to be delayed. Our data do not support this view, as year round residency of the Spanish population is not associated with a higher degree of saturation. Instead, the low residency of Italian crows might reflect the benefit of a floating strategy for both adults and juveniles during the non breeding period in those areas. Under these conditions, Kokko and Lundberg's model predicts

high degree of habitat saturation and lack of kin sociality to co-occur in the populations, which is what we have observed.

We suggest that year round residency might have a more direct role in the expression of delayed dispersal in crows because it confers intrinsic benefits to natal philopatry. The “safe haven hypothesis” (Kokko and Ekman 2002) suggests that the presence of parents makes the natal territory a special place for juveniles, which gain access to defended resources and sometimes protection against predators (Ekman, Sklepkovych & Tegelström 1994, Pravosudova, Grubb & Parker 2001, Kraaijeveld and Dickinson 2001, Griesser 2003). This hypothesis explains the correlation between year round territoriality and delayed dispersal in birds without attributing any role to habitat saturation, and predicts that juveniles will disperse early in life either when parents cannot afford prolonging the care of their offspring or where they switch to non-territorial behaviour after the breeding season, allowing free competition for resources within their home range. Crow parents are tolerant towards their offspring both in Italy in Spain, but, as a consequence of lack of territoriality during the non breeding season, young crows in Italy do not have any incentive to stay at home. Therefore, it might be the case that the ecological factors that promote year round residency in crows (e.g. predictability and defensibility of trophic resources, which are currently under investigation), are the ones that ultimately shape the social organisation.

An alternative explanation might be that living in kin groups allows the crow to defend the territories year round, and that therefore the social system is the cause of the observed pattern of geographic variation in territoriality. However, this seems to be unlikely as Spanish unassisted pairs also live in the territories year-round and we

found no effect of group size on either the occupancy rate of territories or the frequency of conspecific intrusions in Spain during the non breeding period.

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Figure legends

Fig. 1. Proportions of banded offspring remaining on their natal territory throughout their first year in Italy and Spain. Differences were tested with Yates corrected χ^2 adjusted to multiple tests by applying the sequential Bonferroni correction (Holm 1979). Asterisks indicate $p < 0.05$.

Figure 2. a) Territory occupancy rate during the non breeding period in the two populations studied; b) Territory intrusion rate during the breeding and non breeding season.

Table 1. Territory turnover, percentage of individuals competing for territory vacancies in the population and habitat saturation (number of competitors per breeding vacancy) in Spain (2000-2002) and Italy (2001 and 2002).

Year	Turnover (%) (No. of individuals)		Percentage of indiv. competing for vacancies ¹	Sex ratio population $\sigma\sigma : \text{♀♀}$	Habitat saturation (H_0) ¹		
	$\sigma\sigma$	♀♀			$\sigma\sigma$	♀♀	
Spain	2000	20.0 (10)	28.6 (7)	39.8	4.7	1.3	
	2001	20.0 (15)	45.5 (11)	41.1	1 : 0.67	5.0	0.9
	2002	18.2 (11)	16.7 (6)	38.5		4.8	2.3
Italy	2001	22.2 (9)	37.5 (8)	55.8	1 : 0.61	8.1	2.0
	2002	30.8 (13)	37.5 (16)	58.4		6.5	2.2

¹ the proportion of sexes among non breeders was derived from the sex ratio in the population as: proportion of non-breeding males = (proportion of males in the population – 0.5 × proportion of breeders) / proportion of non breeders; proportion of non-breeding females = 1 – proportion of non-breeding males.

Table 2. Proportion of non breeders, occurrence of cooperative breeding and territorial system in well studied European crow populations.

Study area	Subspecies	Breeding density (pp/Km ²)	Percentage of non-breeders	Occurrence of helper at nest	Territorial system	Reference
Northern Spain	<i>Corvus c. corone</i>	2.0	38.5 – 41.1 %	75 % of territories	year-round territoriality	This study
Northern Italy	<i>Corvus c. cornix</i>	6.5	55.8 - 75 %	0 % ¹	Undefended home ranges	This study Bogliani et al., 1994
Switzerland, Zurich airport and surroundings	<i>Corvus c. corone</i>	2.0 – 3.0	Unknown	0%	Estimated maximum occupancy rate during non breeding season = 0.15	Griesser, unpublished data
Switzerland, rural area	<i>Corvus c. corone</i>	6	“high”	0 %	Territories defended only during the breeding season	Richner, 1989
Switzerland, urban area	<i>Corvus c. corone</i>	36	53 - 66 % ³	6 %	year-round territoriality	Richner, 1989 and 1990
Southern Sweden	<i>Corvus c. cornix</i>	1.9 - 2.5	77 % ⁴	0 % ²	Territories abandoned in summer and reoccupied in spring	Loman, 1985
Scotland	Both	2.3 - 3.0	50 - 73 %	0 %	Territories defended only during the breeding season	Picozzi, 1975 Charles, 1972
Germany	<i>Corvus c. corone</i>	3	33 - 42 %	0 %	Territories abandoned in summer and reoccupied in late autumn; undefended in winter	Wittemberg 1988

¹ “Third bird” in two territories, helping role unclear.

² Offspring occasionally retained at home for 1 year.

³ Calculated from Richner, 1990

⁴ Calculated from Loman, 1985 (referred in Cramps and Perrins, 1994).

Table 3. Ecological constraints model's predictions *versus* observed patterns of territory turnover, habitat saturation and variability of territory quality in the two studied crow populations, according to the fact that crows delay natal dispersal and help at the nest only in Spain.

	Ecological constraints hypothesis (according to Emlen 1994)	Ecological constraints hypothesis (according to Arnold and Owens 1998)	Observed
Territory turnover	No specific prediction	Slower in Spain than in Italy	Slower in Spain than in Italy (ns)
Habitat saturation	Higher in Spain than in Italy	Higher in Spain than in Italy	Higher in Italy than Spain
Variability in territory quality	Higher in Spain than in Italy	No specific prediction	Higher in Italy than in Spain (ns)

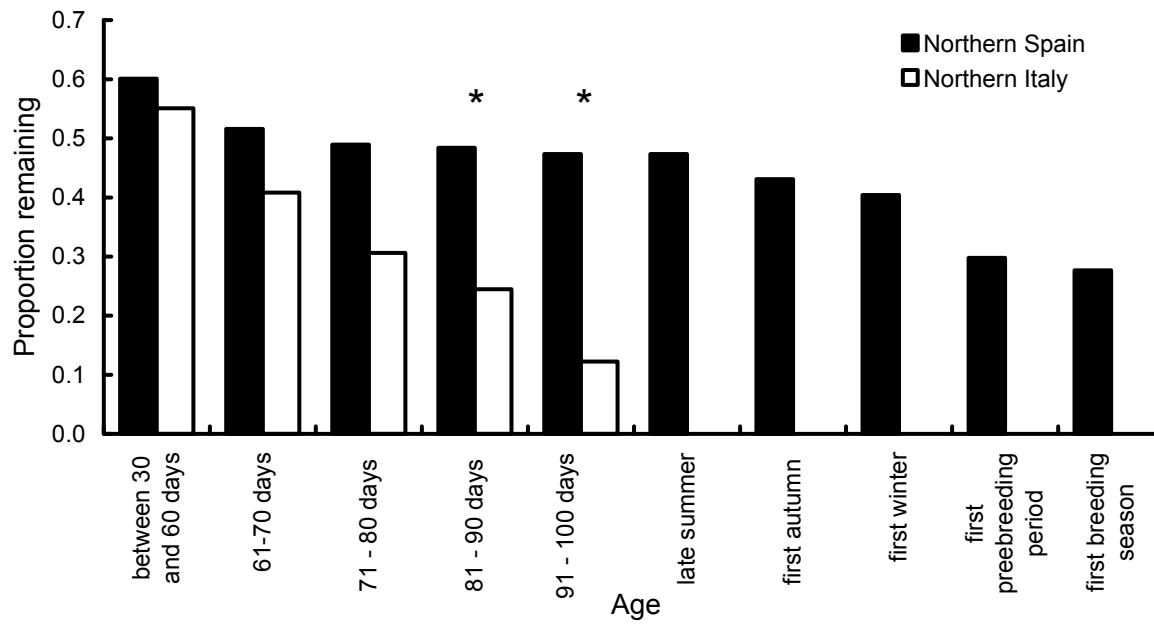


Figure 1

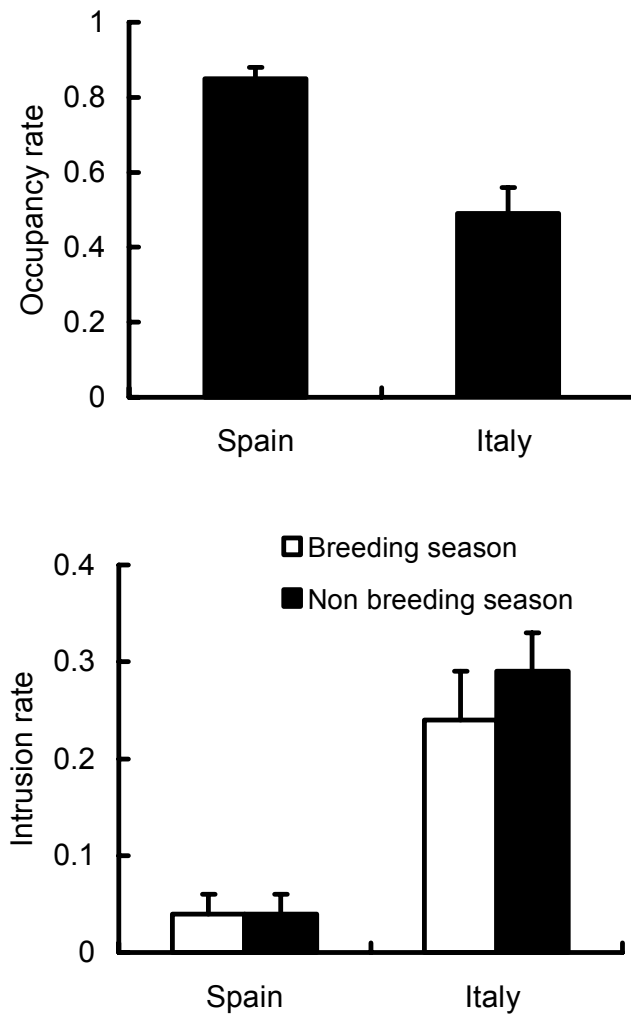


Figure 2