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Linking territory quality and reproductive success in the Red-billed Chough *Pyrrhocorax pyrrochorax*: implications for conservation management of an endangered population

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As changes in land use have been identified as the main factor explaining the decline in Red-billed Chough *Pyrrhocorax pyrrochorax* populations across western Europe, a study was carried out in Ouessant (western France) in order to assess the relationship between territory quality and reproductive success. As such an approach could be hindered by the fact that the birds' reproductive performance could be influenced by their breeding experience, we analysed both inter- and intranest-site variation in fledging success. Territory quality was quantified, combining habitat selection, territory size, the amount of feeding area and distance between nest and feeding area. Feeding habitats selected positively by Red-billed Choughs were characterized by a mean sward height of less than 5 cm. Foraging area was on average 21 557 m^2. Feeding areas (i.e. feeding habitat within foraging area) close to the nest were used preferentially. Fledging success appeared to be influenced neither by the total area of feeding sites in a Chough territory, nor by the mean feeding flight distance. However, fledging success adjusted to nest-site and year appeared to be influenced by feeding area close to the nest: one additional fledgling was expected for each additional 10 000 m^2 of feeding habitat within 300 m of the nest. These first results allowed us to consider recommending landscape management measures to ensure a favourable conservation status of local Chough populations.

Habitat loss and damage linked to changes in agricultural practice are the most frequently reported threats affecting European birds (Newton *et al*. 1990, Shrubb 1993, Tucker 1993, Tucker & Heath 1994, Bignal & McCracken 1996, Pain & Pienkowski 1997, Baillie *et al*. 2001, Gregory *et al*. 2004, Newton 2004). European agriculture has been intensified drastically in recent decades, although, paradoxically, agricultural abandonment has also occurred as an indirect effect of intensification, as some marginal land has become less profitable for farming and has therefore been 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 in respect of 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 affected by agriculture, 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 conservation planning emerging from any such agricultural policy should be determined by comparing the population dynamics

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of species across habitat management treatments (Barber *et al.* 2001, Rodewald & Yahner 2001, Davis 2005, Driscoll *et al.* 2005).

This is especially so for the Red-billed Chough *Pyrrhocorax pyrrhocorax* (hereafter Chough), 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, McCracken *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, in particular, 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 agricultural land use, such as farming intensification or the loss of grazing practices (Rolfe 1966, Garcia-Dory 1989, Dendaletche 1991, McCracken *et al.* 1992, Meyer *et al.* 1994, Blanco *et al.* 1998, Kerbiriou 2001). However, we still have little knowledge of the 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, 2003b). A major long-term study of individually marked Chough, carried out on the isle of Islay (UK) has highlighted the consequences of environmental variability (as temperature and rainfall variations during the pre-breeding season) on demographic 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 regarding the demographic processes affecting the short-term population dynamics of the Chough has shown that the most important explanatory factor is natal weather conditions (Reid *et al.* 2003a), whereas at the population level, the main extrinsic factor cited to explain population trends is the change in land use.

Such differences between the conclusions of studies based on distribution and abundance and those of studies based on demographic parameters are probably explained by the focus of the latter on short-term inter-annual variations, whereas habitat variation occurs over 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 by combining estimation of foraging area and feeding habitat, taking account of the distance to the nest. We then studied variation in breeding success in relation to our measure of territory quality. We used the result to make landscape management recommendations for the Red-billed Chough.

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 & Heath 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; it appears to be one of the smallest clusters, and the most isolated population in Western Europe (Tucker & Heath 1994, Kerbiriou 2001). It suffered a large decrease after the 1960s, from probably 100–150 to about 30 pairs two decades later. Currently, this population seems to be stabilized 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 rarely skip breeding years as observed in previous studies (Roberts 1985, Bignal *et al.* 1997, Reid *et al.* 2003a).

Study area

Our study was conducted on the small island of Ouessant (1541 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 as a result of a decline in the human population that occurred during the 20th century. This led to the complete disappearance of crop farming, and a huge reduction in grazing pressure (sheep numbers decreased from 5900 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 land, dominated by Bracken *Pteridium aquilinum* and Bramble *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 digitized directly from aerial photographs, they were first defined as lines. Field measurements of path width were then made, as well as recording their eventual vegetation cover. A polygon GIS-layer representing all pathways was then created as a buffer along the path linear layer using data on path width as the buffer distance, and keeping the path state as a further descriptive variable. The final Chough habitat cover was obtained by updating the vegetation cover with the pathways. 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, etc.) evolve slowly if at all, and could be considered as perennial vegetation. Restored habitats were located at the southwest tip of the island and account for a small area (77 466 m^2, i.e. 2.9% of the coastal vegetation).

Chough survey and focal sampling of behaviour

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

To assess the distribution of foraging habitat within the territory used by a pair during the breeding period, we conducted several survey sessions each year for each pair during the breeding period (mid April to early July); these totalled 318 sessions from 1998 to 2003 (average 4.5 ± 0.18 se per pair and per year). During a survey session, a team of 2–6 people (depending on preliminary field knowledge of the

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 ranges from 5 cm to 50 cm. 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 proceeds

size of the territory), communicating by radio was positioned close to, but out of, the potential foraging area. Surveys were carried out only in good weather (no rain, light wind and avoiding low or high temperatures). During each session, the pair was surveyed for 1.5 h (1 h 29 ± 3 se min), giving a total of 802 h of male and female survey from 1998 to 2003. Pairs were identified according to the nest they occupied, and in some cases 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 the Chough was noted. Only feeding behaviours were considered further to model territory usage. Every 30 s, the location of the feeding male and habitat used were considered for territory modelling. These feeding observations were then plotted on a digitized 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 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 the 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 continues to regurgitate food to the female, who in turn feeds the newly hatched chicks. During the second half of the rearing period, the male and female forage close together, and make regular foraging trips to areas in their home range to collect food, and then feed the nestlings by regurgitation. The foraging area was modelled by using data from the 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 chose contouring methods to measure Chough foraging area because these methods have considerable advantages 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, and leading to more accurate depictions of space use (Hemson *et al.* 2005). Foraging areas were modelled using the Ranges V package (Kenward & Hodder 1996), using the kernel density estimator, a series of estimators viewed as the most reliable contouring methods in ecology (Worton 1989, 1995, Boulanger & White 1990, Powell 2000, Kernohan *et al.* 2001). Kernel density estimation creates isopleths of the intensity of utilization by calculating the mean influence of data points at grid intersections. 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). The core-weighting kernel method was chosen (rather than the fixed or tail-weighting kernel) because it minimizes the risk of over-estimating the size of foraging area because of isolated outlying locations (Fig. 1; see, for example, Jiguet *et al.* 2000). Such isolated contact points are probably not connected to the main feeding range but correspond to occasional movements of males defending their territories, as suggested by the close proximity of neighbouring breeding pairs. In addition, we considered the isoline of 95% point density to obtain the size of foraging area. We did not consider the 100% point density to model foraging areas because (1) the additional 5% point density doubled the size of the foraging area (by a factor of 2.18 ± 0.13 sd), and (2) 100% foraging areas displayed large overlaps between pairs, which is biologically unlikely given the strong territorial behaviour of the species (Fig. 1).

Randomization tests were used to assess the number of visits necessary to give a robust estimate of foraging area. This was assessed (as the best compromise between effort and precision) to be four survey sessions distributed evenly through the breeding season (see Appendix).

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

The foraging areas of each pair and for each year were mapped on the digitized map using the GIS. We then superimposed the habitat cover onto the foraging areas on the GIS to record specific areas covered by each habitat type in each foraging area. The habitat cover within foraging areas was recorded for each pair in each year of the survey.

Habitat selected for foraging was further studied by comparing the areas (in m^2) present in the territory, deduced from the vegetation map and the time (in s) spent foraging by each member of the pair in

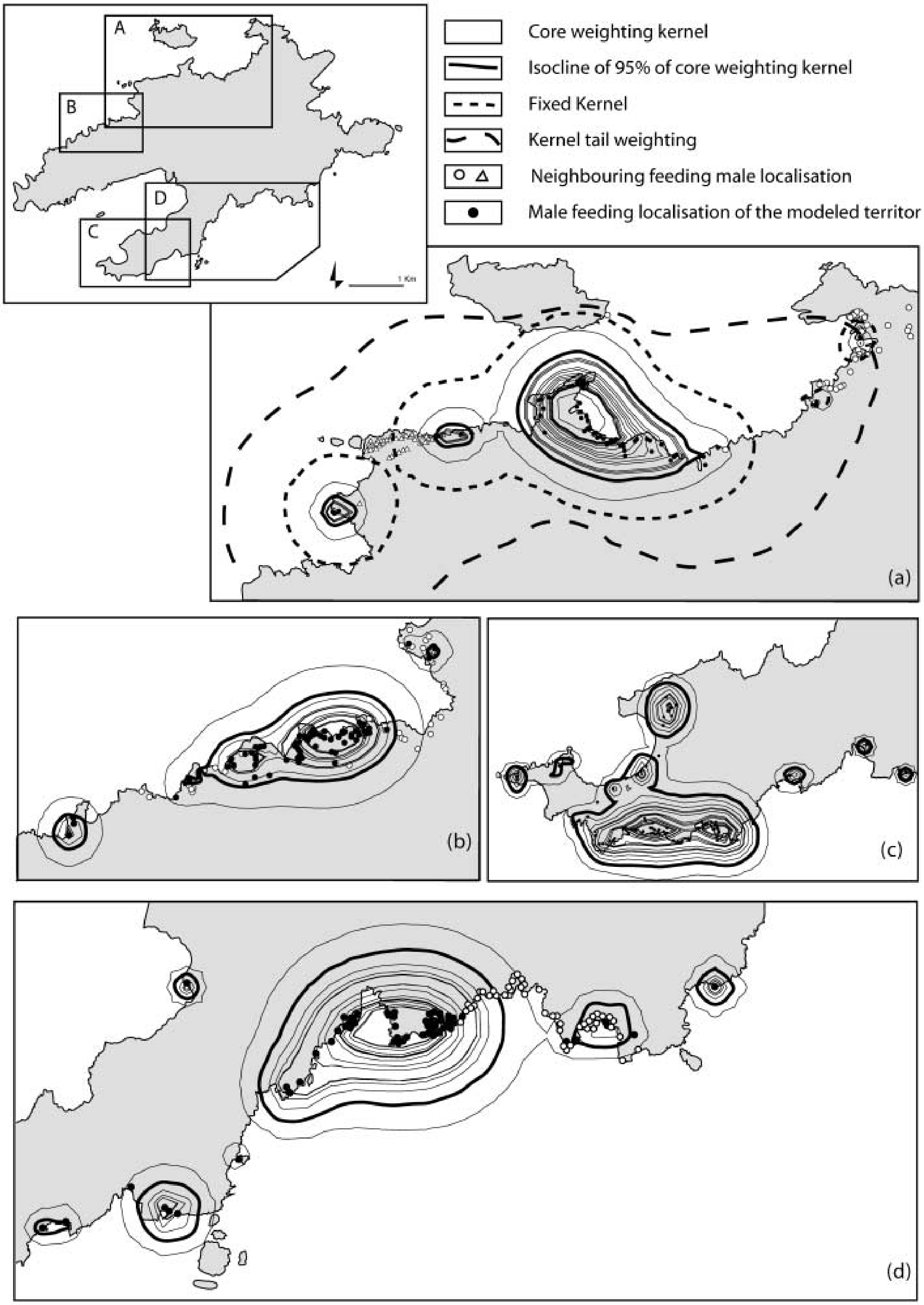

Figure 1. Examples of four modelled Chough breeding territories.

the different habitats recorded during the field survey. Comparison was done on a Logit scale as follows:

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

where n is the number of nest surveys during the study (68), $F_{i,t}$ is the percentage of time spent by a breeding pair i in year t in habitat H, and $S_{i,t}$ is the percentage of area cover by habitat H in the territory of pair i.

Statistical analysis

We used ANOVA to explore variation in fledging success in relation to territory quality. The fledging success of each pair each year was estimated as the number of young fledging (ranging from zero to four young). Territory quality was estimated in three ways: (1) as the total area (m^2) of optimal foraging habitat (with a vegetation height below 5 cm; see Results for the derivation of this) present in the foraging area of each breeding pair; (2) as the mean length of a foraging trip (m); or (3) as the area of optimal foraging habitat present in the foraging area within 300 m of the nest. These analyses were controlled for year effects by including year as a factor.

The study of heterogeneity in demographic parameters among breeders, and how it is linked to variation in territory quality, could be complicated by influences of age, breeding experience, territory ownership duration or pair-bond duration, and on demographic parameters such as reproductive performance (Cam & Monnat 2000, Black 2001, Pyle *et al.* 2001, Reid *et al.* 2003b). Unfortunately, very few individual histories were known in the population studied because most 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 variation (i.e. the average variation between the different nests: tests were nested to the nest-site effect) and intra-nest variation (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 Choughs could be evaluated by comparing areas (m^2) of such habitat in each territory and the time that each breeder spent foraging in the different habitat types. The same three habitats again appeared to be positively selected by Chough (Fig. 2). These three habitat types were pooled and defined as the optimal habitat in subsequent analyses.

Home ranges of breeding pairs

Foraging area sizes estimated by the Core-weighting Kernel method, varied from 3587 to 67 388 m^2 (mean 21 557 m^2 ± 1645 se). Within these foraging areas, the foraging habitat area covered by habitats identified as optimal for foraging varied from 516 to 61 200 m^2 (mean 17 439 m^2 ± 1503 se). The territory with the smallest area of optimal foraging habitat was occupied by a pair that had mostly used secondary habitat.

Year to year changes

Although the vegetation cover at a given location did not vary between years, the foraging area of a pair breeding at the same nest-site could vary considerably (Fig. 3). This was presumably because of changes in local social structure, such as the disappearance of a breeding pair and the appropriation of their territory by the neighbouring breeding pair (e.g. see Fig. 3a). Changes in territory quality can also occur when the degree of agonistic behaviour between pairs changes (e.g. Fig. 3b). These examples (Fig. 3) show that Chough territories are not only constrained by the location of the nest-site, but are also influenced strongly by the presence of breeding Choughs in the neighbourhood.

Distances between nests and feeding areas

The median distance between nests and feeding areas was 230 m, although 59% of breeding Choughs were observed feeding less than 300 m from their nest. Less than 1% of the 3700 observations were further than 1800 m from the nest (the greatest distance

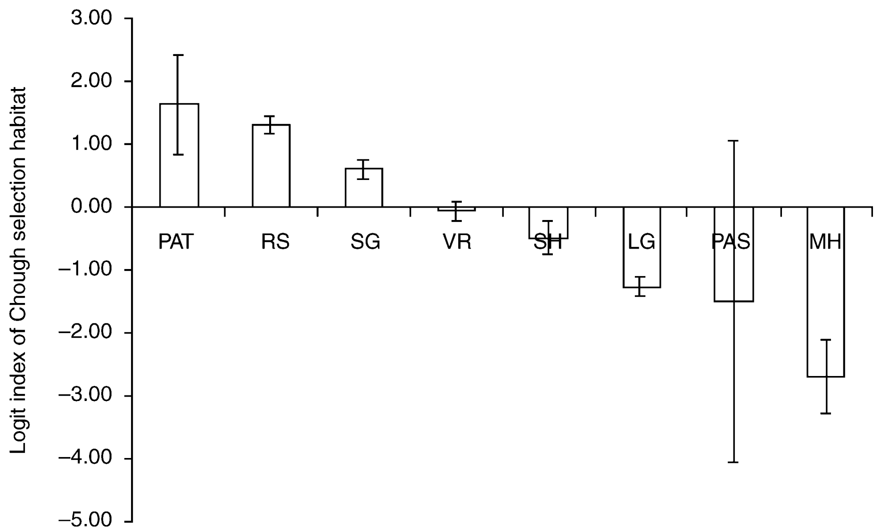

Figure 2. Logit index with standard error of habitat selection by feeding Choughs. PAT, path; RS, rocky and short grassland; SG, short grassland; VR, vegetation in restoration; SH, short heathland; LG, littoral grassland; PAS, pasture; MH, medium heathland.

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

	Within-nest variation			Between-nest variation		
Model	*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

was 5113 m). The average foraging distance varied from 125 to 3128 m (mean 489 m ± 56 se).

Influence of territory quality on fledging success

We analysed variation in fledging success as a function of territory characteristics. Fledging success appeared to be influenced by nest-site identity, but we detected no year effect (Table 2). We attempted to explain inter-nest variation in fledging success by using the average parameter over year calculated for each nest. The total area of optimal foraging habitat in the foraging area appeared not to influence fledging success significantly (Table 2). This was probably due to an important nest-site effect. The average fledging success was not influenced by the mean distance covered by pairs during the breeding period (Table 2). As most Choughs were observed feeding less than 300 m from their nest, we retained this distance class to test for effects of the amount of optimal foraging habitat within a 300-m radius from the nest on fledging success. This measure of territory quality (feeding area close to the nest) also explained no inter-nest variation (Table 2).

Focusing on intra-nest variation in fledging success, fledging success adjusted for nest and year effects appeared not to be influenced by the total area of optimal 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 the breeding period (Table 2), but it did appear to be influenced strongly by the amount of optimal foraging area close to the nest ($R^2 = 0.6196$, Fig. 4; Table 2).

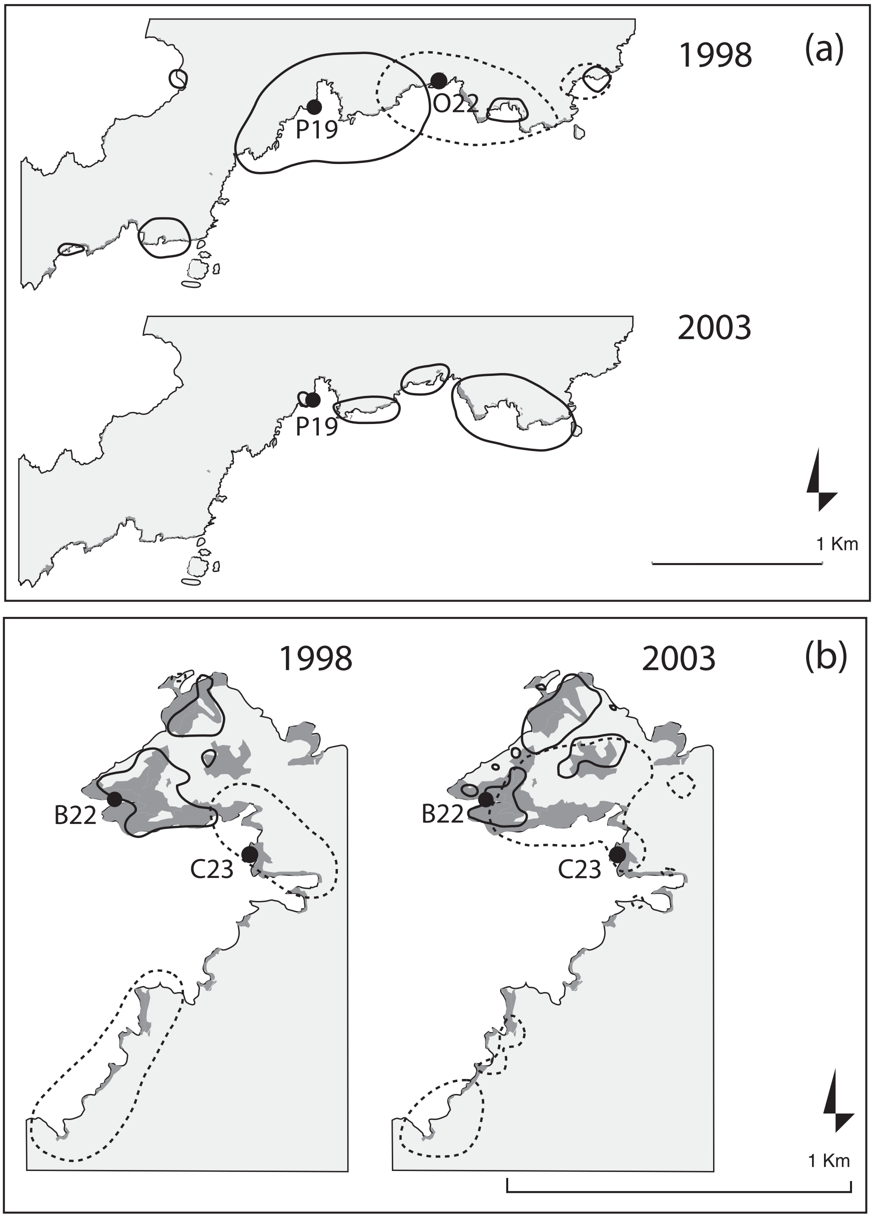

Figure 3. Two examples of territory change. Dark circles are nest locations and dark grey areas represent suitable Chough habitat. (a) The breeding pair P19 settled on the abandoned territory (O22) and thus reduced its long-distance feeding trips. (b) Agonistic behaviour between two pairs had changed: B22 pairs in 1998 had a dominant behaviour status and therefore occupied most of the suitable habitat, expelling the C23 pair and then forcing this pair to feed most of the time far away from its nest. In 2003 the dominance status was reversed, as were territories patterns.

However, it should be noted that the effects of the amount of optimal foraging habitat close to the nest on intra- and inter-nest variation in fledging success showed similar slopes (respectively 1.0 ± 0.7 se and 1.4 ± 0.7 se additional fledgling per 10 000 m^2 of optimal foraging habitat within 300 m of the nest).

DISCUSSION

Habitat selection by breeding Choughs

Because we had accurately modelled the foraging areas using standardized data from focal sampling of

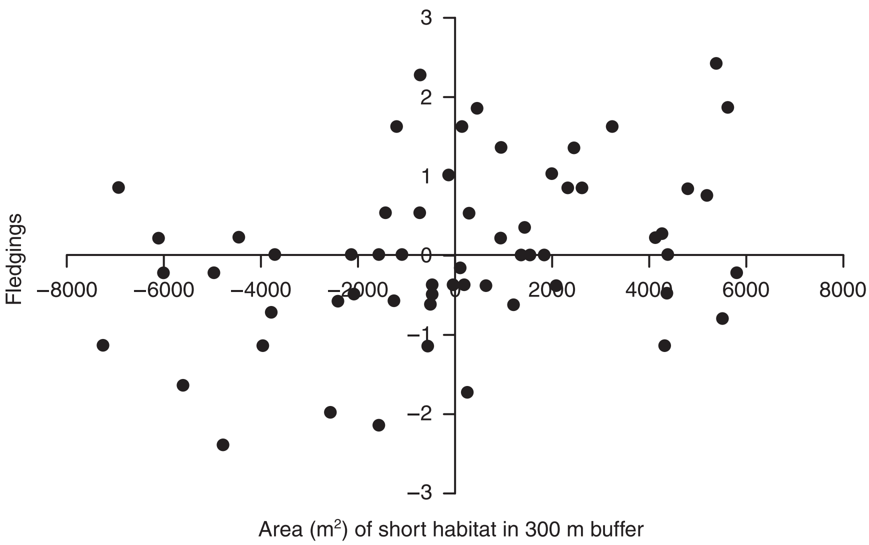

Figure 4. Relationship between territory quality and fledging success.

feeding Choughs, it was possible to estimate which habitats were used preferentially by Choughs when foraging. Maritime turf appeared to be the most selected feeding habitat, whereas heathland and coastal ungrazed grassland were clearly avoided, as had been found in previous studies of coastal populations (Bullock *et al.* 1983, Meyer 1990, Bignal *et al.* 1995, Roberston *et al.* 1995, Whithead *et al.* 2005). Footpath could appear quantitatively as a minor feeding habitat, although it was strongly selected according to availability, as observed by Whithead *et al.* (2005). However, the low frequency of Choughs seen feeding in pasture on Ouessant contrasts strongly with what is observed elsewhere; the major feeding habitat for Chough is generally reported to be agricultural land devoted to low-intensity grazing (Garcia-Dory 1989, Meyer *et al.* 1994, Bignal & Bignal 1999, McKlay & Gruinart 1999). Habitats preferred by feeding Choughs on Ouessant are characterized by a mean sward height of less than 5 cm, whereas habitats with taller vegetation are avoided. Habitat attractiveness is known to decrease when the height of the vegetation increases, and the selectivity coefficient for sward height became null or negative beyond 10 cm (Whithead *et al.* 2005). This could explain why Ouessant pastures submitted to very light grazing (mean 266 kg of life grazing animals/ha in 2002) are avoided, as vegetation height in pastures ranges from 10 to 40 cm. Little information was available previously on the home-range size of Choughs, although there were some data on maximum distances between the main feeding areas and nests. Indeed, Whithead *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 300 m of the nest, observations further than 1 km from the nest being rare.

Territory quality and fledging success

Fledging success was related positively to the amount of feeding habitat, and negatively to the distance between such habitats and the nest. Yearly changes in territory quality, as observed for some pairs, were probably 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 consequence of foraging far from the nest is the decrease that occurs in nest guarding against predators such as Carrion Crows *Corvus corone*. Indeed, complete nest failure, presumably due to depredation, adjusted to nest and year could be in part correlated to mean feeding distance ($F_{1,44}$ = 25.5, χ^2 = 0.06).

Conservation implications

Ouessant has undergone land fallowing due to progressive abandonment of agro-pastoral practices. This inevitably led to the development of unsuitable foraging vegetation for Choughs, such as scrub and bramble. Today, such bushy open areas cover more

Table 3. Variations in breeding success of Choughs in different western European populations.

Region	Fledging success of the whole population	Fledging success of successful breeder	*n*	Reference
Ouessant, France	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.* (2003a)
Central Apennines, Italy		2.68 ± 0.37 se	55	DeSanctis *et al.* (1997)
Cueno and Turin Province, Italy		2.60 ± 0.53 se	8	Laiolo and 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 Island), UK	2.08		91	

than half of the island area. Moreover, most ancient pastures are under-grazed and have become dominated by rank grasslands, which are avoided by feeding Choughs. Optimal feeding habitats are now limited spatially to remnant coastal vegetation, maintained by maritime environmental constraints or localized in areas trampled by tourists. Agricultural abandonment has directly reduced the quantity and quality of suitable habitat and probably partly explains the lower fledging success recorded on Ouessant as compared with other study sites (Table 3). Indirectly, abandonment has also promoted predator colonization. For example, the Carrion Crow did not nest on Ouessant before 1971, because of the lack of bushes and trees in which it could nest. 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 risk and tourist disturbance have all threatened the Chough population, especially through their influence on chick survival, to the point at which the short-term viability of this population is threatened. All these elements point towards the urgent need to apply landscape management in order to maintain this core Chough population in western France.

To define suitable management measures to be undertaken, we needed to identify the demographic determinants of population growth rate. For the Chough population of Islay (Scotland) Reid *et al.* (2004) evaluated the percentage contribution to the total variance in population growth rate of between-year variation in first-year, second-year and adult survival and mean breeding success. This long-term study showed that the three survival parameters each contributed 25% to the total variance in population growth rate, whereas the mean breeding success contributed only 15%. Even if breeding success is not the main factor constraining population growth rate, from a conservation management perspective it would be easier to take appropriate landscape management action to increase breeding success, rather than to increase survival *per se*.

The amount of suitable feeding habitat near the nest is a key factor affecting fledging success. Hence, our results allow us to rank the priority of action for future management. The most important is to halt the 'fallowing' 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 within 300 m of the nests. Each additional 10 000 m^2 of suitable vegetation in this neighbouring area should allow one more chick to fledge from each family. Because of a shortage of nest-sites, we recommend that some attention be paid to sites that have had especially poor average productivity (e.g. in 8 years of survey two breeding sites have produced zero and one young, although both have been occupied for 7 years). Finally, we should also consider the restoration of short vegetation near historical and potential new breeding sites.

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APPENDIX

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 territories that were surveyed on nine occasions in 1998. We randomly chose 2–8 sessions within the available pool of nine, and performed the foraging area analyses to determine how many sampling sessions were necessary to obtain unbiased foraging area size estimates. When considering 2–5 sessions, we made 20 random permutations within the nine sessions, ten when considering 6–7 sessions and the eight possible permutations for eight sessions. Curve stabilization was observed from four sessions onwards for three nests, and from three sessions for the remaining one (Fig. A1).

An ANOVA of foraging area size as a function of nest identity and of the number of surveys indicated a significant correlation between foraging area size and number of surveys up to four (Table A1), whereas from 5–9 samplings no significant correlation could be detected (Table A1).

For these four territories, foraging area size estimated after four sessions was *c.* 90% of the foraging area obtained with the full set of nine sessions. Therefore, we modelled foraging area sizes further only for breeding pairs surveyed at least on four occasions. For the few breeding pairs with more than four survey sessions available, spare sessions were eliminated from the analysis with the following criteria: session with an effective observation lasting less than 1.5 h, or date far from the core reproductive period.

Table A1. Sensitivity of territory size to number of survey.

Number of survey	*F* value	*P*
1–9	$F_{1,469} = 137.2$	> 0.0001
2–9	$F_{1,433} = 78.4$	> 0.0001
3–9	$F_{1,353} = 23.7$	> 0.0001
4–9	$F_{1,272} = 4.3$	> 0.05
5–9	$F_{1,192} = 1.6$	ns

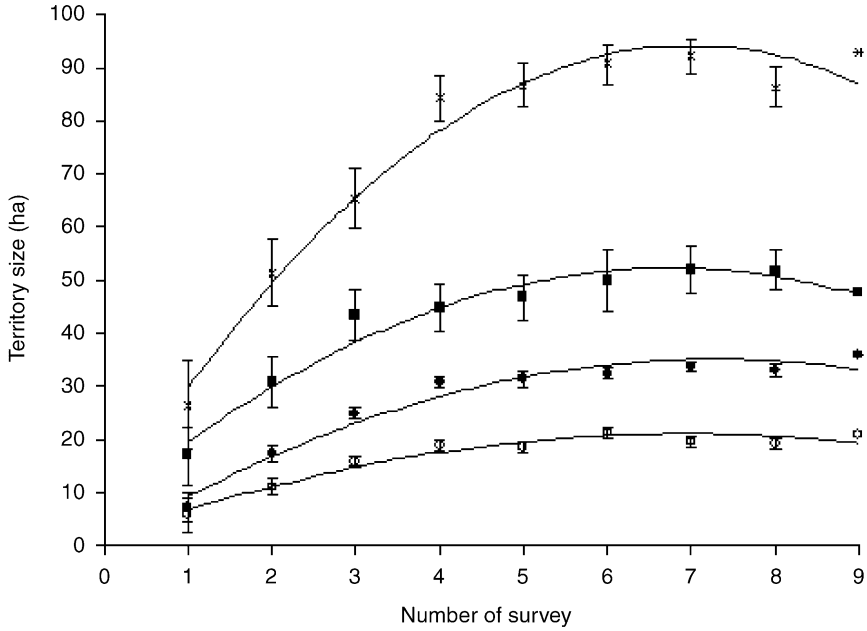

Figure A1. Relationship between estimated home ranges and number of survey sessions considered: (●) nest V11, (×) nest P19, (■) nest F19 and (○) nest I11. The nests are the same as those figured in Figure 1.