

Linking territory quality and reproductive success in the chough (Pyrrhocorax pyrrochorax): implications for conservation management of an endangered population

Christian Kerbiriou, Françoise Gourmelon, Frédéric Jiguet, Isabelle Le Viol, Frédéric Bioret, Romain Julliard

▶ **To cite this version:**

Christian Kerbiriou, Françoise Gourmelon, Frédéric Jiguet, Isabelle Le Viol, Frédéric Bioret, et al.. Linking territory quality and reproductive success in the chough (Pyrrhocorax pyrrochorax): implications for conservation management of an endangered population. Ibis, 2006, 148 (2), pp.352-364. 10.1111/j.1474-919X.2006.00543.x . hal-02554709

HAL Id: hal-02554709
https://hal.science/hal-02554709

Submitted on 26 Apr 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Linking territory quality and reproductive success in the chough (*Pyrrhocorax pyrrochorax*): implications for conservation management of an endangered population

KERBIRIOU Christian, Centre d'Etude du Milieu d'Ouessant 29242 Ouessant FRANCE / UMR 5173, Muséum National d'Histoire Naturelle, CRBPO, 55 rue Buffon, 75005 Paris, France.
e-mail : kerbiriou@mnhn.fr

GOURMELON Françoise, Equipe Géomer (UMR 6554 CNRS – LETG), Institut Universitaire Européen de la Mer (Université de Bretagne Occidentale), 29280 Plouzané, France

JIGUET Frédéric, UMR 5173, Muséum National d'Histoire Naturelle - CRBPO, 55 rue Buffon, 75005 Paris, France

LE VIOL Isabelle, UMR 5173, Muséum National d'Histoire Naturelle, CRBPO, 55 rue Buffon, 75005 Paris, France.

BIORET Frédéric, Equipe Géomer (UMR 6554 CNRS – LETG), Institut Universitaire Européen de la Mer (Université de Bretagne Occidentale), 29280 Plouzané France

JULLIARD Romain, UMR 5173, Muséum National d'Histoire Naturelle, CRBPO, 55 rue Buffon, 75005 Paris, France.

Keywords : territory quality, *Pyrrhocorax pyrrochorax,* Core-weighting kernel method..

Words :

SUMMARY

As changes in land uses have been mentioned as the main factor to explain decline of chough population across western Europe, a study was carried out in Ouessant (western France) in order to link territory quality with reproductive success. As such an approach could be hindered by the fact that reproductive performance of birds could be influenced by their breeding experience, we analysed both inter- and intra-nest site variation in fledging success. Territory quality was quantified combining habitat selection, territory size, amount of feeding area and distance between nest and feeding area.

Feeding habitats positively selected by chough were characterized by a mean sward height lower that 5cm. Foraging area was on average of 21,557 m². Feeding areas (ie. feeding habitat within foraging area) close to the nest were preferentially used. Fledging success appeared not to be influenced by the total area of feeding areas in chough territory, nor by the mean feeding flight distance. But fledging success adjusted to nest site and year appeard to be influenced by feeding area close to the nest : one additional fledging was expected for each additional 10,000 m² of feeding habitat within 300m of the nest. These first results bring elements which allowed us to consider recommend landscape management measures to ensure a favourable conservation status of local chough populations.

INTRODUCTION

Habitat loss and damage linked to changes in agriculture practices are the most frequently reported threats affecting European birds species (Baillie et al. 2001, Bignal & McCracken 1996, Pain & Pienkowski 1997, Newton *et al*. 1990, Shrubb 1993, Tucker 1993, Tucker & Heath 1994, Newton 2004, Gregory *et al* 2004). European agriculture has been intensified drastically in recent decades although, paradoxically, agricultural abandonment has also

occured as an indirect effect of intensification, as some marginal lands became less profitable to farming and are therefore set aside (Bignal 1991, Blanco *et al.* 1998). In order to ensure favourable conservation status for threatened bird species in Europe, the European Commission requires member states to designate Special Protection Areas – SPAs- to protect endangered habitats and species, especially for birds listed in the Directive of the council of the European Community on the conservation of wild birds (Directive 79/409/CE). As most European areas are directly or indirectly concerned by agricultural practices, such conservation measures also receive support from EU countries through management agreements under the agri-environment regulation (EC reg. 1765/92) of the Common Agricultural Policy. The efficiency of the conservation planning emerging from such agricultural policy should be determined by comparing ecological knowledge on population dynamics and the corresponding effects of habitat management. (Barber et al 2001, Davis 2005, Driscoll *et al.* 2005, Rodewald & Yahner 2001),

This is particularly the case for the chough (*Pyrrhocorax pyrrhocorax*), a species listed in Annex I of the European Community Birds Directive. Its populations are scattered and most of them show long-term decline. Many studies have highlighted the ecological needs of the chough in low-intensity farmland habitats, such as undisturbed rough grass and short grazed pasture (Warnes 1982, Mc Cracken *et al.* 1992, Rolando *et al.* 1994, Bignal *et al*. 1995, Robertson *et al.* 1995, Blanco *et al.* 1998, Madders *et al.* 1998, Whithead *et al.* 2005). In addition, local population trends have been linked to a range of factors such as weather conditions (Owen 1989, Reid *et al.* 2003a), human persecution (Owen 1989) and, chiefly, grazing pressure (Bullock et al. 1983, Cullen 1989, Owen 1989, Berrow *et al.* 1993, Cook *et al.* 2001 , McCanch 2000). In general, population declines are believed to be due to changes in land use of agricultural landscapes, such as farming intensification or the loss of grazing practices (Rolfe 1966, Garcia-Dory 1989, Mc Cracken *et al.* 1992, Meyer *et al.* 1994,

Dendaletche 1991, Blanco *et al.* 1998, Kerbiriou 2001). However, we still have little knowledge of possible processes driving these declines in terms of population dynamics, and only a handful of studies have directly examined habitat characters affecting demographic parameters (McCanch 2000, Reid et al. 2003a, Reid et al. 2003b). A major long-term study of individually-marked chough, carried out on Islay (United Kingdom) has highlighted the consequences of environmental variability (as temperature and rainfall variations during the pre-breeding season) on demographics parameters such as fledging success, first-year survival and individual life-time reproductive success (Reid *et al.* 2003a.).

It is puzzling that the main study available about demographic process affecting the short term populations dynamics has shown that the most important explanatory factor is natal weather conditions, (Reid et al. 2003a), whereas at the population level, the main external factor cited to explain population trends is change in land use.

Such differences between conclusions of studies based on distribution and abundance and studies based on demographic parameters are probably explained by the focus of the latter on short-term inter-annual variations, while habitat variation occurs at a longer time scale.

A way to solve this apparent paradox would be to link spatial variation in demographic parameters among breeders and variations in territory quality. Choughs need cavities for nesting and short vegetation for foraging. We predicted variations in territory quality among different breeding pairs according to these parameters. We quantified territory quality combing estimation of foraging area and feeding habitat, taking account distance to the nest. We then studied variation in breeding success in relation with our measure of territory quality. We used our result to suggest landscape management recommendations for chough based on these analyses

METHODS

The biological model

The red-billed chough is a medium-sized corvid with a patchy distribution throughout its European range. The estimated minimum European population size is 16,000 pairs, confined to remote areas mostly in mountains and along coasts. Over half of this population is concentrated in Spain, Greece and Italy, while most other populations are small and declining (Tucker and Health 1994). This scattered distribution results from the ecological needs of the species, involving a combination of suitable nesting sites (shallow caves in cliffs) and suitable foraging areas (short grassland vegetation with low cover; Roberts 1983, Farinha & Teixeira 1989, Rolando *et al.* 1994, Bignal *et al.* 1997, Blanco *et al.* 1998, Whithead *et al.* 2005). The small Western French population is confined to very few localities in Brittany, and appears to be one of the smallest cluster and the most isolated population in Western Europe (Tucker and Heath 1994, Kerbiriou 2001). It suffered a large decrease after the 1960s, from probably 100-150 to about thirty pairs two decades later. Currently, this population seems to be stabilised at a low level of 39-55 breeding pairs (Kerbiriou *et al.* 2005). These birds are highly faithful to site and mate, they breed once each year and they rarely skip breeding years as observed elsewhere (Roberts 1985, Bignal et al 1997, Reid *et al.* 2003a).

Study area

Our study was conducted on the island of Ouessant, a small island (1,541 ha) 20 km from the western tip of Brittany, France (48°28'N , 5°5' W). It shelters one of the cores of the Brittany chough population (Kerbiriou 2001), with an average of 13 breeding pairs. Important land use changes occurred on the island after the decline of the human population since the beginning of the 20th century. This led to a complete disappearance of crop farming, a drastic decrease in grazing pressure (sheep numbers decreased from 5,900 in 1950 to 650 in 2003). Pastures were

formerly located along the coastal strip, but moved inland closer to human settlements, while crop abandonment and low grazing pressure created fallow lands, dominated by bracken (*Pteridium aquilinum*) and brambles (*Rubus fructicosus*) which now occupy more than half of the island area (Gourmelon *et al.* 2001).

Vegetation coverage

A vegetation map was created using field plotting and aerial ortho-photograph (IGN 2002) interpretation, implemented in a Geographical Information System (Arc-Info, Environmental Research System Institut Inc). Chough feeding habitats were categorized according to vegetation cover, vegetation height and floral composition. Seven habitat classes were determined (Table 1). As paths could not be accurately digitalised directly from aerial photographs, they were first defined as lines. In a second step, field measurement of path width were made, as well as a recording of their eventual vegetation cover. A polygon cover of paths was then created as a buffer along the path linear cover using data on path width and state. The final chough habitat cover was obtained by up-dating the vegetation cover with the polygon path cover. Except for restored habitats, changes in coastal vegetation can be considered as insignificant during the study period (1998-2003), most habitats (heathland, short and rocky vegetation, grassland...) evolve slowly or even not at all, and could be considered as perennial vegetation. Restored habitats were located at the south west tip and account for a small area (77,466m², i.e. 2.9 % of coastal vegetation).

Chough survey and focal sampling of behaviour

To allow the study of reproductive performance variation among breeding pairs, all nests (about 12 per year) were found and the number of fledged offspring was recorded yearly from 1998 to 2003 for each pair.

We wanted to assess distribution of foraging habitat within the territory used by a pair during the breeding period. We conducted each year several survey sessions for each pair during the breeding period (mid April to early July), totalling 318 sessions from 1998 to 2003 (average 4.5 ± 0.18 SE per pair and per year). During a survey session, a team made of two to six people (depending on preliminary field knowledge of the size of the territory), connected by radio was settled close to but out of the potential foraging area. Survey were carried only in good weather (no rain, light wind and avoiding low or high temperature). During each session, the pair was surveyed for 1.5 hours(1 h 29 ± 3 SE min), giving a total of 802 hours of male and female survey from 1998 to 2003. Pairs were identified according to the nest they occupied; some were also identified by individual colour-rings. During a session, we performed focal sampling of behaviour (categorized as feeding, resting, flying, parental care, interaction with other choughs or other animals) as well as the time spent for each of these activities. For each foraging behaviour, habitat used by chough was noticed. Only feeding behaviours were further considered to model territory usage. Every 30 seconds, the location of feeding male and habitat used were considered for territory modelling. These feeding observations were then plotted on a digitised map of the study area, using aerial ortho-photographs, implemented in a GIS.

Estimating foraging area of breeding choughs

As defining and estimating foraging area of breeding pairs was crucial for the purposes of this study, we had to assess the reliability of the data and of the method we used to obtain ranges. While the female incubates the eggs, the male forages within home range and feeds the female

at, or close to, the nest. When females feed by themselves, it is mostly close to the nest. After egg-hatching, the male keeps on regurgitating food to the female, who in turn feeds the newly-hatched chicks. During the second half of the rearing period, male and female forage close together, and make regular foraging trips to areas in their home range in order to collect food, and then feed the nestlings by regurgitation. Therefore, foraging area was modelled with data from feeding male only, as female feeding locations could have biased the foraging area delimitation by bringing a set of locations either concentrated around the nest or similar to those of males.

We choose contouring methods to measure chough foraging area because these methods have considerable advantage over other popular home-range estimation methods such as the minimum convex polygon (Hemson *et al.* 2005). They do not rely on outlying points to anchor their corners and are less influenced by distant points, thereby excluding unused areas, leading to more accurate depictions of space use (Hemson *et al.* 2005). Foraging areas were modelled using Ranges V package (Kenward and Hodder 1996), using the kernel density estimator, an estimator viewed as the most reliable contouring methods in ecology (Worton 1989, Boulanger & White 1990, Worton 1995, Powell 2000, Kernohan *et al.* 2001). Kernel density estimation creates isopleths of intensity of utilization by calculating the mean influence of data point at grid intersection. Each isopleth contains a fixed percentage (e.g.95%) of utilization density suggestive of the amount of time that the animal spends within the contour (Hemson *et al.* 2005). Core-weighting kernel method was chosen (rather than fixed or tail-weighting kernel) because it minimises the risk of over-estimating foraging area size because of isolated outlying locations (fig.1; see e.g. Jiguet *et al.* 2000). Such isolated contact points are most probably not connected to the main feeding range but correspond to occasional movements of males defending their territories because of the close proximity of neighbouring breeding pairs. In addition, we considered the isoline of 95% point density to

obtain size of foraging area. Considering the additional 5% point density increased foraging areas sizes more than twice (2.18 ± 0.13 factor). Furthermore, 100% foraging areas are largely overlapping between pairs, which is biologically unlikely due to the strong territorial behaviour of the species (Fig. 1).

Randomisation test were used to assess the number of visits necessary to give robust foraging area estimate: 4 survey sessions distributed along the reproduction season was found as the best compromise between effort and precision (Appendix 1).

This protocol allowed us to model all breeding chough territories of Ouessant from 1998 to 2003, except in 2000 when home ranges could be estimated for only 5 of the 12 breeding pairs. Altogether, 68 different home ranges could be computed.

Feeding areas of each pair and for each year were mapped on the digitalised map using the GIS and the cross-cutting with the habitat cover layer allow then to obtain data on areas covered by each habitat type in each foraging area.

Habitat selected for foraging was further studied through the comparison between the area (in m^2) present in the territory, deduced from vegetation map and the time (in s) spent foraging by each member of the pair in the different habitats recorded during the field-survey. Comparison was done on a Logit scale as follow :

$$\text{Logit Index of Habitat H} = \sum_{i,t} \left[[\ln(S_{i,t}/(100 - S_{i,t})] - [\ln(F_{i,t}/(100 - F_{i,t})] \right] / (n).$$

n is the number of nest survey during the study (68).

$F_{i,t}$ is the percentage of time spend by a breeding pair (i) the year (t) in the habitat H.

$S_{i,t}$ is the percentage of areas cover by the habitat H in the territory of the pair (i).

Statistical analysis

We used ANOVA to explore variations in fledging success in relation with territory quality. The fledging success of a nest was estimated as the number of young fledging from this nest, (ranging from 0 to 4). Territory quality was estimated as the total optimal foraging habitat areas (m^2) present in the foraging area of each breeding pairs, or as the mean lenght of a foraging trip(m) or as the optimal foraging habitats area present in the foraging area close to the nest (within a radius of 300 meters). These analyses were controlled for year effect (year was considered as a factor).

The study of heterogeneity in demographic parameters among breeders, and its link to variations in territory quality, could be complicated by influences of age, breeding experience, territory ownership duration or pair bond duration, on demographic parameters such as reproductive performance (Reid *et al.* 2003b, Cam & Monnat 2000, Black 2001, Pyle, *et al.* 2001). Unfortunately, very few individual histories were known in the studied population because must breeders were not colour ringed. When relationships between habitat quality and demographic parameters were analysed we attempted to avoid this pitfall by considering inter-nest variations (the average variations between the different nests, test were nested to the nest site effect) and intra-nest variations (i.e. residual variation after controlling for nest site effect) separately.

.

RESULTS

Habitat selection.

In order to evaluate the feeding quality of each territory, it was first necessary to identify which habitats were used by feeding choughs. Breeding birds spent 71% of their foraging time in various habitat types all characterized by vegetation under 5 cm high : paths, rocky short

grasslands and short grasslands . Secondary habitats used for foraging were short heathland and littoral grasslands. Other habitats such as pastures and medium heathland represented less than 1% of the observations. Habitat selection by foraging chough could be evaluated through the comparison between the areas (m^2) present in each territory and the time each breeder spent foraging in the different habitat types. Again the same three habitats appeared to be positively selected by chough (Fig. 2). These three habitat types were pooled together to describe territory quality in subsequent analyses.

Home ranges of breeding pairs

Foraging areas sizes estimated with Core-weighting Kernel method, varied from 3587 to 67,388 m^2 (mean : 21,557 m^2 ± 1 645 SE). Within these foraging areas, the foraging habitat area covered by habitats identified as optimal for foraging (i.e. with a vegetation height below 5cm) varied from 516 to 61 200m^2 (mean : 17,439 m^2 ± 1 503 SE). The territory with the smallest optimal foraging area come from a pairs which had used mostly secondary habitat.

Year to year changes.

Vegetation cover at given place did not vary between year. But foraging area of pair breeding at the same nest site could vary quite much (Fig.3) presumably because of changes in local social structure, such as disappearance of a breeding pairs and the appropriation of territory by the neighbouring breeding pair as illustrated in Figure 3a. Changes in the territory quality can also occur when dominant behaviour between two pairs change as showed in Figure 3b. These examples (Fig. 3) show that chough territory is not only constrained by the location of nest site, but mostly influenced by the presence of breeding choughs in the neighbourhood.

Distances between nests and feeding areas.

The median value of the distances measured between nests and feeding areas was 230 m, while 59% of breeding choughs are observed feeding less than 300 m from their nest. Only less than 1% of the 3700 observations were farther than 1800 m from the nest (the largest distance was 5113 m). Average foraging distance varied from 125 to 3128 m (489 ± 56 SE m).

Influence of quality territory on fledging success.

We analysed variation in fledging success as a function of territory quality with fledging success. Fledging success appeared to be influenced by nest-site identity, but we did not detected any year effect (Table 2). We attempted to explain inter-nest variation in fledging success with the average parameter over year calculated for each nest. Total area of favourable foraging habitat in foraging area appeared not to influence significantly fledging success (Table 2), very likely due to important nest-site effect, but the correlation was slightly positive. Average fledging success was not influenced by the mean distance covered by pairs during breeding period (Table 2). As most choughs were observed feeding less than 300 meters away from their nest, we retained this distance class, to test the possible effects of the amount of optimal foraging habitats within a 300m radius from the nest on fledging success. But again this estimated of territory quality (feeding area close to the nest), did not explain inter-nest variation (Table 2).

A second approach focussed on intra-nest variation in fledging success : Fledging success adjusted to nest and year appeared not to be influenced by the total area of favourable foraging habitat in foraging area (Table 2). Fledging success adjusted to nest and year was not influenced by the mean distance covered by pairs during breeding period (Table 2). But fledging success adjusted to nest and year appeared to be influenced by the amount of optimal

foraging area close to the nest, a quite important variation is explain by this effect : R^2 = 0.6196 (Fig.4 ; Table 2).

However, it can be noted that intra and inter-variation of fledging success according to optimal favourable habitat close to the nest showed a similar slope (respectively 1.0 ± 0.7 SE and 1.4 ± 0.7 SE additional fledging per 10,000 m^2 of optimal foraging habitat within 300m of the nest).

DISCUSSION

Habitat selection in breeding choughs

Thanks to the accurate modelling of foraging areas using standardized data from focal sampling of feeding choughs, it was possible to estimate which habitats were preferentially used by choughs when foraging. Maritime turf appeared to be the most selected feeding habitat, whereas heathland and coastal ungrazed grassland were clearly avoided, as found in previous studies of coastal populations (Bignal et al 1995, Bullock *et al.* 1983, Meyer 1990, Roberston *et al.* 1995, Whitehead *et al.* 2005). Footpaths could appear as a quantitatively minor feeding habitat, though it was strongly selected according to their availability, as observed by Whitehead et al. (2005). However, the low frequency of choughs seen feeding in pasture on Ouessant strongly contrasts with what is observed elsewhere, as it is generally cited in previous studies, that the major feeding habitat for chough is agricultural land devoted to low-intensity grazing (Garcia-Dory 1989, Meyer *et al.* 1994, McKlay & Gruinart 1999, Bignal & Bignal 1999). Habitats preferred by feeding choughs on Ouessant are characterized by a mean sward height lower that 5cm, whereas habitat with taller vegetation are avoided. Habitat attractiveness is known to decrease when the height of the vegetation increases and selectivity coefficient for sward height became null or negative beyond 10cm (Whitehead *et al.* 2005). This could explain why Ouessant pastures, submitted to a very low grazing pressure (mean

266kg of life grazing animals / ha in 2002), are avoided, as vegetation height in pastures ranges from 10 to 40cm. Few data were previously available about home-range size of choughs, though there were some information on maximum distances between main feeding areas and nests. Indeed, Whitehead *et al.* (2005) found a similar decreasing frequency of habitat use with distance from the nest in a Welsh population, where choughs foraged mostly in habitats within 300m of the nest, with observations further than one kilometre from the nest being rare.

Territory quality and fledging success.

Fledging success was positively related to the amount of feeding habitat and negatively to the distance between such habitats and nest. Yearly changes in territory quality as observed for some pairs were likely due to changes in the local social interactions, such as the disappearance of a breeding pair and the consequent appropriation of its former territory by a neighbouring pair. Another awkward consequence of feeding far from the nest is the decrease in nest guarding against predators such as crow (*Corvus corone*). Indeed, complete nest failure, presumably due to depredation, adjusted to nest and year could be in part correlated to mean feeding distance ($F_{\text{binomial}1,44}=25.5$, $Chisq=0.06$).

Conservation implication

Ouessant has undergone a fallowing land due to progressive abandonment of agro-pastoral practices. This inevitably led to development of unsuitable foraging vegetation covers for choughs, like scrubs and brambles. Nowadays, such bushy open areas cover more than half of the island area. Moreover, most ancient pastures are under-grazed and become long-grass lands, which are also avoided by feeding choughs. Optimal feeding habitats are now spatially limited to remnant coastal vegetation, maintained by maritime environmental constraints or

localised in areas trampled by tourist. Agricultural abandonment has directly reduced the quantity and quality of suitable habitat and probably partly explains the lower fledging success recorded at Ouessant when compared to other study sites (Table 3). Indirectly, abandonment has also promoted predator installation. As an example, the Carrion Crow did not nest on Ouessant before 1971, because of the lack of bushes and trees for potential breeders. From the first breeding pairs in 1971, 30 pairs were breeding on the island in 1984 and about 50 pairs in 2002. Habitat loss, increasing predation risks but also tourism disturbance threatened the chough population, especially through decrease of young survival, to the point where this population short-term viability is concerned (Kerbiriou et al in prep.). All these elements point towards the urgent need to apply landscape management in order to maintain this core population of chough in Western France.

To define suitable management measures to be undertaken, we needed to identify the demographic determinants of population growth rate. On the chough population of Islay (Scotland) Reid *et al.* (2004) have evaluate the percentage of contribution of between-year variation in first-year, second year and adult survival and mean breeding success to total variance of population growth rate. This long-term study show thethree survivals parameters contributed each to 25 % of total variance in population growth rate whereas mean breeding success contribute only for 15%. Even if breeding success is not the main factor constraining population growth rate, from a conservation management point of view it would certainly be more easy to make appropriate landscape management measures aiming at an increase in breeding success, rather than an increase in survival.

The amount of suitable feeding habitat next to the nest is a key factor affecting fledging success. Hence, our results allow us to suggest, optimise and establish a scale of priority for

future management efforts. The first priorities consist in stopping on going fallow land process and soil erosion (due to heavy tourist trampling around breeding sites). Next, the restoration of short vegetation through mowing or livestock grazing must be planned close to known active nests, especially in a 300m radius circles from the nests. Each additional 10,000 m^2 of suitable vegetation in this neighbouring area should allow to add one more young to the fledging family. Because of nest-site shortage, we recommend focusing on site with weak average productivity. (for example, in 8 years of survey two breeding sites have produced respectively 0 and 1 young but have been occupied 7 years). Finally, we can also consider the restoration of short vegetation on historical and potential new breeding sites.

ACKNOLEDGEMENTS

Special thanks are due to Jacques Nisser who helped with defining the ringing techniques and Hélène Pouliquen for is help with English language. In addition we wish to thank the following for their participation in breeding chough survey sessions : A. Audevard, R. Baeta, C. Caïn, B. Combot, C. Constantin, R. Couix, N. Le Clainc'h, A. Guillaume, P. Laurent, V. Le Pennec, R. Morin, G. Ruiz, S. Tessier and L. Therin. We thank two anonymous referees for comments on earlier drafts of this manuscript.

REFERENCES

Baillie, S. R., Crick, H.Q.P., Balmer, D.E., Bashford, R.I., Beaven, L.P., Freeman, S.N., Marchant, J.H., Noble, D.G., Raven, M.J., Siriwardena, G.M., Thewlis, R. & Werham, C.V. 2001. Breeding birds in the wider countryside : their conservation status 2000. *BTO Research Repport N°252*, Thetford: http://www.bto.org/birdtrends.

Barber, D. R., Martin, T.E., Melchiords, M.A., Thill, R.E. & Wigley T.B. 2001. Nestling success of birds in different silvicultural treatments in southeastern U.S. pine forest. *Conservation Biology*. **15**: 196-207

Berrow, S.D., Mackie, K.L., O'Sullivan, O., Shepherd, K.B., Mellon, C. & Coveney, J.A. 1993. The second international Chough survey in Ireland, 1992. *Irish Birds* **5**: 1-10.

Bignal, E. 1991. Transhumance in Spain. In: *Birds and pastoral agriculture in Europe*. , ed. by D.J. Curtis, E.M. Bignal and D.I. McCracken, 18-21. Peterborough, Joint Nature Conservation Committee.

Bignal, E., McCracken, D. I., Stillman, R. A. & Ovenden, G. N. 1995. Feeding behavior of nestling choughs in the Scottish Hebrides. *Journal of Field Ornithology* **67**: 25-43.

Bignal, E. & McCracken, D. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* **33**: 413-424.

Bignal, E., Bignal S. & McCracken D. 1997. The social life of the Chough. *British Wildlife* **8**: 373-383.

Bignal, S. & Bignal, E. 1999. Long term studies of social organisation and behaviour. *In Chough & Farming Seminar, Islay 15-16 September 1999*, ed. by Royal Society for Protection of Birds and Scottish Natural Heritage.

Black, J.M. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioural Ecology* **12**, 640-645.

Blanco, G., Tella, J.L. & Torre, I. 1998. Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrocorax* conservation in a Spanish pseudo steppe landscape. *Journal of Applied Ecology* **35**: 232-239.

Boulanger, J.G. & White, G.C. 1990. A comparison of home-range estimators using Monte Carlo simulation. *J. Wildl. Manag.* **54** : 310-315.

Bullock, I. D., Drewett, D. R. & Mickleburgh, S. P. 1983. The chough in Britain and Ireland. *British Birds* **79**: 377-401.

Cam, E. & Monnat, J.Y. 2000. Apparent inferiority of first-time breeders in the kittiwake : the role of heterogeneity among age classes. *Journal of Animal Ecology* **69**: 380-394.

Cullen, J.P.1989. The history and present status of the chough in the Isle of Man. 19-22pp *In:* Bignal E., Curtis D. Chough and Land use in Europe. Proceeding of an International Workshop on the Conservation of the Chough, Pyrrhocorax pyrrhocorax in the EC. 11-14 November 1988.

Cook, A.S., Grant, M.C., McKay, C.R. & Peacock, M.A. 2001. Status, distribution and breeding success of the Red-billed Chough in Scotland in 1998. *Scottish Birds* **22:** 82-91.

Davis, S.K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor*. **107:** 605-616.

Dendaletche, C. 1991. Alpine Chough and Choughs : biological integrators of agro-pastoralism ecosystems in the Pyrenees. *In*: Birds and Pastoral Agriculture in Europe (Eds Curtis D.J, Bignal E. and Curtis M.A) pp. 68-70.

DeSanctis, A., De Marinis, F., Limongelli, L., Pellegrini, M. & Spinetti, M. 1997. The status and breeeding biology of the chough (*Pyrrhocorax pyrrocorax* Linnaeus) in the Central Apennines-Abruzzo-Italy. *Avocetta* **21**: 157-164.

Driscoll M.J.L., Donovan, T., Mickey, R., Howard, A. & Fleming, K.K. 2005. Determinants of wood thrush nest success: a multi-scale, model selection approach. *Journal of Wildlife Management*. **69**:699-709.

Farinha J.C. & Teixeira, A.M. 1989. the chough in Portugal – Status and distribution. 25-28pp *In:* Bignal E., Curtis D. Chough and Land use in Europe. Proceeding of an International Workshop on the Conservation of the Chough, Pyrrhocorax pyrrhocorax in the EC. 11-14 November 1988.

Garcia-Dory, M.A. 1989. Datos sobre la ecologia del genero Pyrrhocorax (P. pyrrhocorax y P. graculus) en el parque Nacional de la Montana de Covodonga, Asturias. *Alytes* **1** : 411-448.

Gourmelon, F., Bioret, F. & Le Berre, I. 2001. Land-use changes and implications for management of a small protected island off the coast of Bretagne. *Journal of Coastal Conservation* **7**: 41-48.

Gregory, R.D, Noble, D.G. & Custance, J. 2004. The state of play of farmland birds : population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* **146** : 1-13.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. & MacDonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with lest-square cross validation. *Journal of Animal Ecology*. **74** : 455-463.

Jiguet, F., Arroyo, B. & Bretagnolle, V. 2000. Lek mating system a case study in the little bustard *Tetrax tetrax. Behavioural process* **51**: 63-82.

Kenward, R.E. & Hodder, K.H. 1996. RANGES V: An Analysis system for biological Location Data; Institute for Terrestrial Ecology, Wareham, Dorset, U.K.

Kerbiriou, C. 2001. Originalité de la population bretonne de crave à bec rouge dans un contexte européen. *Alauda* **69** : 25-42.

Kerbiriou, C. Thomas, A., Floc'h P., Beneat, Y., Floté, D., Gager, L. & Champion, M., 2005. Recensement 2002 de la population bretonne de crave à bec rouge (Pyrrhocorax pyrrhocorax). *Ornithos* **12**:113-122

Kerbiriou, C., Gourmelon, F., Le Viol, I. & Julliard, R. Tourist impact on an endangered bird : from behavioural response of individuals to viability of the population. *in prep.*

Kernohan , B.J., Gitzen, R.A. & Millspaugh, J.J. 2001. Analysis of animal space use and movements. Radio tracking and Animal Populations (eds J.J. Millspaugh & J.M. Marzluff) pp. 125-166. Acadecmic Press, San Diego.

Laiolo, P. & Rolando, A. 2001. A comparative analysis of the breeding biology of the red-billed Chough *Pyrrhocorax pyrrocorax* and the Alpine Chough P. graculus coexisting in the Alps. *Ibis* **143**: 33-40.

Pain, D.J. & Pienkowski, M.W. 1997. Farming and birds in Europe. Academic Press, London.

Powell, R.A. 2000. Animal home ranges and territories and home range estimators. Research Techniques in Animal Ecology: Controversies and Consequences (eds L. Boitani & T.K. Fuller), pp.65-110. Columbia University, New York.

Pyle, P., Sydeman, W.J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology* **70**: 1088-1097.

Madders, M., Leckie F.M., Watson J, & McKay, C.R. 1998. Distribution and foraging habitat preferences of Choughs on the Oa peninsula, Islay. *Scottisch Birds* **19**: 280-289.

McCanch, N. 2000. The relationship between Red-Billed Chough *Pyrrhocorax pyrrhocorax* (L) breeding populations and grazing pressure on the Calf of Man. *Bird Study* **47**: 295-303.

McKlay, C. & Gruinart, L. 1999. Chough, habitat and land use on islay. *In Chough & Farming Seminar, Islay 15-16 September 1999*, ed. by Royal Society for Protection of Birds and Scottish Natural Heritage.

McCracken, D.I., Foster, G.M., Bignal, E.M. & Bignal, S. 1992. An assement of chough Pyrrhocorax pyrrhocorax diet using multivariate analysis technique. *Avocetta* **16**: 19-29.

Meyer, R. M. 1990. Observations on two red-billed choughs *Pyrrhocorax pyrrocorax* in Corwall: habitat use and food intake. *Bird Study* **37**: 199-209.

Meyer, R.M, Buckland, P.C. & Monaghan, P. 1994. The diet of the chough Pyrrhocorax pyrrhocorax as indicated by analysis of digested prey remains. Avocetta 18: 95-106.

Newton, I., Wyllie, I. & Freestone, P. 1990. Rodenticides in British Barn Owls. *Environmental Pollution* **68**: 101-117.

Newton I ., 2004. The recent declines of farmland bird populations in Britain : an appraisal of causal factors and conservation actions. *Ibis* **146** : 579-600.

Owen, D. 1989. Factors affecting the status of the chough in England and Wales; 1780-1980. 72-80pp *In:* Bignal E., Curtis D. Chough and Land use in Europe. Proceeding of an International Workshop on the Conservation of the Chough, Pyrrhocorax pyrrhocorax in the EC. 11-14 November 1988.

Reid, J.M, Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. 2003a. Environemental variability, life-history covariation and cohort effects in the red-billed chough. *Journal of Animal Ecology* **72**: 36-46.

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003b. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax* : patterns and processes in a natural population. *Journal of Animal Ecology* **72**: 765-776.

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2004 Identifying the demographic determinants of population growth rate : a case study of red-billed choughs *Pyrrhocorax pyrrhocorax. Journal of Animal Ecology* **73**: 777-788.

Roberston, A., Jarvis, A. M. & Day, K. R. 1995. Habitat selection and foraging behaviour of breeding choughs *Pyrrhocorax pyrrhocorax* L. in county Donegal. *Biology and Environment: Proceedings of the Royal Irish Academy* **95**: 69-74.

Roberts, P.J. 1983. Feeding habitats of the chough on Barsey Island (Gwynedd). *Bird Study* **30**: 67-72.

Roberts, P.J. 1985. The Choughs of Bardsey. *British Birds* **78**: 217-232.

Rodewald, A.D. and Yahner, R.H. 2001. Avian nestling success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* **118**: 1018-1028.

Rolando, A. Patterson, I., Laiolo, P. 1994. The foraging behaviour of the chough *Pyrrhocorax pyrrhocorax* in two contrasting habitats *Avocetta* **18**: 41-51.

Rolfe, R. 1966. Status of the Chough in Scotland. *Scottish Birds* **12**: 238-246.

Shrubb, M. 1993. The Kestrel. Hamlyn Species Guides, Hamlyn London.

Tucker, G.M. 1993. Effects of agricultural practices on filed use by invertebrate-feeding birds in winter. *Journal of applied Ecology* **29**: 779-790.

Tucker, G. M. & Heath, M. F. 1994. Birds in Europe their conservation status. Cambridge, U.K. Birdlife Conservation serie 3600p.

Warnes, J.M. 1982. A study of the ecology of the Chough Pyrrhocorax pyrrhocorax L. on the isle of Islay, Argyll, 1980-1981. M.Sc. Thesis, University of Stirling.

Whithead, S., Johnstone, I. & Wilson, J.D. 2005. Choughs *Pyrrhocorax pyrrhocorax* breeding in Wales select foraging habitat at different spatial scales. *Bird Study* 52:193-203.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* **70**: 164-168.

Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* **59**: 794-800.

Table 1. Classification of coastal habitats used by chough.

Habitat class	Vegetation structure and composition
Rocky and short grassland	vegetation with many rocky outcrops under 5 cm high, dominated by *Armeria maritima, Plantago coronopus, Festuca rubra pruinosa, Sedum anglicum, Jasione montana*, lichen (*Cladonia sp*), and also a large part of annual species
Short grassland	vegetation with a total covering and under 5 cm high, dominated by *Plantago coronopus, Festuca rubra pruinosa, Agrostis stolonifera maritima, Chamamelum nobile, Scilla verna, Centaurium erythraea*
Path	vegetation under 5 cm high, created by human use and dominated by *Plantago coronopus, Festuca rubra, Bellis perennis, Lolium perenne, Agrostis tenuis, Cynosurus cristatus*
Short heathland	vegetation height included between 5 cm and 15 cm and dominated by *Erica cinerea, Calluna vulgaris, Danthonia decumbens, Pedicularis sylvatica, Thymus drucei*
Littoral grassland	vegetation height included between 5 cm and 15 cm and dominated by *Festuca rubra pruinosa, Agrostis stolonifera maritima, Holcus lanatus, Plantago lanceolata, Daucus carota gummifer, Lotus corniculatus, Silene maritima*
Pasture	vegetation grazed by sheep, but with a low pressure of grazing, height included between 10 cm and 40 cm and dominated by *Dactylis glomerata, Holcus lanatus, Trifolium repens, Lolium perenne*
Medium heathland	vegetation height included between 15 cm and 50 cm and dominated by *Erica cinerea , Calluna vulgaris, Ulex gallii*
Vegetation in restoration	vegetation under management operation, is at least mowed twice annually. This vegetation height range from 5 cm to 50cm. This vegetation is dominated by fallow land species (*Pteridium aquilinum, Rubus sp, Dactylis glomerata, Ulex europaeus*). Progressively changing to grassland species (*Dactylis glomerata, Holcus lanatus, Anthoxantum odoratum, Trifolium repens)* as management proceed.

Table 2. Modelling fledging success. Model c, d, e are adjust to nest-site and year, but are not adjust between them.

Model	Within nest variation			Between nest variation		
	df	**F**	*P*	*df*	*F*	*P*
(a) Nest-site	16,45	3.37	0.0006			
(b) Year	5,45	1.42	0.23			
(c) Area of foraging habitat in the foraging area	1,44	0.86	0.35	1,15	3.34	0.07
(d) Mean distance covered by breeding pairs	1,44	0.01	0.98	1,15	0.97	0.33
(e) Areas of foraging habitat in the foraging area and close to the nest (within a 300 m radius)	1,44	4.36	0.04	1,15	1.92	0.18

Table 3. Variations in breeding success of choughs in different West European populations.

Region	Fledging success of the whole population	Fledging success of successful breeder	n	Reference
Ouessant-Fance	1.46 ± 0.13 SE	2.44 ± 0.11 SE	114;68	this study
Islay-Scotland-UK	2.02 ± 0.1 SE			Reid *et al.* 2003
Central Apennines-Italy		2.68 ± 0.37 SE	55	De Sanctis et al 1997
Cueno & Turin Province-Italy		2.60 ± 0.53 SE	8	Laiolo & Rolando 2001
Ireland		2.85 ± 0.36 SE	67	Bullock *et al*. 1983
Isle of Man	1.88±0.44 SE		67	Bullock *et al*. 1983
Wales (inland) -UK	2.05±0.46 SE		79	Bullock *et al*. 1983
Wales (coastal)-UK	2.68±0.33 SE		160	Bullock *et al*. 1983
Wales (Bardsey)-UK	2.08		91	

Figure 1. Examples of four modelled chough breeding territories.

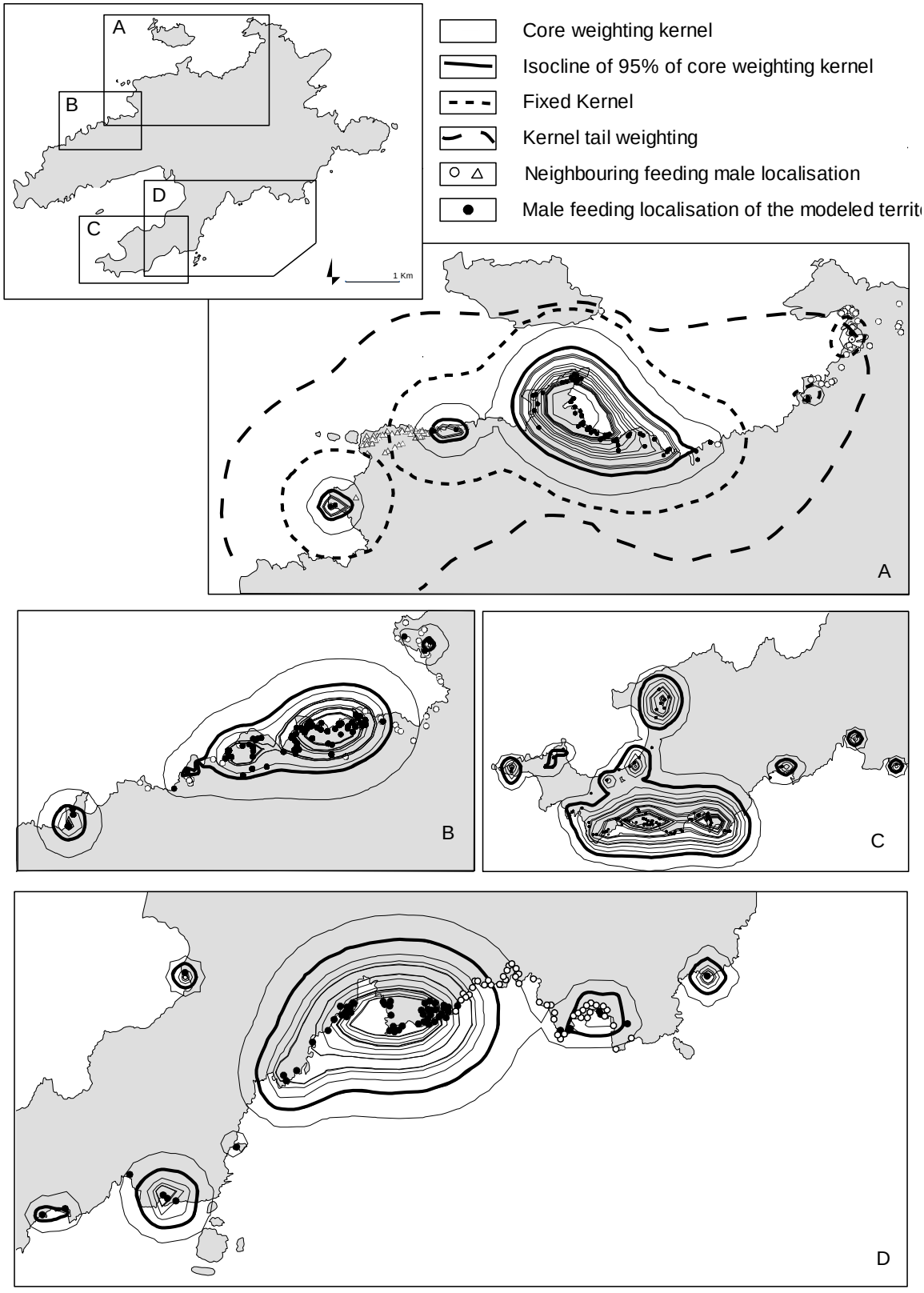


Figure 2. Logit index with standard error of habitat selection by feeding chough. PAT : path, RS : Rocky and short grassland, SG : Short grassland, VR : Vegetation in restoration, SH : Short heathland, LG : littoral grassland, PAS : Pasture, MH : Medium heathland.

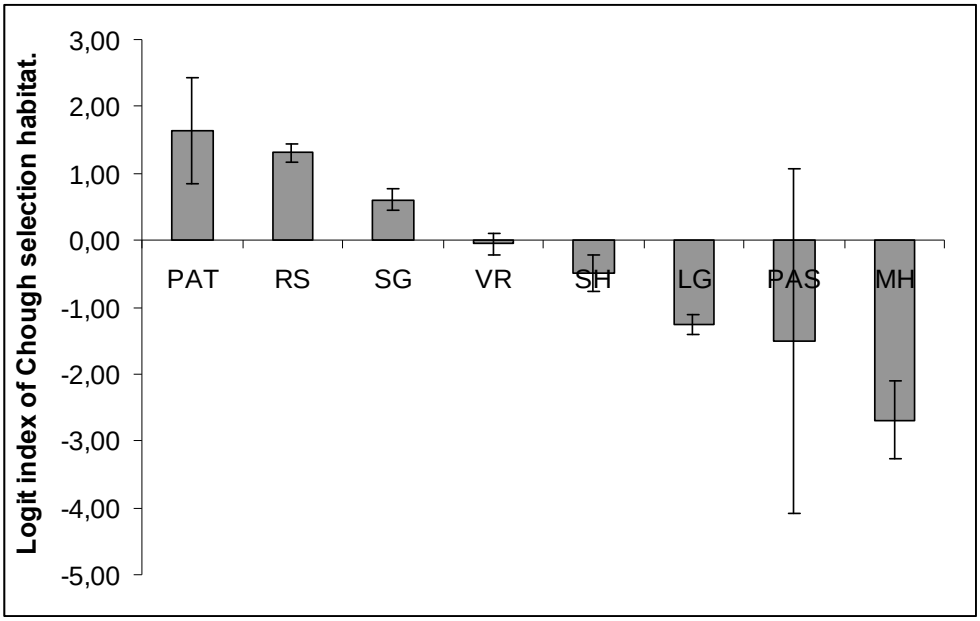
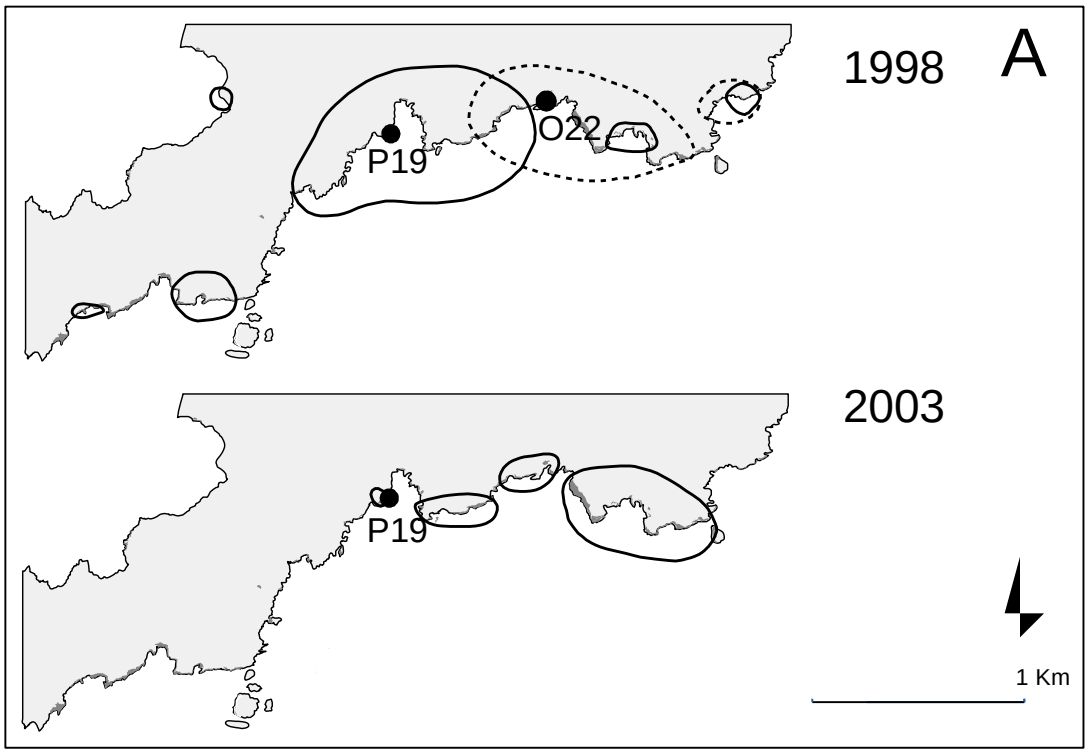


Figure 3. Two examples of territory change dark circle are localisation of nest and dark grey areas represent suitable chough habitat.
(a) The breeding pair P19 settled on the abandoned territory (O22) an thus reduced its long distance feeding trip.
(b) Dominant behaviour between two sites had changed : B22 pairs in 1998 had a dominant behaviour status and therefore occupied the majority of the suitable habitat expelling the C23 pair and then forcing this pairs to feed most of the time far away from its nest. In 2003 the dominant behaviour status was inverted and so were territories patterns.



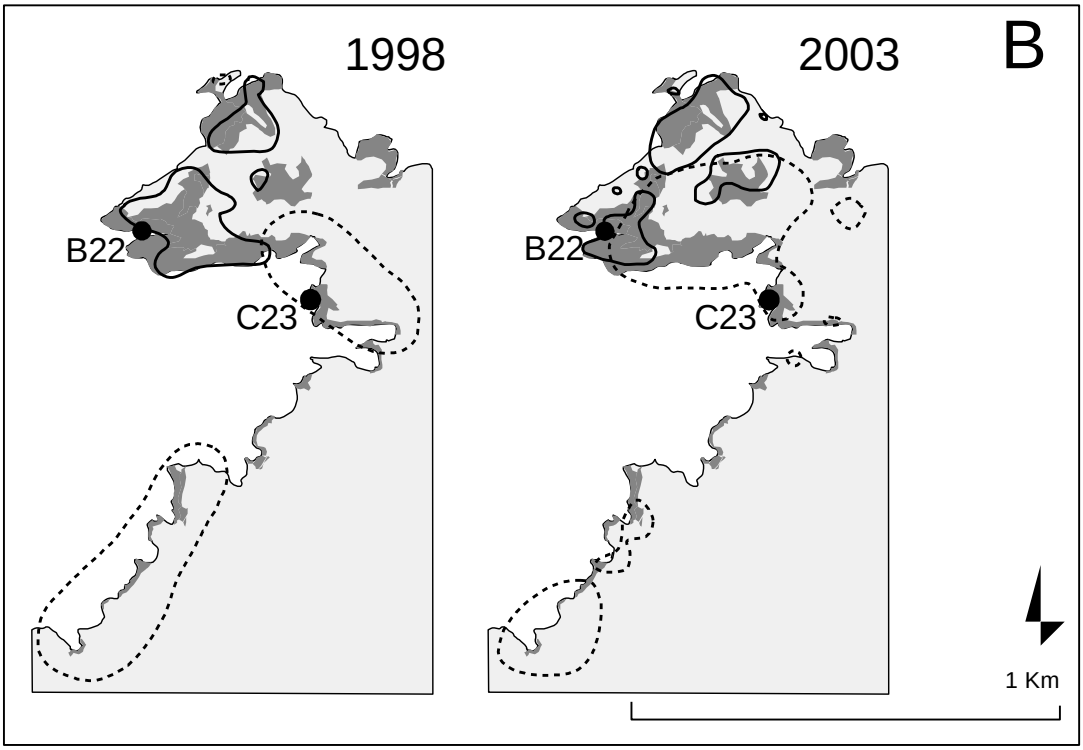
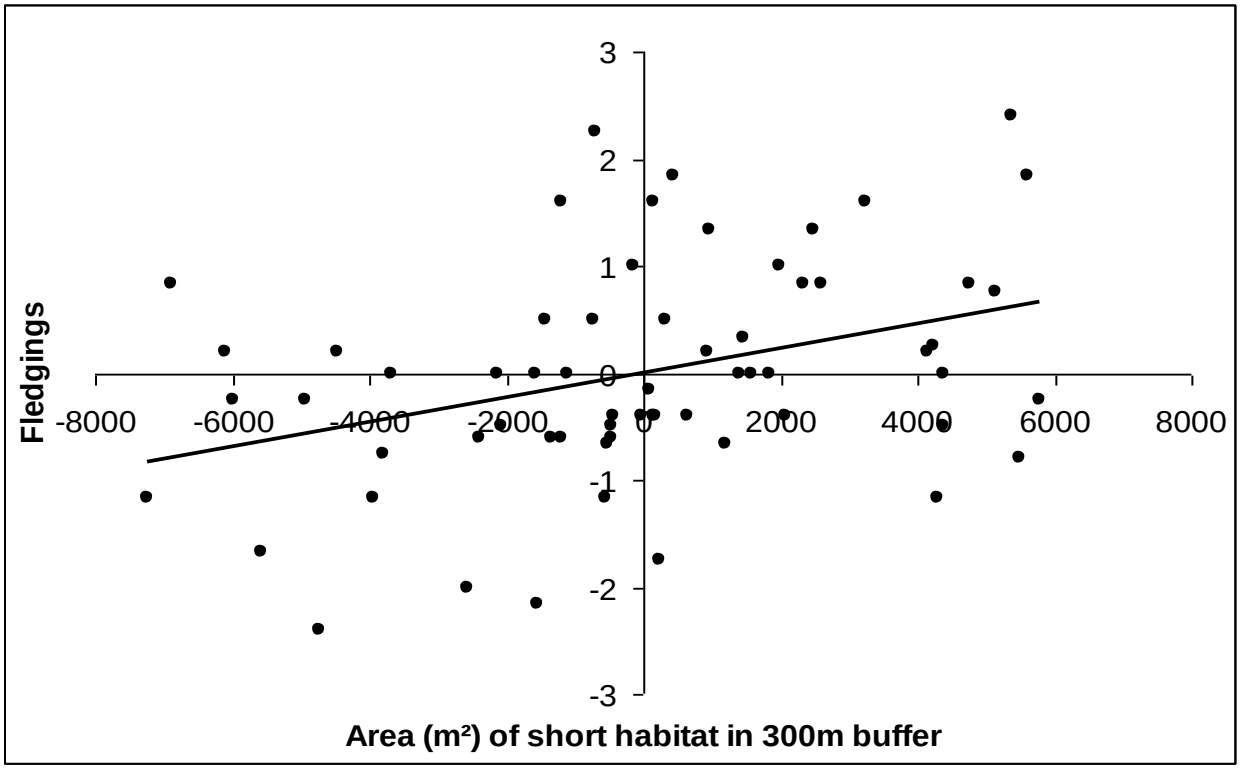


Figure 4. Relationship between territory quality and fledging success.



APPENDIX I

We tested whether modelled foraging area size was sensitive to the number of sampling sessions we made in the field. To do this, we used data from four that were surveyed on nine occasions in 1998. We randomly chose 2 to 8 sessions within the available pool of 9, performed the foraging area analyses to determine how many sampling sessions were necessary to obtain unbiased foraging area size estimates. When considering 2 to 5 sessions, we made 20 random permutations within the 9 sessions, 10 when considering 6 to 7 sessions and the 8 possible permutations for 8 sessions. Curve stabilisation could be observed from 4 sessions onwards for three nest, and from 3 sessions for the remaining one(Fig. i).

ANOVA analysis of foraging area size as a function of nest identity and of the number of survey indicated a significant correlation between foraging area size and number of survey until 4 (Table i.), whereas from 5 to 9 sampling no significant correlation could be detected (Table i).

For these four territories, foraging area size estimated after 4 sessions was c.a. 90% of the foraging area obtained with the full set of 9 sessions. Therefore, we further modelled foraging areas sizes only for breeding pairs surveyed at least at 4 occasions. For the few breeding pairs with more than 4 survey sessions available, spare sessions were eliminated from the analysis with the following criteria: session with an effective observation lasting less than 1h30, or date far from the core reproductive period.

Table i . Sensitivity of territory size to number of survey.

Number of survey	F Value	Pr
1-9	$F_{1,469} = 137.2$	$Pr > 0.0001$
2-9	$F_{1,433} = 78.4$	$Pr > 0.0001$
3-9	$F_{1,353} = 23.7$	$Pr > 0.0001$
4-9	$F_{1,272} = 4.3$	$Pr > 0.05$
5-9	$F_{1,192} = 1.6$	NS

Figure i. Relationship between estimated home ranges and number of survey sessions considered, (Δ) nest V11, (o) nest P19, (•) nest F19 and (Δ) nest I11. Same nests as those figured in fig.1.

