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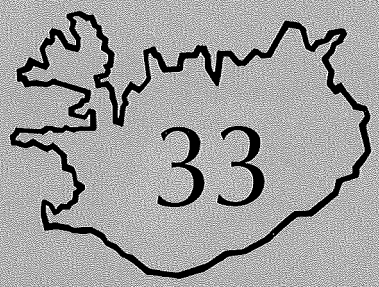

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Breeding biology, movements, and persecution of ravens in Iceland

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Abstract. We studied Common ravens (*Corvus corax*) in Iceland from 1981-85. This paper describes (1) the breeding biology of three local raven populations in Southwest, Northeast, and East Iceland, respectively, (2) movements and mortality of non-breeding ravens, (3) composition of non-breeding and wintering flocks, and (4) impact of human persecution on the raven population in Iceland.

(1) The range of mean breeding densities for 7 regions in Iceland was 1.5 – 6.8 pairs/100 km^2. There was no significant annual variation in occupancy rates of territories and nest success; mean occupancy rates for the Southwest (72%) and East (67%) were significantly higher than in the Northeast (59%). On average, 9% of occupied territories were occupied by non-breeding birds. The mean clutch size was 4.6 eggs, and the mean brood size was 3.3 young per successful pair. Brood size did not differ among areas but was significantly different among some years; the annual means ranged from 3.0 young (1983) to 3.7 young (1981). Nest success was significantly higher in the East (89%) than in the Northeast (77%). The mean nest success for all years and areas combined was 83%, among the highest recorded for ravens anywhere. One female initiated breeding at 2 years.

(2) The overall recovery rate of 587 raven nestlings banded in our study was 42%; rates were highest for nestlings banded in the Northeast (47%), followed by the East (43%) and Southwest (18%). Recovery rate did not depend on brood size, laying date or, hence, fledging date. Ravens recovered during their first year represented 62% of the total number recovered. The median interval between banding and recovery differed significantly among ravens in the three study areas; 295, 195, and 312 days in the Southwest, Northeast, and East, respectively. Recoveries peaked in August-October (45%) and April-May (24%). The majority (87%) of recovered ravens was killed by humans. Distances between banding and recovery locations of ravens differed significantly among the banding areas; median distances were 73 km for the Southwest, 30 km for Northeast, and 70 km for East. Ninety six percent of the recoveries in the Northeast came from within 80 km of the banding place, compared to 64% in the Southwest and 57% in the East. The longest movement was 386 km. Most ravens (87%) recovered during summer were inland (>10 km from the coast), but during winter 81% were coastal (<10 km from the coast).

(3) Raven young dispersed from their parents' territories about 4-6 weeks after fledging and joined non-breeding flocks for up to 6 years. The percentage of ≤1-year-old birds killed in non-breeding flocks declined significantly from fall (56%) to spring (44%).

(4) A large-scale raven control program began in Iceland in 1976. The estimated kill during 1981-85 averaged 4116 ravens each year. A minimum 43% of all ravens banded in the Northeast and 36% banded in the East were killed by humans. Over 80% of the annual reproductive output of the estimated 2000 raven pairs in Iceland was needed to compensate for the annual persecution. This level of persecution did not seem to affect numbers of breeding pairs as the occupancy of territories remained stable throughout our study. In the Northeast, however, where ravens were heavily persecuted, data suggested a declining non-breeding population. There, ravens differed significantly in some of their life-history characteristics from ravens in the other two study areas: they had lower occupancy rate of territories and lower nest success; nestlings were recovered at an earlier age and after dispersing shorter distances.

CONTENTS

INTRODUCTION

The Common Raven (*Corvus corax*) is a conspicuous bird in Iceland, breeding in all lowland areas up to 500-600 m a.s.l., but mostly absent from the barren interior (Fig. 1). The territorial raven population is estimated around 2000 pairs (Skarphédinsson et al. in press). The raven is an opportunistic omnivore, a scavenger, and a predator; eggs, nestlings, and adult birds form a considerable part of its diet in Iceland during spring and summer. During fall and winter, however, the raven appears to be more of a scavenger (Nielsen 1986; unpubl. material).

There are more folk-tales, beliefs, and superstition, usually associated with the raven's intelligence, playful, and sometimes bold behavior, than of any other bird species in Iceland. Because ravens are alleged to be pests by many people, they are unprotected and persecuted in Iceland. Raven-related problems can to a large extent be attributed to insufficient disposal of organic waste, as ravens often concentrate around such locally abundant food supplies. Non-breeding birds are nomadic and aggregate at garbage dumps, fish factories, and slaughter houses, especially during the winter months. In spring, they gather at nesting areas of colonial waterbirds where they prey mainly upon eggs.

Killing newborn lambs (*Ovis aries*) was formerly regarded as the major raven depredation in Iceland. Due to improved husbandry, relatively little damage now occurs; most lambs are born under careful supervision and are housed during their first days of life. The loss of newborn lambs to ravens and Great Black-backed Gulls (*Larus marinus*) was estimated to be less than 0.1% of all lambs born in 1974 (Jónsson 1974). Ravens also occasionally attack weak or sickly sheep, and even mares (*Equus caballus*) during foaling, causing fatal injuries.

It has been speculated by some non-biologists that predation by ravens, Great Black-backed Gulls, and the introduced Mink (*Mustela vison*) on Common Eiders (*Somateria mollissima*), their eggs, and young is the main reason for the decline in the recorded harvest of eider down from an all-time high (4700 kg/yr) in 1911 to an all-time low (about 1700 kg/yr) during the late 1960s (Snaebjörnsson 1988). Decreased eider husbandry, however, probably did contribute more to the decline (cf. Gardarsson 1982). The recorded eider down harvest has gradually increased since the late 1970s (3100 kg/yr in 1988; Árni Snaebjörnsson, pers. comm.). Recent studies did not show any significant effect of raven egg predation on the eiders' reproductive output, but ravens caused disturbances in the colonies (Skarphédinsson and Temple, unpubl. material). In 1969 eider farmers were licensed to use poisons to control pest birds. The chemical currently in use is phenobarbitalum, but strychnine was used off and on in the colonies from 1889-1965. Poisoning can only be carried out in eider colonies during the eiders' breeding season (15 April – 1 August), and poison can only be placed in eggs. The purpose of this restriction is to avoid accidental poisoning of the rare White-tailed Eagle (*Haliaeetus albicilla*) which inhabits western Iceland.

Ravens are common nest predators, and it is sometimes claimed that they are a serious threat to some non-game bird populations. Raven depredation on non-game birds seems at most to cause very local and temporary effects

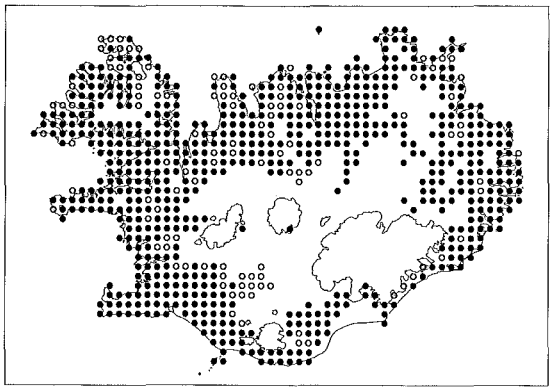


Fig. 1. The breeding distribution of ravens in Iceland, based on a 10x10 km grid system and data collected mostly during 1981-90. Filled circles: breeding confirmed; open circles: breeding probable, but not confirmed.

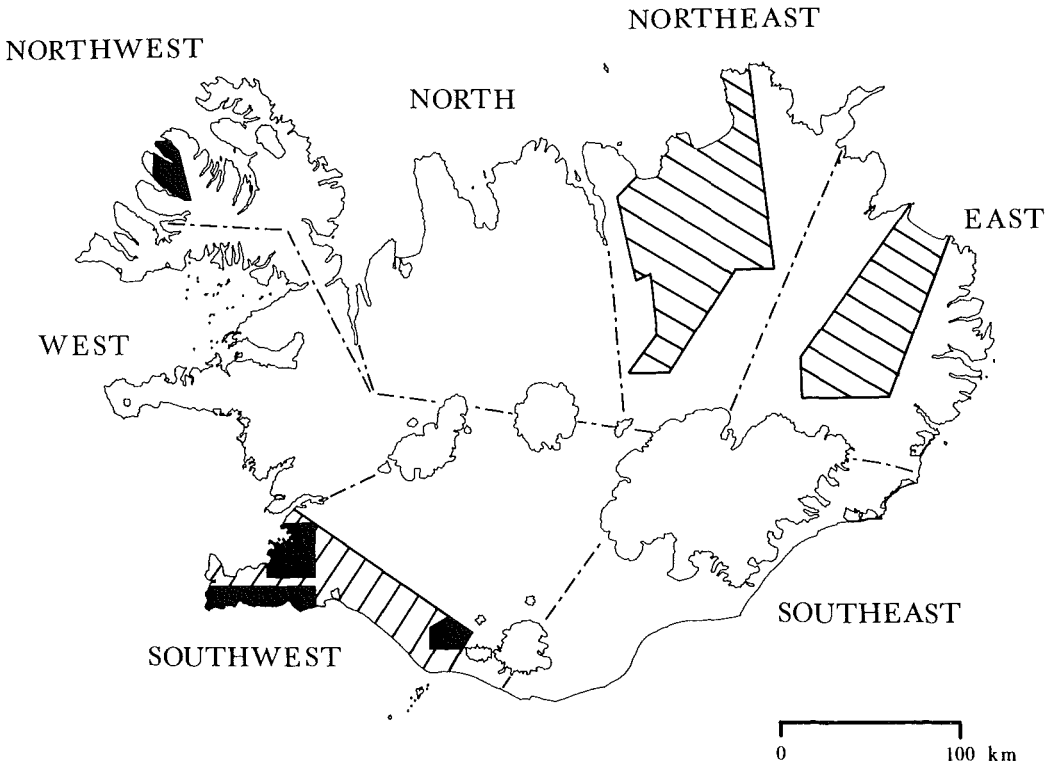


Fig. 2. Study areas in Iceland and regional boundaries employed. Crosshatched: the three main study areas; black: areas where densities of breeding ravens were measured, including a study site in the Northwest which otherwise was excluded from this study. Also shown, are major glaciers.

(cf. Petersen 1979). Similarly, raven depredation on newly planted seeds of oats (*Avena sativa*) and barley (*Hordeum vulgare*), and trees in plantations (Petersen 1971, Jónsson 1974, Óskarsson 1986) constitutes only a minor problem.

Ravens feed on and damage stock-fish while the fish is being dried on open-air racks. This fish product has been a fluctuating but sometimes important export item in Iceland for centuries, e.g., 12.5% of the national gross export in 1981 (Statistical Bureau of Iceland 1982).

Since 1976 the Icelandic government has sponsored raven control programs through the Wildlife Damage Control Unit. The stated goal is to reduce raven depredation, mainly on stock-fish, by locally controlling raven numbers, especially the non-breeding flocks. The Unit uses poison placed in offal to kill ravens and gulls year-round near garbage dumps and fish factories and operates in most parts of Iceland, except in the breeding areas of the White-tailed eagle in western Iceland. A few municipalities have also organized their own raven control programs, and certain individuals, especially eider farmers, kill many birds. Bounties have also been paid for killing ravens by local organizations and municipalities, a practice now uncommon, but dating back to the late 1800s. Currently, the eider farmers of Breidafjördur in the West pay the equivalent of $2 for each raven killed in their area.

Raven persecution has increased in Iceland during the past decade, but so far, little effort has been made to estimate the extent of the damage caused by ravens, and no information exists on the effectiveness of current control programs. Furthermore, the biology of the raven in Iceland is poorly known. Our objectives in this paper are to describe: (1) the breeding biology of three local raven populations, (2) the movements and mortality of non-breeding ravens, (3) the composition of non-breeding and wintering flocks, and (4) the impact of

persecution on the dynamics of the raven population in Iceland.

STUDY AREAS

We studied ravens in three regions of Iceland (Fig. 2): the Southwest, Northeast, and East, respectively. The 4600 km^2 Southwest region (Fig. 3) is basically the southwestern corner of Iceland, including the barren Reykjanes peninsula (mostly postglacial lava fields); the Reykjavík area (low hills and coastal cliffs); and finally the Southwest lowlands, west of Markarfljót river and mainly south of Highway 1 (partly drained wetlands, previously sedge fens and bogs, now pastures and meadows inhabited by dairy and sheep farmers). In the Southwest lowlands, nest sites for ravens are scarce; the sites being used are mostly on low cliffs, often close to human dwellings, and on man-made structures.

The 5900 km^2 Northeast region (Fig. 4) has its northern boundary set by the coastline and its southern boundary by the northern fringe of the Central Highlands. The western and eastern boundaries are the valley of Fnjóskadalur and the major glacial river Jökulsá á Fjöllum, respectively. Also included in this region is the district of Öxarfjördur and the western part of the peninsula Melrakkaslétta. The general topography is flat, with rolling hills rising from the coast to 600-800 m a.s.l. at the southern edge of the study area, 100 km inland. This relief is interrupted by several valleys, isolated mountains, and larger mountain masses.

Owing to land-use practices, most of the climax vegetation, which is typically birch (*Betula pubescens*), has been converted to heaths dominated by dwarf shrubs (*Empetrum nigrum, Betula nana,* and *Salix* spp.) and grasses. Soil erosion has completely devegetated large expanses of the uplands. Coastal plains, valleys, and some of the uplands are inhabited by sheep and dairy farmers. On the coast, there are two fishing villages, Húsavík and Kópasker.

The 4750 km^2 East region (Fig. 5) consists of the gradually narrowing lowland of the Hérad which stretches some 100 km southward from the 20-km-wide Héradsflói. Most of the field work was carried out in Jökuldalur, a 60-km-long, narrow valley, surrounded by the tundra plateaus of Jökuldalsheidi and Fljótsdalsheidi (550-700 m a.s.l.). The glacial river, Jökulsá á Dal, runs in a gorge through the valley. Together with the ravines of its tributaries, the river gorge offers ample nest sites for ravens. About 30 sheep farmers reside in the valley. The lowland vegetation is primarily heaths, but the highlands are barren grounds with some sedge-bogs. The Eastfjords are separated from Hérad by a stretch of 800 to 1240-m-high mountains. There, we studied non-breeding ravens, mainly at the towns of Eskifjördur and Reydarfjördur.

METHODS

We studied raven breeding biology and banded nestlings from 1981-85 in the Northeast and East and from 1982-84 in the Southwest. Each year, we sampled raven territories in our study areas to estimate occupancy rates, nest success, and young production, and to band young. A part of the research in the Northeast was done in conjunction with Nielsen's (1986) studies on Gyrfalcons (*Falco rusticolus*).

We defined a breeding territory as an area containing one or more nest sites that either were used during the course of our study or had historical evidence of raven occupancy. Nesting sites that were less than 2.5 km apart, were assigned to separate territories only if they were in simultaneous use on one or more occasions during the study.

A pair was considered to be breeding if we found at least a lined nest in their territory; we never found more than one lined nest in a raven territory. Raven nests are conspicuous and relatively easy to find. Thus, if no lined nest was found in a territory, but a pair of birds was

Fig. 3 (page 6). The Southwest study area with major lakes and rivers; the broken line indicates the boundaries. Dots refer to raven territories with nest sites on cliffs; squares refer to territories with nest sites on man-made structures. The feint dashed lines are the 400 m contour; major towns and urban areas are crosshatched.

Fig. 4 (page 7). The Northeast study area. As Gyrfalcons have bred in most of the raven nesting territories, their distribution is not shown on the map. The feint dashed lines are the 400 m contour.

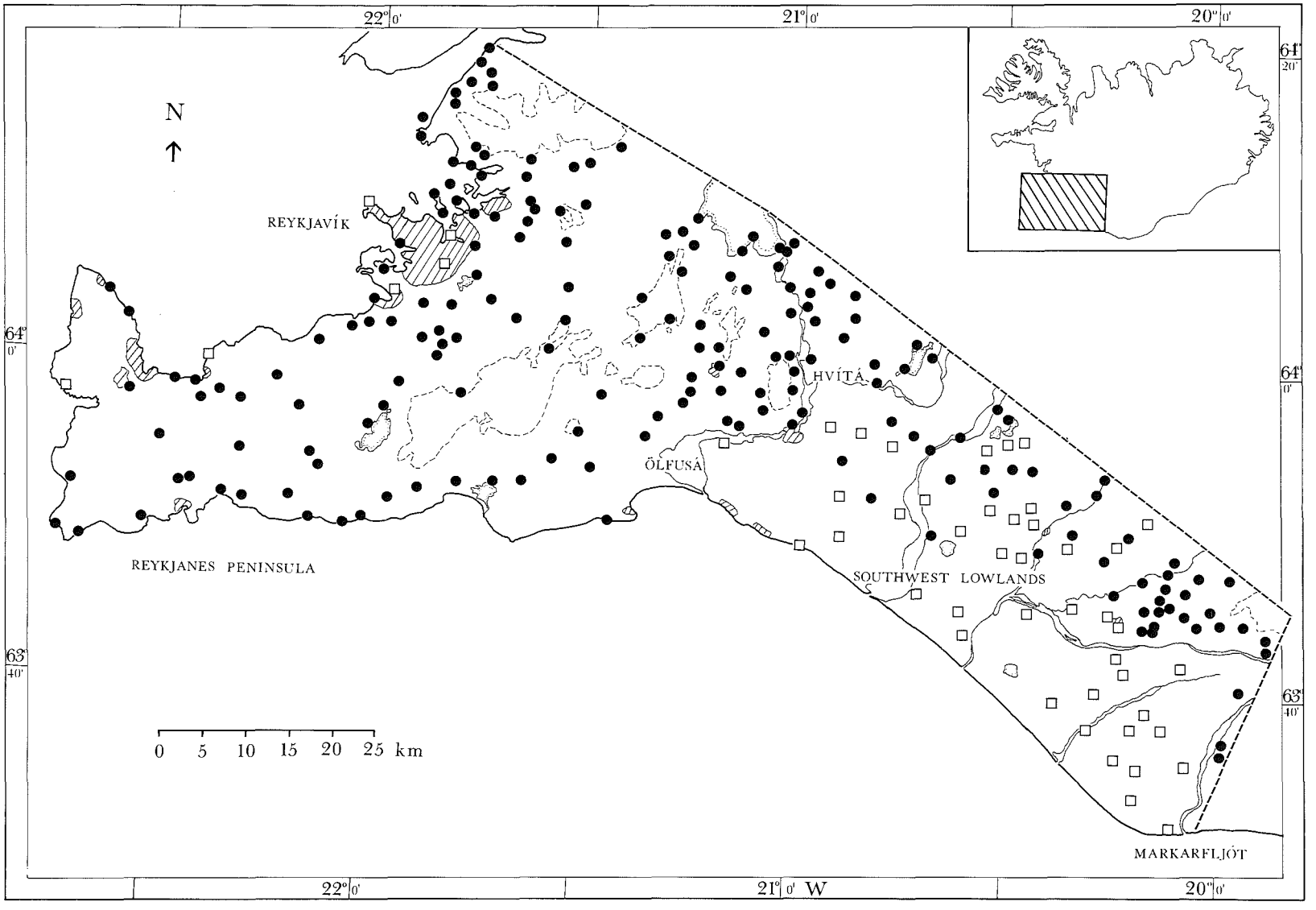

22° 0'
21° 0'
20° 0'
64° 20'
64° 0'
63° 40'
N
REYKJAVÍK
HVÍTÁ
ÖLFUSÁ
REYKJANES PENINSULA
SOUTHWEST LOWLANDS
MARKARFLJÓT
0 5 10 15 20 25 km
W

Fig. 3.

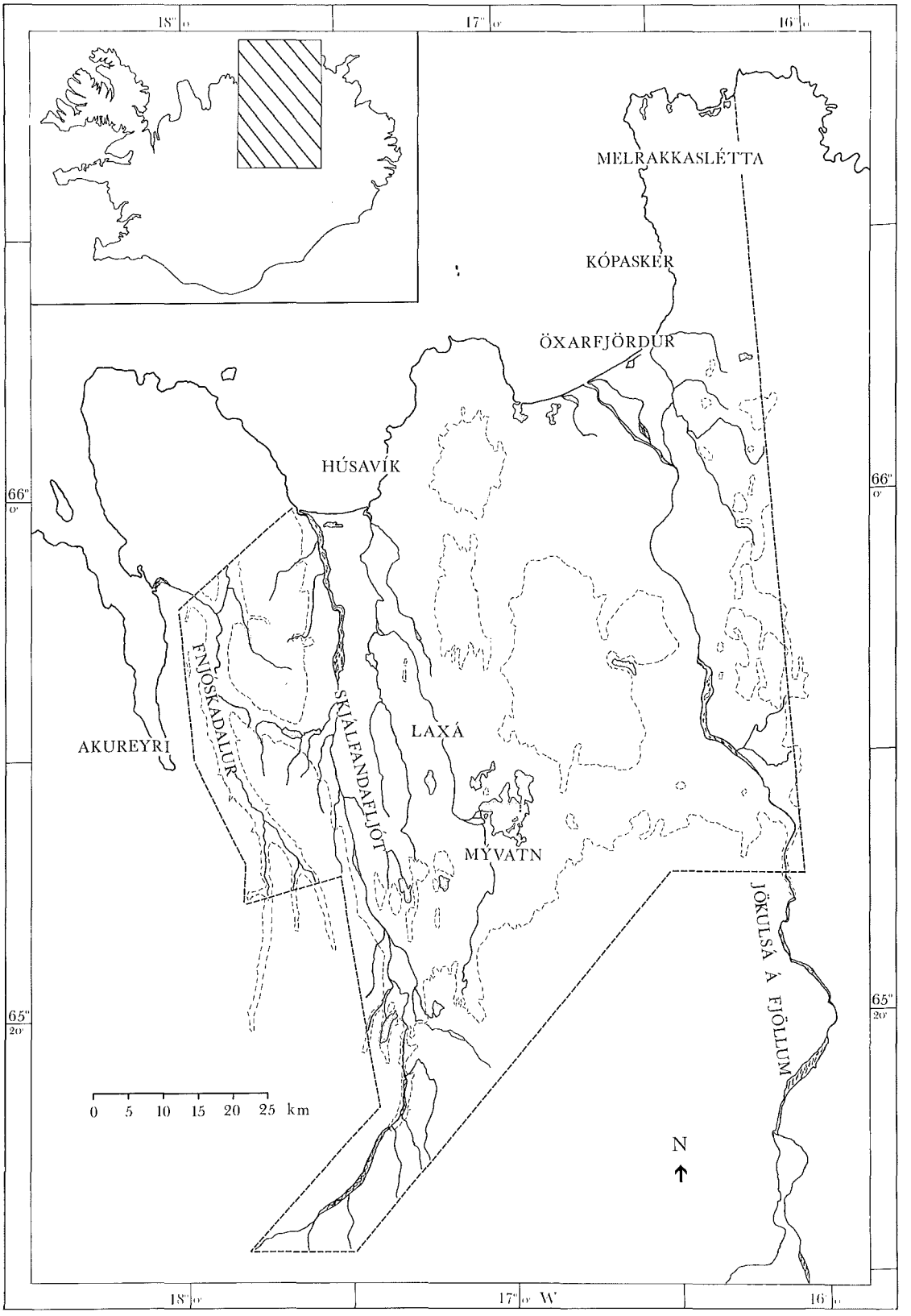

18° 0'
17° 0'
16° 0'
MELRAKKASLÉTTA
KÓPASKER
ÖXARFJÖRDUR
HÚSAVÍK
66° 0'
FNJÓSKADALUR
SKJÁLFANDAFLJÓT
LAXÁ
AKUREYRI
MÝVATN
JÖKULSÁ Á FJÖLLUM
65° 20'
0 5 10 15 20 25 km
N
18° 0'
17° 0' W
16° 0'

Fig. 4.

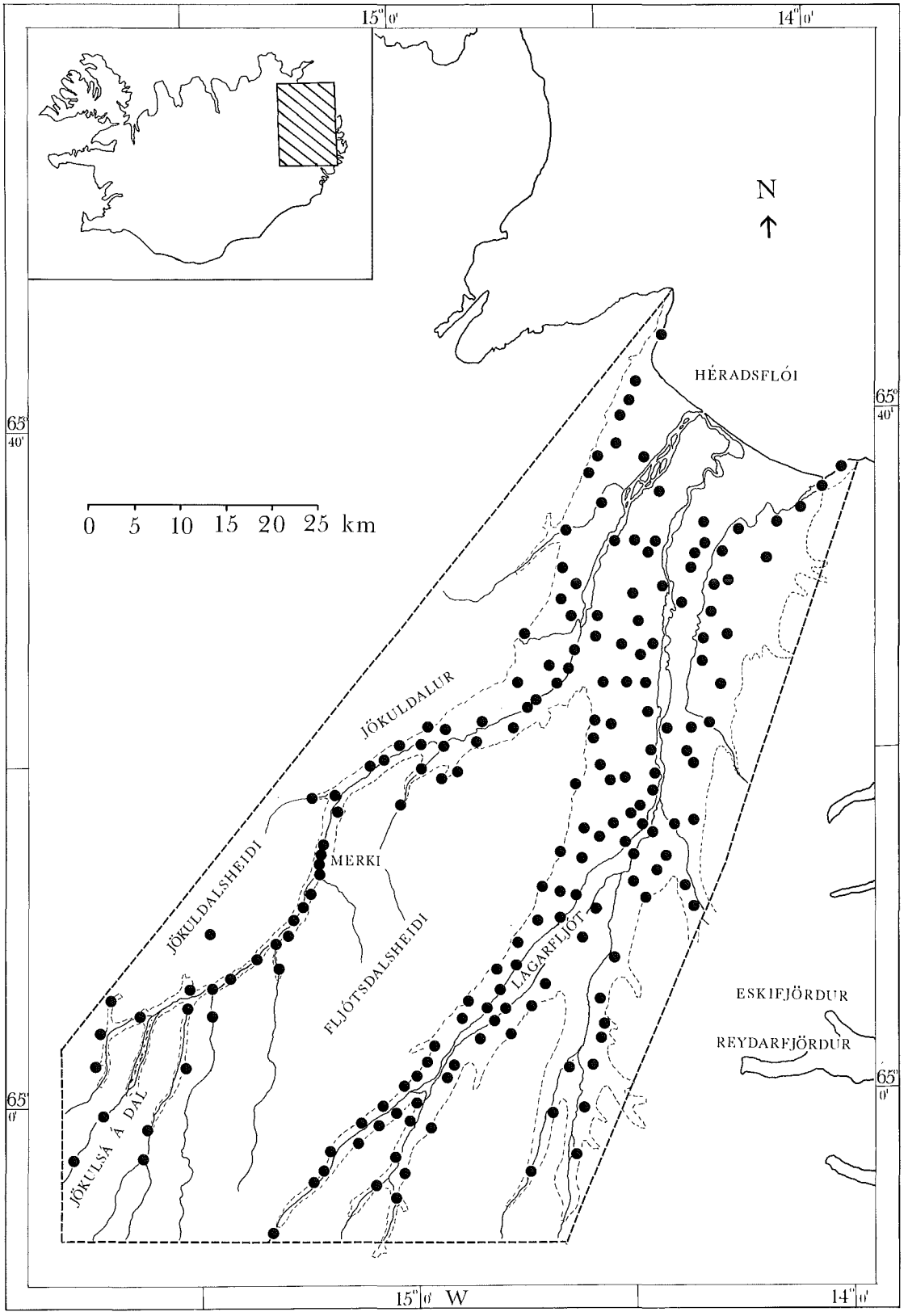

15° 0'
14° 0'
N
HÉRADSFLÓI
65° 40'
0 5 10 15 20 25 km
JÖKULDALUR
JÖKULDALSHEIDI
MERKI
FLJÓTSDALSHEIDI
LÁGARFLJÓT
ESKIFJÖRDUR
REYDARFJÖRDUR
65° 0'
JÖKULSÁ Á DÁL
15° 0' W
14° 0'

Fig. 5.

observed, they were regarded as a non-breeding pair. If only one bird was seen, the territory was judged to be occupied by a single bird. Other signs of raven activity in the absence of a lined nest (e.g., white-wash on cliffs, fresh pellets, or freshly molted feathers) were used only to indicate that the territory was occupied.

We measured breeding densities of ravens in four areas (Fig. 2); furthermore, we used occupancy rates of raven territories to estimate the total breeding population and densities of ravens in our three major study areas.

The laying date of the first egg was usually back-calculated from partially laid clutches, partially hatched broods, or the estimated age of young nestlings (based on length of tarsi, remiges, etc. from nestlings of known age). We assumed that one egg was laid daily, the incubation period was 21 days, and incubation started with the second egg laid (Stiehl 1985).

The number of young fledged from successful nests was usually considered as the number of banded nestlings or young near fledging, unless otherwise indicated. This figure somewhat overestimates the number of fledged young because some mortality takes place just prior to fledging (e.g., at least 3 young of fledging age became entangled in nest material and died while still in the nest).

We banded 587 raven nestlings in the study areas during 1981-85: 78 in the Southwest, 275 in the Northeast, and 234 in the East. We also banded 26 full-grown birds, mostly non-breeders (App. 1). Ravens were banded with numbered stainless steel bands provided by the Icelandic Museum of Natural History. During 1982-85, we also placed unique combinations of plastic color leg-bands on ravens banded in the Southwest and East study areas. Ravens were checked for color bands, both in the study areas and sporadically in other parts of Iceland. By 31 December 1988, 244 recoveries of the ravens we banded as nestlings were available, and they form the basis for our banding analysis. For comparisons, we also used other raven recoveries (n = 46) from the files of the Icelandic Museum of Natural History. A total of 841 ravens, including our 613 birds, were banded in Iceland between 1928 and 1987; 86% of these have been banded since 1981, and 94% were nestlings (App. 1). Six banded pet ravens were omitted from the totals. Details of a few of the oldest recoveries of ravens have been published (Björnsson 1936, 1940; Skovgaard 1937), but no banding summaries have been published for the past 40 years.

We were unable to calculate age-specific survival rates from these banding records because almost all the recoveries were ravens banded as nestlings (cf. Brownie et al. 1985).

We used plumage and palate color to determine the age of ravens killed in non-breeding and wintering flocks (Kerttu 1973, Boersma 1978). As ravens are sexually dimorphic, members of some pairs could be sexed in the field. In Iceland, male ravens (1453 ± 94 g, range 1240-1625 g, n = 30) were on average 17% heavier than females (1228 ± 98 g, range 1010-1398 g, n = 35; based on non-breeding birds caught in May and June, 1984-85).

Data on the numbers of ravens killed were obtained from the Wildlife Damage Control Unit and a few additional individuals who kept accurate records of their raven control activities.

Statistical analysis were performed with a statistical software package (Systat by Systat, Inc., version 3.0; Wilkinson 1986). As we had unequal sample sizes in our ANOVA-tests, we followed up significant ANOVA's with Tukey's honestly significant difference (HSD) test.

RESULTS AND DISCUSSION

Breeding biology

Nesting habitat

The breeding range of ravens in Iceland is mostly confined to the lowland areas, i.e. below 400 m a.s.l. (Figs 1, 3, and 5). All but one of the nest sites in the Southwest, 94% in the Northeast, and 90% in the East, respectively, were below 400 m a.s.l. (Figs 3 and 5). In the Northeast and East study areas, however, individual raven pairs nested between 500-600 m a.s.l.; one historical nest site in the East, never used during our study, was 840 m a.s.l.

Fig. 5 (page 8). The East study area with major rivers; the broken line indicates the boundaries. Dots refer to raven territories; the feint dashed lines are the 400 m contour.

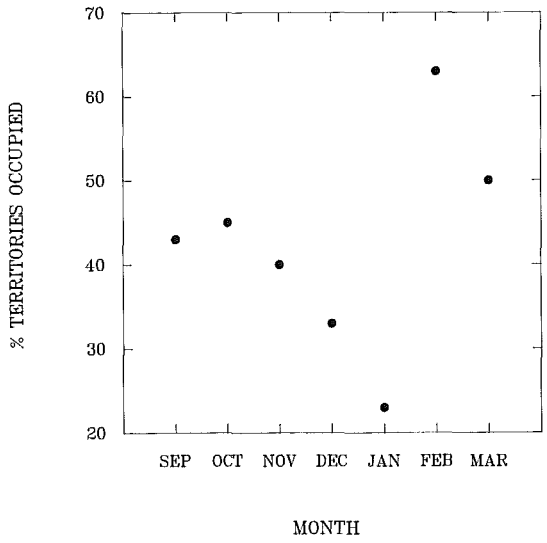


Fig. 6. Occupancy rate of raven territories during the non-breeding season (September-March) in Northeast Iceland, combined for 1983-85. Number of territories checked during each month ranged from 10-20.

Most of the raven nests were built on various types of cliffs. In the Southwest lowlands, east of the Ölfusá-Hvítá river, 48% (43/89) of pairs used man-made structures, e.g., electric transmission towers, abandoned farm dwellings, barns, and grass silos (Fig. 3). There are only scattered records of such nests in other parts of the country (Skarphédinsson et al. in press). A few tree-nesting ravens have been found in the Southwest, North, Northeast, and East. Several historical raven nest sites in the expanding urban areas in the Southwest have been abandoned, probably due to human disturbance, or because the nest sites have been destroyed.

Occupancy of territories

Ravens in the Northeast were seen in their territories in all months during the non-breeding season, September- March (App. 2). The percentage of occupied territories did not change significantly among months (Fig. 6; $\chi^2 = 5.53$, df = 6, $P < 0.50$). The overall mean occupancy rate of raven territories under observation throughout the year in the Northeast was 44% during the non-breeding season. We regard these occupancy figures from the non-breeding season as minimal; ravens probably spend most of the daylight hours foraging during the short days of winter and only return to roost in their territories after dark (cf. No. 12 in App. 2). We, therefore, believe that most raven pairs stay in, or close to their territories year round. This conclusion is supported by anecdotal observations from the Southwest and East. In other parts of their range, where ravens have been observed in similar fashion, most pairs appeared to stay in their territories throughout the year, e.g. in the British Isles

Table 1. Occupancy of territories and nest success of ravens in Southwest Iceland, 1982-84.

Parameter	1982		1983		1984		Overall mean
Number of territories checked	67		59		30		
Number occupied[a]	47	(70%)	44	(75%)	21	(70%)	(72%)
Number of successful pairs[b]	38	(81%)	33	(75%)	15	(71%)	(77%)
Number of unsuccessful pairs	7	(15%)	9	(20%)	3	(14%)	(17%)
Number of non-breeding pairs	2	(4%)	2	(5%)	2	(10%)	(5%)
Number of non-breeding bird(s)					1	(5%)	(1%)
Nest success[c]	84%		79%		83%		82%
Young/successful pair	3.6		3.2		3.6		3.5
Young/breeding attempt	3.0		2.5		3.0		2.9
Young/occupied territory	2.9		2.4		2.5		2.7

[a]Differences in occupancy rates among years; $\chi^2 = 0.31$, df = 2, NS.
[b]Differences in proportions of successful pairs among years; $\chi^2 = 0.57$, df = 2, NS.
[c]Differences in nest success among years; $\chi^2 = 0.26$, df = 2, NS.

Table 2. Occupancy of territories and nest success of ravens in Northeast Iceland, 1981-85.

Parameter	1981		1982		1983		1984		1985		Overall mean
Number of territories checked	100		117		135		135		109		
Number occupied[a]	63	(63%)	68	(58%)	79	(58%)	84	(62%)	56	(51%)	(59%)
Number of successful pairs[b]	40	(63%)	50	(73%)	49	(62%)	53	(63%)	42	(75%)	(67%)
Number of unsuccessful pairs	18	(29%)	8	(12%)	15	(19%)	18	(21%)	9	(16%)	(20%)
Number of non-breeding pairs	2	(3%)	4	(6%)	9	(11%)	10	(12%)	1	(2%)	(7%)
Number of non-breeding bird(s)	3	(5%)	6	(9%)	6	(8%)	3	(4%)	4	(7%)	(6%)
Nest success[c]	69%		86%		77%		75%		82%		77%
Young/successful pair	3.7		3.0		3.1		3.2		3.5		3.2
Young/breeding attempt	2.6		2.6		2.4		2.4		2.9		2.5
Young/occupied territory	2.3		2.2		1.9		2.0		2.6		2.1

[a]Differences in occupancy rates among years; $\chi^2 = 3.83$, df = 4, NS.
[b]Differences in proportions of successful pairs among years; $\chi^2 = 7.58$, df = 4, NS.
[c]Differences in nest success among years; $\chi^2 = 5.97$, df = 4, NS.

(Ratcliffe 1962, Newton et al. 1982, Dare 1986, Ewins et al. 1986); northern Germany (Schmidt 1957, Gothe 1961, Prill 1983); Northwest Territories, Canada (Poole and Bromley 1988); and Maine (Heinrich 1989). Some pairs, however, left their territories temporarily in either mid-winter (Wales; Newton et al. 1982, Wyoming; Dorn 1972, Oregon; Stiehl 1978, 1985), or late summer and early fall (northern Germany; Emeis 1951, Gothe 1961).

Occupancy rates of raven territories during the breeding season in our three study areas remained relatively stable and did not differ significantly among years during 1981-85 (Tables 1-3). Overall occupancy rates were 72%, 59% and 67% in the Southwest, Northeast, and East, respectively. The occupancy rate in the Northeast was significantly lower than in either the East ($\chi^2 = 4.94$, df = 1, $P < 0.05$) or the Southwest ($\chi^2 = 8.40$, df = 1, $P < 0.005$) which were not significantly different from each other ($\chi^2 = 0.87$, df = 1, $P < 0.50$). In 1987, occupancy rates of raven territories in the Southwest and East study areas were 70% (n = 63) and 70% (n = 130), respectively.

In other areas where comparable information was available, occupancy rates of raven territories were considerably higher than in

Table 3. Occupancy of territories and nest success of ravens in East Iceland, 1981-85.

Parameter	1981		1982		1983		1984		1985		Overall mean
Number of territories checked	53		52		58		64		45		
Number occupied[a]	32	(60%)	34	(65%)	40	(69%)	45	(70%)	31	(69%)	(67%)
Number of successful pairs[b]	28	(88%)	26	(76%)	31	(78%)	34	(76%)	26	(84%)	(80%)
Number of unsuccessful pairs	2	(6%)	2	(6%)	5	(12%)	6	(13%)	3	(10%)	(10%)
Number of non-breeding pairs	2	(6%)	3	(9%)	2	(5%)	5	(11%)	1	(3%)	(7%)
Number of single birds			3	(9%)	2	(5%)			1	(3%)	(3%)
Nest success[c]	93%		93%		86%		85%		90%		89%
Young/successful pair	3.8		3.5		2.6		3.3		3.3		3.3
Young/breeding attempt	3.5		3.2		2.2		2.8		3.0		2.9
Young/occupied territory	3.3		2.7		2.0		2.5		2.8		2.6

[a]Differences in occupancy rates of territories among years; $\chi^2 = 1.79$, df = 4, NS.
[b]Differences in proportions of successful pairs among years; $\chi^2 = 2.24$, df = 4, NS.
[c]Differences in nest success among years; $\chi^2 = 1.07$, df = 4, NS.

Table 4. Breeding densities of ravens in Iceland, 1981-87.[a]

Study area	Year(s) censused	Area (km^2)	Raven pairs present	Raven pairs/ 100 km^2
Fljótshlíd, SW	1983	236	16	6.8
Southern Reykjanes, SW	1987	680	21	3.1
Reykjavík, SW	1982	450	19	4.2
Önundarfjördur, NW	1985	428	23	5.4
Southwest[b]	1982-84	4600	169-181[c]	3.7-3.9
Northeast	1981-85	5900	76-97[d]	1.3-1.7
East	1981-85	4750	113-126[e]	2.4-2.7

[a]For geographic boundaries of regions employed, see Figs 2-5.

[b]Includes the Fljótshlíd, southern Reykjanes Peninsula, and Reykjavík areas.

[c]Calculated using the percentage of raven territories occupied by pairs (70-75%; Table 1), and the total number of raven territories known in the area (n = 241; Fig. 3).

[d]Calculated using the percentage of raven territories occupied by pairs (47-60%); Table 2), and the total number of raven territories known in the area (n = 162).

[e]Calculated using the percentage of raven territories occupied by pairs (60-67%; Table 3), and the total number of raven territories known in the area (n = 188; Fig. 5).

our study areas, but as in Iceland, they were relatively stable among years; Central Wales 80-86%; Northern Wales 91%; Orkney 84-93%; Switzerland 89-94%; Oregon (75-80%); Idaho 1974-78: 84-100%, but dropped to 71% in 1979 (App. 3).

Breeding density

Raven breeding densities in Iceland are difficult to estimate because of the patchy dispersion of raven habitat and the concentrations of nesting pairs along sea cliffs, river valleys surrounded by barren highlands, or heathlands devoid of potential nest sites. The estimated mean densities in our 3 main study regions (Figs 2-5) ranged from 1.5 pairs/100 km^2 in the Northeast to 3.7 pairs/100 km^2 in the Southwest (Table 4). All study regions had some habitat that was unsuitable for nesting ravens, mainly high ground (above 500 m a.s.l.). Direct measurements of breeding densities of ravens in smaller areas of more or less continuous raven habitat within the Southwest region and in the Northwest, gave somewhat higher figures (3.1-6.8 pairs/100 km^2; Table 4).

With the exception of high breeding densities in some areas of Wales and the Scottish Isles (up to 14 pairs/100 km^2), and some sections along the Snake River, Idaho, most reported densities of breeding ravens ranged from 2-6 pairs/100 km^2 (App. 3). Densities over 7 pairs/km^2 have otherwise only been reported from relatively small study areas (<150 km^2). This could indicate a bias towards selecting either small study areas with high breeding densities, or areas too large for adequate search of breeding pairs (cf. Village 1984). Also, large study areas tend to be less homogenous than small ones; consequently they generally include relatively more unsuitable habitat.

Breeding phenology

Territorial behavior (i.e., aerial pursuits of conspecific intruders) was seen in the Southwest as early as late January. An unusually early pair was observed nest-building in the Southwest lowlands about 10 February 1985, but deserted before the nest was completed. During 1981-85, nest-building ravens were observed in the East as early as 15 March (1985). Ravens initiated egg-laying in the first week of April, and by 21 April, 86% of raven pairs in the Southwest and 82% of those in the East (excluding 1983) had laid their first egg (Fig. 7). The mean laying date of the first egg in the Southwest was 16 April, both in 1982 and 1983. Laying dates of the first egg were significantly different among years in the East

(ANOVA, F= 10.997, df = 4,82, P < 0.001); 1983 (mean = 29 April) differed significantly from all the other years (means = 13-18 April; Tukey's HSD test). In the cold spring of 1983, one of the coldest on record in Iceland (Icelandic Meteorological Office 1983), ravens in the East laid, on average, two weeks later than in other years (Fig. 7).

Clutch size

Because we visited most raven nests only during the nestling period, our data on clutch sizes were too few for comparisons. Combined for all areas and years, with some additional clutches from other years, the mean clutch size was 4.6 (n = 73), and the modal clutch size 5 (Table 5). This is rather small; most studies have reported between 5 and 6 eggs per clutch (App. 4). Some clutches observed by us were from late nesting ravens, and the eggs were often counted late in the incubation period after losses could have already occurred. Clutch size in ravens is inversely correlated with laying date; the earliest clutches have been reported to be the largest (Marquiss et al. 1978). Also, there was a significant negative correlation between brood size and initiation of laying in the East (Spearman's rank correlation test, r_s = -0.381, n = 81, P < 0.01). In many different groups of birds, both clutch and brood sizes decrease with later laying dates (Newton and Marquiss 1984).

Some ravens in Iceland renested if their original nests were destroyed during the early incubation period. In the Northeast, 7 out of 8 pairs that lost their nests in a snowstorm in April, 1984, relaid; all 7 pairs built new nests for the second clutch. Most of the renesting attempts occurred within the same stretch of cliffs as the first nesting attempt. Four of the 7 new nests were 2-200 m from the old nests; the others were 800, 1000, and 2500 m apart. None of the above birds were individually marked; the birds were, however, closely observed during the early nesting period. Ravens in the Northeast relaid as soon as 10 days after the old nest was destroyed, similar to ravens in northern Germany (usually within 11-14 days; Emeis 1951) and Oregon (some completed second clutch within 11 days; Stiehl 1978).

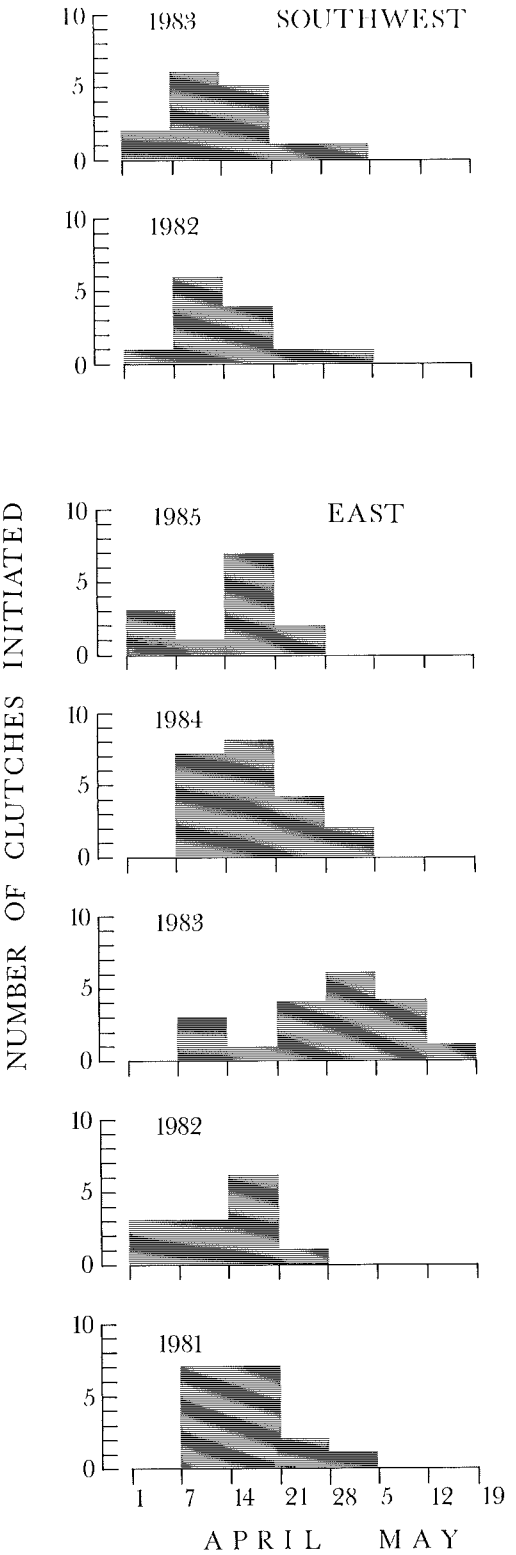


Fig. 7. Initiation of laying for ravens in Southwest (1982-83) and East Iceland (1981-85).

Table 5. Clutch sizes of ravens in the three study areas in Iceland, 1977-87.

Area	Years	Number of clutches examined[a]	Number of clutches of indicated size						Mean clutch size ± SD
			2	3	4	5	6	7	
Southwest	1982-83	12		1	2	4	5		5.1 ± 1.0
Northeast	1977-85	33	1	4	13	9	4	2	4.5 ± 1.1
East	1981-87	28	1	3	7	13	3	1	4.6 ± 1.1
All	All	73	2	8	22	26	12	3	4.6 ± 1.1

[a]Probably includes some second clutches.

Brood size

Brood size in Icelandic ravens is relatively high compared to most other studies, in which 1.4 to 4.0 fledglings per successful nest have been reported (App. 4). In this study, the mean number of fledglings per successful raven pair for all areas and years combined was 3.3 (Table 6). The modal brood size for all areas in most years was 4. No significant differences in brood size existed among areas (ANOVA, $F = 1.229$, $df = 2,252$, $P = 0.294$), but brood size differed among years (ANOVA, $F = 2.855$, $df = 4,252$, $P = 0.024$). Significant differences were between 1981 (mean = 3.7) vs. 1982 (mean = 3.2) and 1983 (mean = 3.0), and 1983 vs. 1985 (mean = 3.4; Tukey's HSD test). We used ANOVA on several subsets of our data to test if there were any interactions between years and areas, but none was found.

The difference between mean clutch size and mean number of fledglings was probably due to eggs failing to hatch or mortality during the early nestling stages (cf. Ratcliffe 1962, Newton et al. 1982, Stiehl 1985).

Non-breeding pairs

The overall mean percentage of non-breeding territorial pairs for all areas and years was

Table 6. Brood sizes of ravens in the three study areas in Iceland, 1981-85.

Area	Year	Number of broods examined	Number of nests with indicated brood size						Mean brood size ± SD
			1	2	3	4	5	6	
Southwest	1982	13	1	2	3	4	1	2	3.6 ± 1.5
	1983	12	1	2	3	5	1		3.2 ± 1.1
	1984	5		1	1	2	1		3.6 ± 1.1
	All	30	2	5	7	11	3	2	3.5 ± 1.3
Northeast	1981	21		3	7	6	4	1	3.7 ± 1.1
	1982	32	5	7	6	10	4		3.0 ± 1.3
	1983	36	6	6	8	12	3	1	3.1 ± 1.3
	1984	30	1	8	7	11	3		3.2 ± 1.1
	1985	17	1	3	5	4	2	2	3.5 ± 1.5
	All	136	13	27	33	43	16	4	3.2 ± 1.3
East	1981	17		1	6	6	4		3.8 ± 0.9
	1982	12	1	1	3	5	2		3.5 ± 1.2
	1983	22	4	6	8	2	2		2.6 ± 1.2
	1984	26	2	4	7	10	3		3.3 ± 1.1
	1985	16	3	2	2	5	4		3.3 ± 1.5
	All	93	10	14	26	28	15		3.3 ± 1.2
All	All	259	25	46	66	82	34	6	3.3 ± 1.2

Table 7. Causes of nest failures of ravens in the three study areas in Iceland, 1981-85.

Parameter	Southwest		Northeast		East	
Number of breeding attempts monitored	105		302		163	
Destroyed by humans	14	(13%)	50	(17%)	7	(4%)
Deserted	0		0		1	(1%)
Catastrophic events[a]	0		6	(2%)	4	(2%)
Unknown[b]	5	(5%)	12	(4%)	6	(4%)
Total number of failed nest	19	(18%)	68	(23%)	18	(11%)

[a]Inclement weather, nest collapsed, etc.
[b]Probably none of the nests in this category were destroyed by humans; most of them failed in the early nesting stages.

9%; in the Southwest, 4-10% (mean = 5%; Table 1); Northeast, 8-19% (mean = 13%; Table 2); and East, 6-18% (mean = 10%; Table 3). Two of 5 non-breeding pairs were yearlings, according to their plumage.

In a 5-year study in Central Wales, 8-17% (mean = 11%) of territorial raven pairs were non-breeding each year (Newton et al. 1982). In Idaho 0-19% (mean = 9%) of raven pairs were non-breeding during 8 breeding seasons (Kochert et al. 1980, 1981). Although the percentage of non-breeding pairs varied among years, the mean values for all areas in Iceland and both Wales and Idaho were similar (9-11%). The tendency to refrain from breeding during the first year as a territory holder has been observed in the Eurasian Crow (*Corvus corone*); (Loman 1984, 1985) and the Black-billed Magpie (*Pica pica*; Högstedt 1980).

Nest success

We observed no difference in nest success among years, i.e., the proportion of breeding pairs fledging at least one young. Nest success was significantly higher ($\chi^2 = 8.44$, df = 1, $P < 0.005$) in the East (89%) than in the Northeast (77%; Tables 2 and 3). This difference was almost entirely due to a higher level of human persecution in the Northeast, where, on average, 17% (range = 11-28%) of all the nesting attempts were destroyed annually by humans. This compares to mean values of 13% and 4% in the Southwest and the East, respectively (Table 7). In some localities in the Northeast (e.g., in the waterfowl nesting areas of Lake Mývatn and Laxárdalur), raven nests were destroyed systematically, whereas in the Southwest, destruction of raven nests appeared more as a result of vandalism rather than conscious control measures. The overall mean number of young produced per occupied territory in the Northeast (2.1) was lower than in the Southwest (2.7) and the East (2.6; Tables 1-3). The overall mean nest success for Icelandic ravens in all years and areas, despite persecution of breeding pairs, was 83%, one of the highest ever recorded for ravens (App. 4).

Dispersal of young

We saw young ravens away from their parents' territories and unaccompanied by adults as early as 10 June. Of 20 groups of young observed between 16 July and 9 August, 10 were not associated with adults, 6 were in non-breeding flocks, and 4 were in their natal territories (App. 5). The last date on which young were definitely seen in association with their parents was 18 July. The last date young were seen in their natal territory was 1 August (Table 8). Most raven young, therefore, seemed to disperse away from their parents' territories about 4-6 weeks after fledging, or in the second half of July in Iceland. This pattern is, furthermore, verified by band recoveries (Fig. 8); the distances between banding and recovery locations of juvenile ravens increased significantly from June to late September (Spearman's rank correlation test, $r_s = 0.423$, n = 62, $P < 0.01$).

Stiehl (1985) and Dorn (1972), both working in the western United States, observed about the same post-fledging dependency period as

Table 8. Breeding phenology of ravens in a closely observed territory, Merki in East Iceland, 1982-83.

Parameter	1982	1983
Initiation of laying	15 April	11 April
Number of young fledged	4	3
Date last young fledged	19 June	15 June
Young roosting in nest until	23 June	19 June
Young last seen	28 July (3 young)	1 August (1 young)

we did, about 4-6 weeks. In contrast to this pattern, others (e.g., Emeis 1951, Schmidt 1957, Gothe 1961, Prill 1983, all working in Germany; Hauri 1956, 1958, working in Switzerland; Dement'ev and Gladkov 1970 and Goodwin 1976) claim that young ravens remain under parental care from 3-8 months, but none of them used individually marked birds. In Idaho, 5 transmitter-equipped juvenile ravens joined communal roosts that were up to 61 km away from their natal areas, within 6 weeks of fledging (Young and Engel 1988). Post-fledging dependency of raven young is relatively short compared to some other *Corvus* species where young may stay in their parents territory for more than a year (App. 6).

Recruitment to the breeding population

Each year, 1983-85, and in 1987, we checked ravens in 10-20 territories in the East for individuals color-banded as nestlings. We found only a single color-marked bird that had been recruited into the breeding population during that period, a female according to size (the smaller member of the pair) and behavior (did most of the incubating). This bird, banded as a nestling in 1983 at Merki in Jökuldalur, East Iceland, returned to its natal territory in March, 1984. In the spring of 1985, at 2 years of age, this bird bred and raised young; it nested again in 1986 and 1987. Besides, three of our banded ravens were shot in their territories in late winter or spring, all at Lake Mývatn in the Northeast, but none of the birds laid eggs. A 6-year-old female banded in the East was shot at her nearly completed, but empty nest in the Northeast in May of 1988, 112 km from the banding location. Ravens have either not been present, or were killed in this territory annually since 1979 (Egill Freysteinsson, pers. comm.), hence this bird was probably breeding for the first time. The other cases involve two banded birds, both paired when shot at the same raven breeding site in March 1987 within 19 days of each other; they were 3 and 5 years old, and had dispersed 34 and 31 km from their natal areas, respectively (Ingi Yngvason, pers. comm.). The only other published records of first breeding in wild ravens are of a 2-year-old female that bred unsuccessfully in Idaho (Kochert et al. 1977) and a 6-year-old male in Orkney, Scotland (Booth 1986).

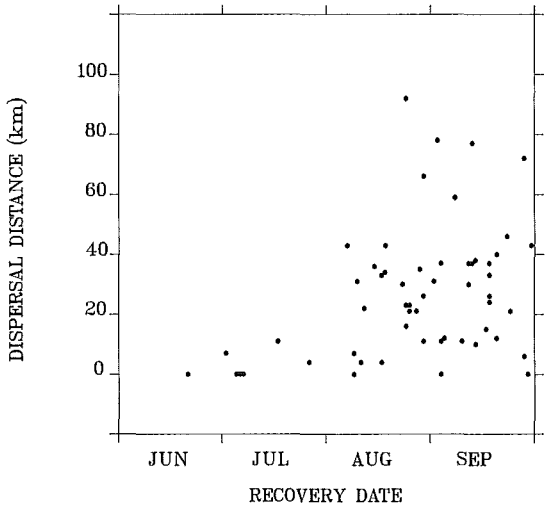


Fig. 8. Dispersal distances of juvenile ravens in Iceland recovered during June-September, 1981-85 (n = 62).

Recoveries of banded birds

Recovery rate

The overall band-recovery rate of 587 ravens banded as nestlings in the study areas during 1981-85 was 42%. The rates differed significantly among areas (Table 9; χ^2 = 21.31, df =

Table 9. Number of ravens banded and recovered in Iceland, 1928-87.[a]

Parameter	Nestlings banded in: Southwest 1982-84	Northeast 1981-85	East 1981-85	Other 1928-80	Other 1981-87	Adults banded 1957-85	All
Number banded	78	275	234	99	108	47	841
Number recovered	14 (18%)	130 (47%)	100 (43%)	13 (13%)	25 (23%)	8 (17%)	290 (34%)
Number reported within a year and percentage of total band recoveries	10 (71%)	92 (71%)	50 (50%)	9 (69%)	20 (87%)	4 (50%)	185 (64%)
Number reported killed by humans	12 (86%)	118 (91%)	84 (84%)	8 (62%)	19 (76%)	6 (75%)	247 (85%)

[a]Recoveries were tallied through 31 December 1988.

2, $P < 0.001$); they were highest for young banded in the Northeast (47%), followed by the East (43%) and the Southwest (18%). The Northeast and East did not differ from each other ($\chi^2 = 0.87$; df = 1, $P < 0.50$). In addition to the recoveries reported in Table 9, we were told of at least 31 more banded ravens that were killed during 1981-85, but the bands had either not been returned or were lost. Eighteen of those were killed around fledging age. In general, we believe that most bands were returned; we knew most of the controllers personally and regularly contacted them to get recovered bands.

The recovery rates of ravens banded as nestlings in Iceland before 1980 (13%) and full-grown birds (17%) were much lower than for raven nestlings banded during 1981-87 (39%; Table 9). The level of human persecution in Iceland was lower in the past, and recoveries are probably more frequently reported nowadays than in the past. Current recovery rate of ravens in Iceland is far above those reported from other countries, with the exception of Greenland (37%); most banding schemes reported recovery rates of <10% (App. 7). As in Iceland, there are no deterrents to killing ravens in Greenland, or to reporting the recoveries. Raven control has been subsidized by the Greenland authorities; bounties were paid for up to 4000 ravens annually, and until recently, Greenlanders were paid, both for banding birds and turning in the recoveries (Salomonsen 1967). The recovery rate of ravens in Iceland was much higher than for some *Corvus* species elsewhere (2.3 – 17.5%; Rowley 1971: Table 8) and most other persecuted pest birds, raptors included (e.g., Newton 1979: Tables 55 and 57).

Recovery rates of ravens during their first year after banding (Table 9), differed significantly between the East (50% of total recov-

Table 10. The effect of brood size on recovery rate of raven nestlings banded in the three study areas in Iceland, 1981-85.

Parameter	Brood size 1	2	3	4	5	6	Total
Number banded	21	58	135	216	75	18	523
Number recovered[a]	8	27	46	106	35	6	228
Percentage recovered	38%	47%	34%	49%	47%	33%	44%

[a]Included are band recoveries from broods in which all young banded are presumed to have fledged, and recoveries after 15 July of the banding year when most raven young have gained independence.

Table 11. The effect of laying date on recovery rate of raven nestlings banded in East Iceland, 1981-85.

	Laying initiated during		
	1-15 April	16-30 April	1-15 May
Number of young banded	88	87	20
Number recovered[a]	37	38	10
Percentage recovered	42%	44%	50%

[a]Included are accurately aged broods from which all young were presumed to have fledged, and recoveries after 15 July of the banding year when most raven young have gained independence.

eries) and Northeast (71%; $\chi^2 = 9.39$, df = 1, $P < 0.005$). The overall mean first-year recovery rate (62%) was similar to those recorded for ravens in Northern Europe and Greenland (56-68%; App. 8). First-year recovery rates are commonly high for birds banded as nestlings, including crows (cf. Rowley 1971: Table 10).

Recovery rate of raven nestlings in Iceland did not depend on brood size (Table 10; $\chi^2 = 9.05$, df = 5, $P < 0.50$). This finding is in agreement with that found by Newton and Moss (1986) for the Sparrowhawk (*Accipiter nisus*), but contrary to studies of many other bird species in which recovery rates, as a measure of juvenile survival, varied with brood size (summarized in Newton and Moss 1986). Similarly, recovery rate did not depend on the laying date or, hence, the fledging date of young, (Table 11; $\chi^2 = 0.43$, df = 2, $P < 0.50$).

Seasonal variation in recovery rate

Combined for all years, recoveries of ravens banded as nestlings, peaked in late summer and early fall (August – October) and again in spring (April – May) with 45% and 24% of the recoveries coming from these respective peri-

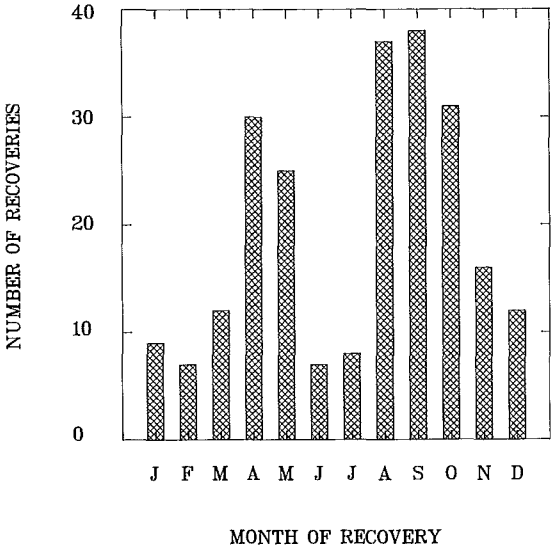


Fig. 9. Monthly distribution of raven recoveries in Iceland where date of death was known within 2 weeks accuracy (n = 231).

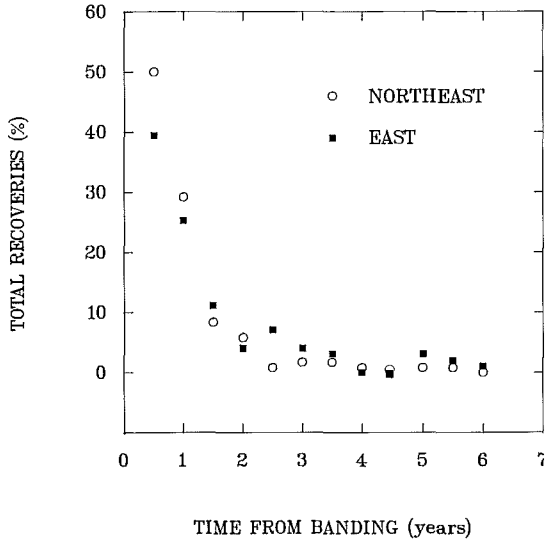


Fig. 10. Differences in recovery rates of raven nestlings banded in Northeast (n = 120 recoveries) and East Iceland (n = 100). Based on recoveries where date of death was known within 2 months accuracy. The beginning of the raven year is set at 1 June. Omitted are recoveries of three 8-year-old ravens received just before the publication of this paper.

ods (Fig. 9). This pattern reflects vulnerability of naive ravens to shooting (August – October), and persecution of ravens in eider colonies and other waterfowl nesting areas (April – May). High recovery rates for ravens during fall have been reported elsewhere where ravens are unprotected, such as in Finland and Greenland (App. 8).

Age of recovered ravens

As stated before, 62% of the recoveries came during the ravens' first year of life (Table 9); additional 25% came during their second year (cf. Fig. 10). Hence, according to band recoveries, only 13% of raven nestlings survived to breeding age (≥2-year-old).

There was a significant difference in the mean age of birds when recovered among the 3 banding areas (Fig. 11; log-transformed data; ANOVA, $F = 3.861$, $df = 2,228$, $P = 0.022$). Only the Northeast and East, however, were significantly different from each other (Tukey's HSD test). The median (mean) interval between banding and recovery was 295 (371) days for raven nestlings banded in the Southwest, 195 (311) days in the Northeast, and 312 (456) days in the East, respectively. The median (mean) interval, combined for all areas, was 254 (376) days. The differences between recovery age of nestlings banded in the Northeast and East was primarily due to higher recovery rate of Northeast juveniles during their first 6 months after fledging (57% of the totals, compared to 39% for the East nestlings; Fig. 10). This difference reflects the higher level of human persecution in the Northeast.

Raven nestlings in Britain and Sweden were recovered, on average, 550 days and 488 days after banding, respectively (Ratcliffe 1962, Strandberg 1980). Persecution of ravens in those two countries appears to be at much lower levels than in Iceland.

Insofar, the oldest ravens recovered in Iceland were 3 birds killed in their eight winter (December – March), 7, 14, and 33 km from their natal areas, respectively. As large scale banding of ravens only started in 1981, these records are not unexpected. This compares to longevity records of 12-16 years for ravens from other banding schemes (Holyoak 1971, Saurola 1977, Rydzewski 1978, Clapp et al. 1983).

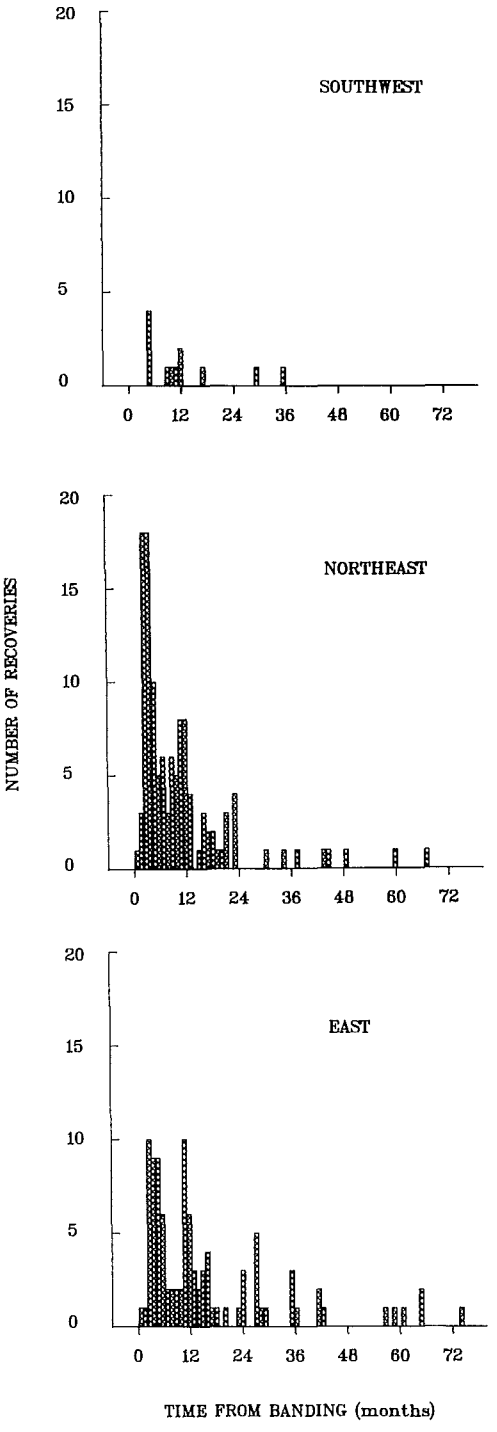


Fig. 11. Time between banding and recovery of raven nestlings from the three study areas in Iceland. Based on the same data as Fig. 9. Omitted from the figure are recoveries of one 8-year-old (= 94 months old) raven from the East and two 8-year-old ravens (91 and 93 months old) from the Southwest, received just before the publication of this paper.

Table 12. Reported causes of death of recovered ravens banded in Iceland, 1981-87.[a]

Parameter	Recovered in the following regions of Iceland:[b]						All regions	
	SW	W	N	NE	E	SE		
Government control program	5	0	4	30	8	3	50	(18%)
Local control programs	0	3	6	78	15	3	105	(39%)
Killed by others	1	3	7	37	32	3	83	(30%)
Accidents	0	0	1	2	5	0	8	(3%)
Unknown	3	0	2	11	11	1	28	(10%)
All causes	9	5	20	157	71	10	274	

[a]This table is based on 260 recoveries of raven young banded in the three study areas in Iceland during 1981-87; 9 recoveries of young banded in other regions of Iceland during 1981-87 and 5 recoveries of adults and subadults banded in the Northeast and East during 1981-85. In addition, 16 ravens were recovered during 1931-77; 9 were shot, 1 broke its wing, and 6 died of unknown causes.
[b]For geographic boundaries of regions employed, see Fig. 2.

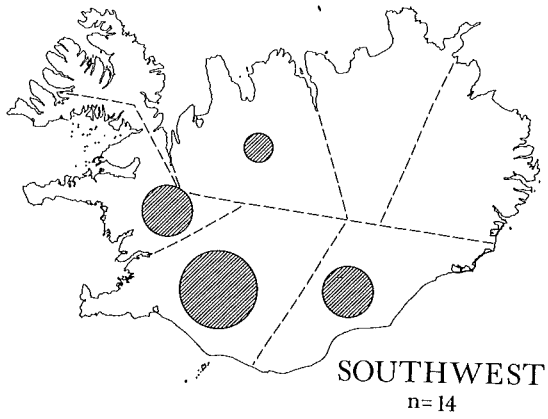
Causes of death

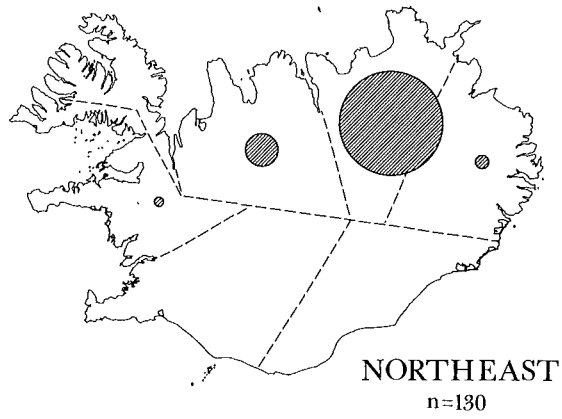
The vast majority (87%) of ravens recovered in Iceland, 1981-88, were reported killed by humans (Table 12). Governmental controllers were responsible for 18% of the recoveries; local controllers took 39% and others 30%. When governmental controllers and eider farmers used poisons to kill ravens, they made extensive searches for drugged birds as most of the ravens did not die immediately. Intoxicated birds were usually shot and all carcasses either burned or buried. Consequently, most banded birds killed with poisons were likely to be recovered and reported. Death due to unknown causes (10% of the total) probably included some birds that had been deliberately killed. The few ravens that died accidentally were caught in leg-hold traps set for mink, collided with powerlines, or were fledglings that became entangled in synthetic nest material. As in Iceland, human persecution was the most important mortality cause for ravens banded in other schemes (App. 7); the percentage of recoveries resulting from this factor, however, was considerably lower than in Iceland.

Dispersal pattern

As expected, most raven recoveries were from those regions where the banding effort was greatest, the Northeast and East (Fig. 12). Most of the recoveries were from the Northeast, mainly from two locations where ravens were heavily persecuted: Lake Mývatn and the coastal town of Húsavík, with 82 (35%) and 32 (14%) of the recoveries from the Northeast and East regions, respectively.

The distances moved by ravens between banding and recovery locations differed significantly among study areas (Fig. 13; log-transformed data; ANOVA, $F = 11.532$, df = 2,257, $P < 0.001$). Young from the Northeast travelled shorter distances (median = 30 km) than young from Southwest (median = 73 km) or East (median = 70 km; Tukey's HSD test). The Northeast young tended to stay in their banding regions, with 96% of the recoveries coming from within 80-km-radius of the banding locations (Figs 12 and 14). Only two long-distance movements were recorded; a juvenile was shot in October, and a 2-year-old bird was shot in April, 263 km and 162 km to the west of their banding locations, respectively. On the other hand, 64% and 57% of the young from the Southwest and East, respectively, were recovered within 80 km of the banding locations. Two young from Jökuldalur in the East were recovered in the Southwest, 386 km and 328 km from their natal areas. Two young from the Southwest were recovered in the West during their first fall, 200 km and 209 km from their natal areas, and one 3-year-old bird in March, 218 km from the banding place, respectively. Also, one young from the Southwest was recovered in the North in its first spring, 171 km





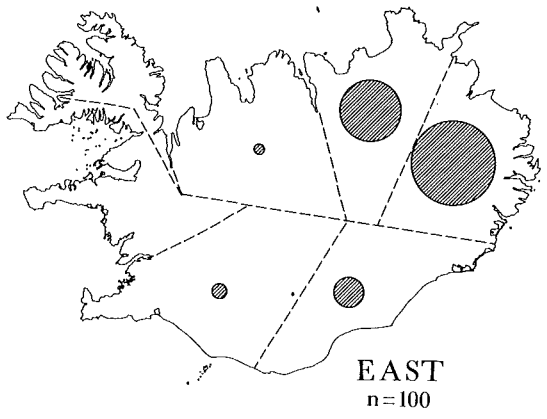


Fig. 12. Regional distribution of recoveries of raven nestlings banded in Southwest, Northeast and East Iceland during 1981-87. Circle area represents percentage of recoveries within each region of Iceland (cf. Fig. 2).

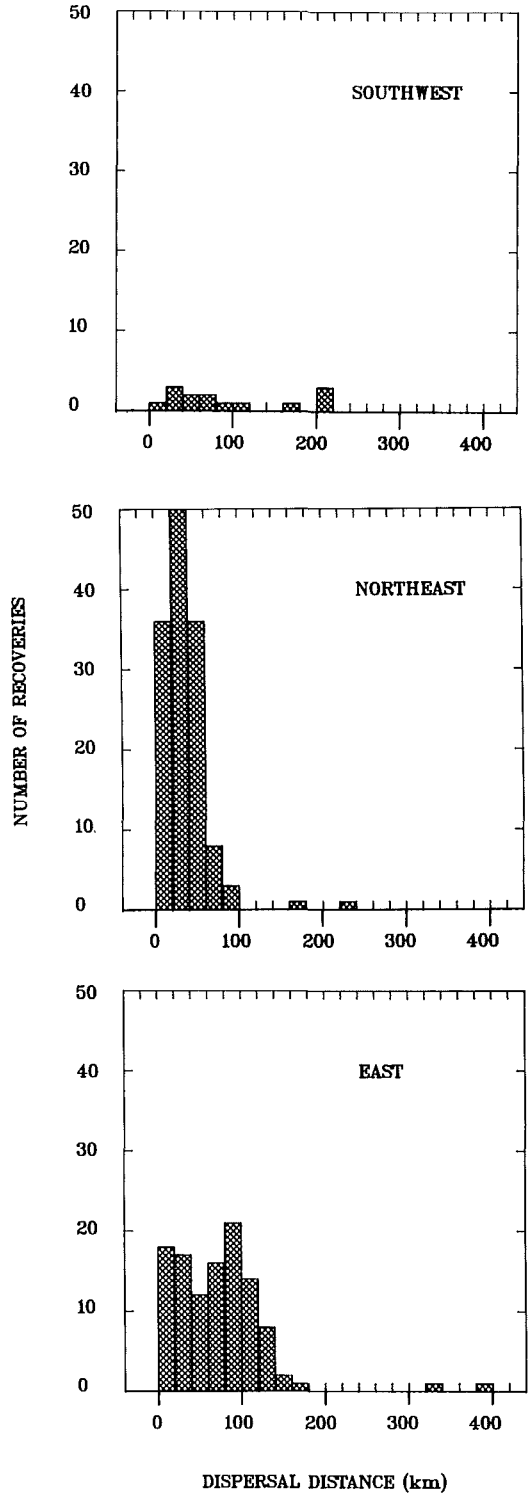
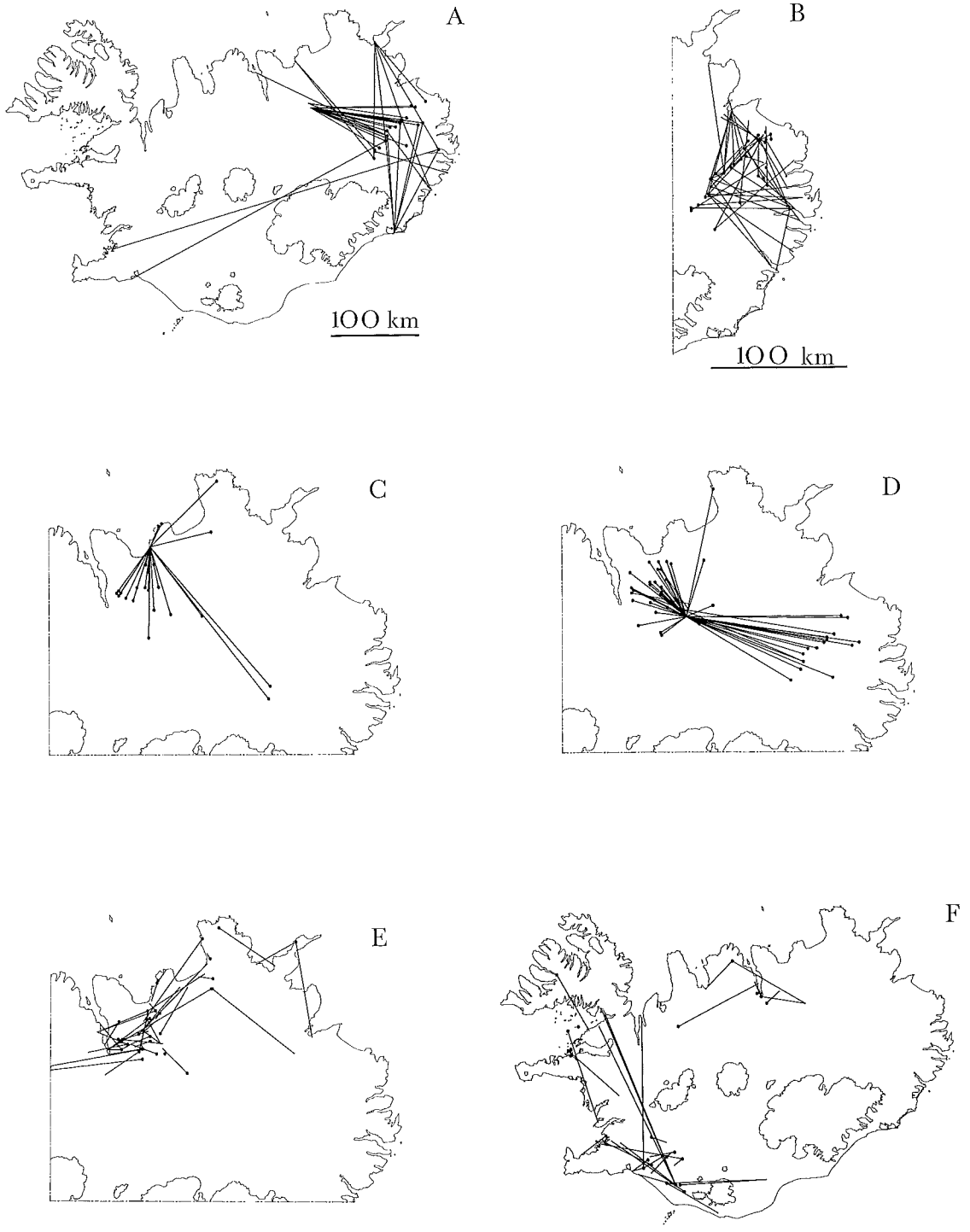


Fig. 13. Dispersal distances of raven nestlings banded in the three study areas in Iceland.


A
100 km
B
100 km
C
D
E
F

from its natal area. The maximum straight-line distance that a raven could possibly travel in Iceland is about 510 km.

Dispersal distances of raven nestlings increased with time during their first post-fledging months (June-September; Fig. 8). Otherwise, we found no significant relationship between overall dispersal distances and time from banding to recovery (ANOVA, F = 1.643, df = 1,225, P = 0.201). Similarly, we found no significant interactive effect of the banding regions and time from banding that influenced the distances moved by ravens (ANOVA, F = 0.846, df = 2,225, P = 0.431).

The differences in dispersal patterns of raven young from the Northeast and East were probably due to combination of the following:

1. The waterfowl nesting area of Lake Mývatn in the Northeast is the major inland attraction site for non-breeding ravens from early spring to late fall. The lake is within 30-40 km from most of the banding sites in the Northeast. No comparable site exists in the East, consequently, the East ravens disperse further than their Northeast counterparts to find similar feeding areas.

2. The level of human persecution of ravens is higher in the Northeast than East; 35% of the total raven recoveries came from the Mývatn area alone. The shooting of ravens during the post-fledging months is more common among the local people of the Northeast than in other parts of Iceland (cf. Table 12); many of them have animosity towards ravens because of their alleged sheep depredation. As a result, ravens in the Northeast are more likely to be shot in their natal areas.

Fig. 14. Dispersal patterns of ravens banded as nestlings in Iceland, 1928-87, and recovered through 1988. The dots are banding locations; some lines refer to more than one individual, banded and recovered at the same locations. *A* East ravens recovered >80 km from the banding locations; *B* East ravens recovered <80 km from the banding locations; *C* Recoveries from Húsavík, NE- Iceland; *D* Recoveries from Lake Mývatn, NE-Iceland; *E* Ravens banded in Northeast Iceland and recovered at other locations than shown on *C* and *D*; two birds were recovered 162 and 226 km to the west; *F* Recoveries of ravens banded outside the Northeast and East regions. Note: the scale on *A* and *F* is the same; and the scale on *B, C, D,* and *E* is the same.

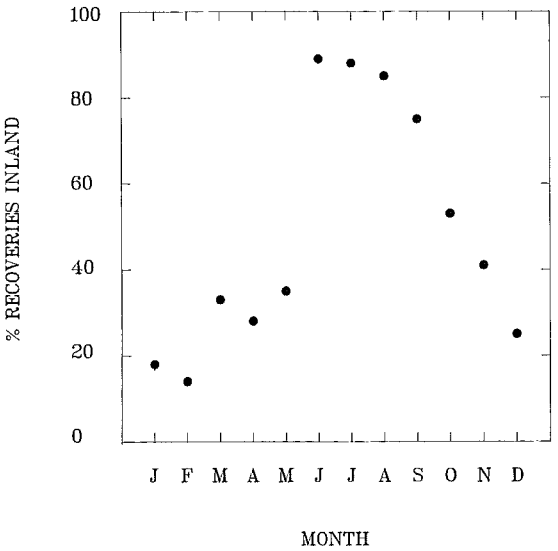


Fig. 15. Seasonal variation in percentage of ravens recovered inland (>10 km from the coast) in Iceland. Based on the same data as Fig. 9.

3. Raven fledglings in the East may disperse further, because suitable habitat in the East is saturated with breeding ravens. Greater dispersal distances of juvenile ravens from the East could, therefore, be an enforced response to local food shortage (cf. Eden 1987). Intraspecific competition is probably reduced in the Northeast where turnover rate in the raven population is higher as a result of persecution.

We divided recoveries into coastal (<10 km from coast) and inland (>10 km from coast) recovery locations (Fig. 15). Most ravens (87%) recovered during summer (June-August) were inland. This percentage declined steadily until December-February (19%). Seasonal differences in the ratio of ravens recovered inland and on the coast were highly significant ($\chi^2 = 52.14$, df = 11, $P < 0.001$). This pattern probably reflects seasonal variations in the distribution of nomadic immature ravens rather than seasonal difference in the levels of persecution between inland and coastal areas; during winter, ravens in Iceland are more abundant in the latter areas.

There is relatively little geographical variation in raven dispersal patterns in Europe and North America (App. 8). Adult ravens move short distances; juveniles disperse during their first year, and 70-80% of them do not move beyond 80 km from their banding locations. Apart from some northern populations, where

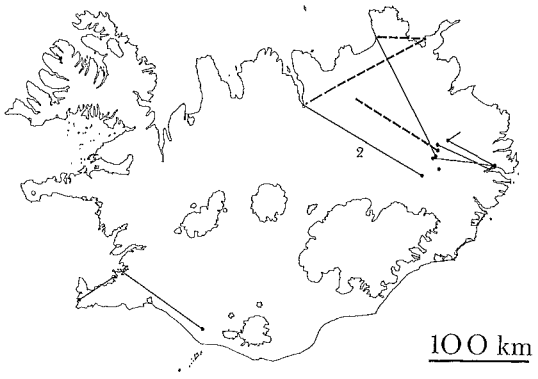


Fig. 16. Resightings of color-marked ravens. The dots are banding locations; solid lines connect banding and resighting locations; dashed lines connect resighting and recovery locations. Based on App. 9.

juveniles tended to disperse southward and longer distances than their southern counterparts, raven dispersal was random. This contrasts with some other *Corvus* species in which individuals of some populations are year-round residents but others show strong migratory behavior (Kalmbach and Aldous 1940, Busse 1969, Holyoak 1971).

Sibling associations

Dispersal distances of sibling ravens correlated significantly (Spearman's rank correlation test, $r_s = 0.622$, $n = 136$, $P < 0.01$), but the birds often moved in different directions. Distances between recovery locations of siblings recovered within a month of each other did not increase significantly with time from banding (Spearman's rank correlation test, $r_s = 0.203$, $n = 22$, NS). These recoveries ranged from 66-801 days after banding, and the siblings were 0-245 km apart when recovered. Ten of these sibling groups were recovered at the same place, and 5 were more than 100 km apart. The remaining 7 were recovered 6-49 km apart. Two siblings banded at Jökuldalur in the East were shot at Lake Mývatn, 92 km to the northwest, 11 days apart, in late summer of their third year. From these data, siblings appear likely to stay in the same general area throughout their nomadic pre-breeding years, and they may even associate with each other.

Sightings of color-marked ravens

A total of 263 ravens were color-marked in the Southwest and East during 1982-85. We did not observe any losses of color bands; some of our birds retained their color-bands for at least 5-6 years. We obtained 52 observations of color-marked ravens; on 37 occasions we positively identified the birds, which involved 24 individuals (9% resighting rate). These birds showed the same general dispersal patterns as ravens that were recovered; we observed movements of up to 140 km from the banding locations (Fig. 16; App. 9).

Non-breeding flocks

Juvenile ravens in Iceland started to join flocks of non-breeding ravens around 20 July, or 4-6 weeks after fledging (App. 5). Non-breeding ravens concentrate in large numbers at garbage dumps, fur-farms, and slaughter houses. The dumps can serve as both feeding grounds and staging areas for birds leaving or entering nearby roosts. Several large roosts (up to 400-500 birds) are known in Iceland; most are frequented by ravens that concentrate on garbage dumps during the day. The largest aggregations occur in mid-winter; e.g., 423 birds were observed at Reydarfjördur in the East in early January 1983 (Thórisson 1984), but their numbers declined to about 120 birds in June 1983.

The origin of non-breeding ravens in the Northeast

Lake Mývatn in the Northeast is about 50 km inland and adjacent to the Central Highlands. Loose aggregations of ravens occurred at the lake from spring to fall; juveniles started to show up in late July, with a major influx in August. This influx included mainly young ravens from nearby breeding areas in the Northeast, but also a few young from the East which had crossed 80-100 km of barren ground to reach the area. The number of ravens produced in the East comprised only 13% (4/30) of the juveniles recovered at Mývatn, but rose to 38% (11/29) and 59% (10/17) among yearlings and older birds, respectively.

The situation in the coastal town of Húsavík was different. All recoveries, that could be accurately dated, were from November to May, coinciding with the activity of the Wildlife Damage Control Unit at that particular location, and only 2 of 31 recoveries were of ravens banded in the East. Therefore, it seems that few juvenile ravens from the East dispersed to the Northeast during their first fall and few of them spent the winter there. In the following spring and later in life, however, they dispersed to the Northeast.

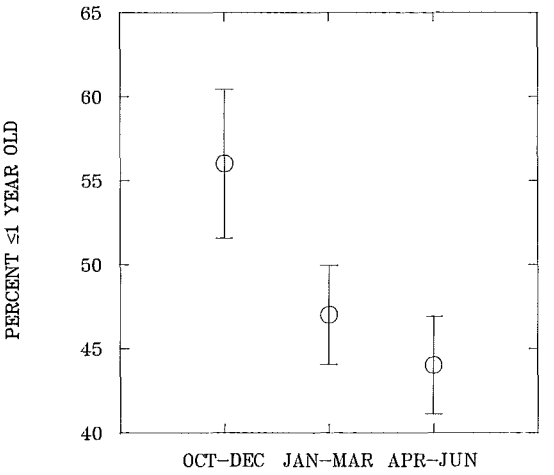


Fig. 17. Seasonal differences in percentage of ≤1-year-old ravens killed in non-breeding flocks in Iceland, 1982-85, all areas and years combined. Percentages are given with one standard error. Based on App. 10.

Age composition of the non-breeding flocks

The percentage of ≤1-year-old ravens killed in flocks of non-breeding ravens varied among locations (App. 10). Combining all samples, the percentage of ≤1-year-old birds declined significantly from October-December (56%) to April-June (44%) (Fig. 17). We do not know if these percentages reflected the actual age composition of the flocks, or if they overestimated the proportion of yearlings because of their greater vulnerability to human persecution.

The only comparable information from wintering flocks of ravens comes from North America; in Nova Scotia, percentages of ≤1-year-old ravens were relatively stable at 63-70% for 3 consecutive winters (November-March; Boersma 1978). A similar percentage (69%) of ≤1-year-old birds was observed in a group of ravens caught in Maine in mid-winter (Heinrich 1988).

Pairing and sexual maturity of non-breeders

Ravens up to 5-6 years of age, seemed to stay in non-breeding flocks (cf. App. 9 and recoveries of non-breeding ravens at Lake Mývatn). This is comparable to the Eurasian Crow in which birds up to 5 years old remain in flocks (Charles 1972). Some of the ≥3-year-old ravens in the non-breeding flocks in the East behaved as if they were paired (e.g. they allopreened and begged for food; App. 9). Several authors (e.g., Kramer 1932, Gwinner 1964, and Jollie 1976) state, without giving specific examples, that pairing of ravens occurs in non-breeding flocks during the raven's second or third year. In the Eurasian Crow, pairs are both formed in non-breeding flocks and in the territories (Loman 1985), but birds less than 20 months old were never paired (Charles 1972). Similarly, in the Jungle Crow (*Corvus macrorhynchos*), pairs are formed in the non-breeding flocks (Kuroda 1977). Pairing of Eurasian crows in non-breeding flocks is thought to be important, as both occupation of vacant territories and establishment of new ones was done by pairs, not unmated birds (Charles 1972), but see Loman (1985).

Congregations of ravens during the breeding season were mostly comprised of non-breeding birds; none of 15 female ravens, ≥2-year-old, that were killed in flocks in late spring during 1984-85, had developed gonads. Only one of 21 similarly aged males from the same sample had developed gonads.

Movements of ravens in non-breeding flocks

Seven of 16 color-marked ravens first seen in June 1984 in a non-breeding flock that frequented a garbage dump in the coastal town of Eskifjördur in the East were seen there again in March 1985. Two additional individuals from the same flock were shot 107 km to the south in October 1984 and 41 km inland in January 1986. During the summer of 1984, when we observed this flock frequently, some of

Table 13. Raven kill in Iceland estimated from registered kill and band recoveries, 1981-85.

Parameter	1981	1982	1983	1984	1985
Registered raven kill[a]	1581	2971	1773	2956	2676
Number of band recoveries from registered kill[b]	6	23	32	28	25
Percentage of recovered ravens killed by humans, coming from registered kill	50%	58%	68%	61%	54%
Estimated total annual raven kill[c]	3162	5122	2607	4846	4956

[a]From App. 11.
[b]All bands taken are assumed to be reported.
[c]Calculated using the formula: total annual raven kill = registered raven kill/percentage of recovered ravens killed by humans coming from registered kill.

these birds moved up to 8 km to another garbage dump on a day-to-day basis.

Non-breeding ravens can move considerable distances in relatively short periods. A color-marked yearling, observed at Akureyri in North Iceland on 30 March 1984, was shot 15 days later at Thórshöfn, 139 km to the northeast (Fig. 16).

In Nova Scotia, some marked, immature ravens in wintering flocks moved up to 75 km on a daily basis during winter (Boersma 1978). In Idaho, ravens moved from 9-60 km/day, averaging 22 km, and ranged up to 24 km from their roosts (Young and Engel 1988); one raven flew from its roost area to another roost 54 km away and then flew back to its original roost to spend the night (K. Engel, pers. comm.). Radio-tagged ravens in Fairbanks, Alaska made regular daily 130-km round-trip between a roost and a landfill near town (Heinrich 1989: 165). Several authors (e.g., Cushing 1941, Schultz-Soltau 1962, Stiehl 1978, Heinrich 1988, 1989) reported daily movements of ravens between roosting and foraging sites that were 20-45 km apart.

Persecution

Raven control programs

Since 1976, the Icelandic government has sponsored intensive raven control programs through the Wildlife Damage Control Unit. During 1981-85, this program and some local controllers, were responsible for almost 60% of the estimated annual raven kill (App. 11, Tables 12 and 13). Indiscriminate killing of ravens usually occurs at garbage dumps, staging areas, roosts, and where ravens concentrate around at locally abundant food. In addition, eider farmers began using stupefying drugs (mainly phenobarbitatum) in 1969; as a result many of them claim they are now more effective at killing ravens than when they only used firearms and strychnine. This level of persecution is unprecedented in Iceland and represents a dramatic increase in the number of raven killings.

The number of ravens killed and registered each year during 1981-87 ranged from 1581 to 2971 (mean = 2385; App. 11). About 70% of the ravens killed by the Wildlife Damage Control Unit were poisoned, the rest were shot (Thorvaldur Björnsson, pers. comm.). In addition, there were unknown numbers of ravens killed by others but not registered. So far, no accurate statistics are available on these killings. We used the percentage of band recoveries resulting from the registered kill (50-68%) to obtain a conservative estimate of the number of ravens killed annually in Iceland during 1981-1985 (Table 13). The estimated kill averaged 4116 (2607-5122) ravens each year.

There is geographical variation in the intensity of raven persecution in Iceland. In the Southwest and Southeast regions shooting ravens by the general public appears to be less common than in the Northeast and East, consequently, most recoveries in the Southwest

and Southeast were made by governmental or local controllers (Table 12). Furthermore, the recovery rate of ravens banded in the Southwest (18%) was much lower than for ravens banded either in the Northeast (47%) or East (43%; Table 9), indicating a much lower level of persecution of ravens in the Southwest. In the West and Northwest, however, eider farmers killed the majority of the registered birds; up to 230 ravens have been killed in a single eider colony in one year (Jónsson 1974).

The impact of persecution on ravens

A minimum 43% of all ravens banded in the Northeast and 36% of those banded in the East were reported killed by humans (Tables 9 and 12). Although little information exists on other mortality factors, human persecution undoubtedly is the single most important mortality factor for immature ravens in Iceland.

So far, the majority of ravens killed by humans are immature birds, an age group with high natural mortality. Nonetheless, in some areas of Iceland (e.g., Breidafjördur in the West and Thingeyjarsýsla in the Northeast) many breeding ravens are also killed. Occupancy rates of raven territories were constant throughout our study in all three study areas (Tables 1-3). It appears, therefore, that current persecution levels have had little impact on numbers of breeding ravens. The size of non-breeding flocks also appears to have remained relatively stable; the number of birds killed in a given area did not fluctuate much from year to year even where control measures were carried out regularly for some time (e.g., in the North, Northeast and East; App. 11). The one noticeable exception (Fig. 18) was a constant and significant decline from 1978-84 in the numbers of ravens killed per hunting day during the winter months at Húsavík in the Northeast (Spearman's rank correlation test, $r_s = -0.929$, $n = 7$, $P < 0.01$). It is, therefore, worth looking at the situation in more detail.

During 1981-85, the estimated mean annual production of raven young in the Northeast was 205 young. Using the proportion of banded birds in the registered kills, we estimate that on average approximately 367 ravens were killed annually in the Northeast during 1981-85 (Table 14). Some of these birds were immigrants; e.g., 22% of the recoveries in the Northeast were from nestlings banded in the East (cf. Figs 12 and 14), including a 6-year-old female shot at her nest 112 km from her natal territory. The persecution level of ravens in the Northeast must, however, be approaching or even surpassing the production of raven young in the region. This leads to the conclusion that the raven population in the Northeast might not be self-sustaining, but instead maintaining itself by ingress of ravens from other parts of Iceland.

Given a stationary breeding population of ravens in Iceland, on average, all young produced annually by 1738 territorial raven pairs

Table 14. Estimated annual raven kill and young production in Northeast Iceland, 1981-85.

Parameter	Estimated value for Northeast	Source
Mean annual registered raven kill in the Northeast, 1981-85	264	This study, see App. 11
Percentage of recovered ravens killed by humans in the Northeast, comming from registered kill	72%	This study
Estimated total annual raven kill in the Northeast	367	Calculated as in Table 13
Mean number of raven young produced annually in the Northeast, 1981-85	205	This study[a]

[a]Calculated using number of known territories in the region (n = 162), the annual mean percentages of territories occupied by successful pairs (40%), and annual mean brood size (3.2); all values from Table 2.

Table 15. Estimated reproductive output needed to compensate for human persecution of ravens in Iceland, 1981-85.

Parameter	Estimated value for Iceland	Source
Percentage of territorial pairs breeding	91%	This study; Tables 1-3
Percentage of successful breeding pairs	83%	This study; Tables 1-3
Young fledged/successful nest	3.3	This study; Table 6
Estimated survival rate of raven fledglings until independence in late July	95%	Guess[a]
Mean annual raven kill, 1981-85	4116	This study; Table 13
Mean number of raven pairs needed annually to compensate for human persecution[b]	1738	

[a]Post fledging mortality of ravens (i.e., before the young dispersed) of ten intensively studied sites in Idaho was 6% (Kochert et al. 1977).
[b]Calculated using the formula: pairs needed to compensate for persecution = annual kill/(percentage of territorial pairs breeding x percentage of successful breeding pairs x mean number of young fledged per successful pair x estimated young survival till late July).

were needed to compensate for the mean annual human persecution during 1981-85 (Table 15). The breeding population of ravens in Iceland was estimated about 2000 pairs in 1985 (Skarphédinsson et al. in press). If this is accurate, about 87% of the annual reproductive output of Icelandic ravens was lost to human persecution during this period.

There are few quantitative examples of how direct persecution has affected other raven populations (but see, Larsen and Dietrich 1970, Littlefield and Thompson 1987). Ravens have been incidentally killed in poisoning programs aimed at crows and mammalian predators (e.g., Kenyon 1961, Dobrowolski et al. 1962, Mead 1986: p. 73-74), but with few exceptions (Schultz-Soltau 1962, Weir 1978, Mitchell 1981, Littlefield and Thompson 1987) consequent changes in raven abundance have not been accurately quantified. In Iceland, control measures have usually only depressed raven numbers for a few months at a time, with the possible exception of the non-breeding flock at Húsavík (Fig. 18). There are, however, several unquantified accounts from various parts of Iceland on how strychnine-poisoning programs, mainly aimed at killing Arctic foxes (*Alopex lagopus*), reduced raven numbers for some years. These accounts date back from the initiation of these programs (late 1880s) to their latest expansion (1957-64; Skarphédinsson et al. in press). Since then, use of strychnine and the poisoning of foxes has been made illegal in Iceland.

Raven numbers and population regulation

No noticeable decline in raven numbers has been observed in Iceland in recent years. On the contrary, biologists and laymen alike, have claimed for decades without providing any quantitative data that the raven population is actually on the rise (cf. Skarphédinsson et al. in press). Even in the early 1940s, naturalists in West, Northeast, and East Iceland were concerned with expanding raven populations in their respective regions. Allegations of raven depredation being more common were usually attached to these claims (Skarphédinsson et al. in press). Increased offal and garbage available to ravens during winter may have improved overwinter survival of immatures, hence, larger numbers occur in the nomadic flocks. An alternative explanation is that ravens are

increasingly concentrated around feeding sites at dumps and, therefore, more conspicuous but not necessarily more numerous.

Currently there is only scanty information for ravens on such important population parameters as adult survival, age structure, or recruitment to the breeding population. Using rather crude data derived from band recoveries, first calendar-year mortality has been estimated to be 37% and 45% for British and Swedish ravens, respectively (Holyoak 1971, Strandberg 1980). First year mortality was estimated to be 64% for North European ravens, again on the basis of band recoveries (Busse 1969).

Some ravens are physiologically capable of breeding at 2 years of age, and do so. Other ravens stay in the non-breeding flocks up to 5-6 years, which implies that they may be unable to gain access to good quality territories.

Thirty to 40 percent of the known raven territories in our study areas were un-occupied each year, but this does not necessarily mean that there were as many vacancies for breeding birds. Many of the unoccupied territories have remained unoccupied for a long time, because they are probably unsuitable for ravens in most years. Stability of the breeding cohort of ravens in Iceland, despite heavy persecution, mainly of immature ravens, implies that some factor other than subadult survival regulates raven breeding numbers.

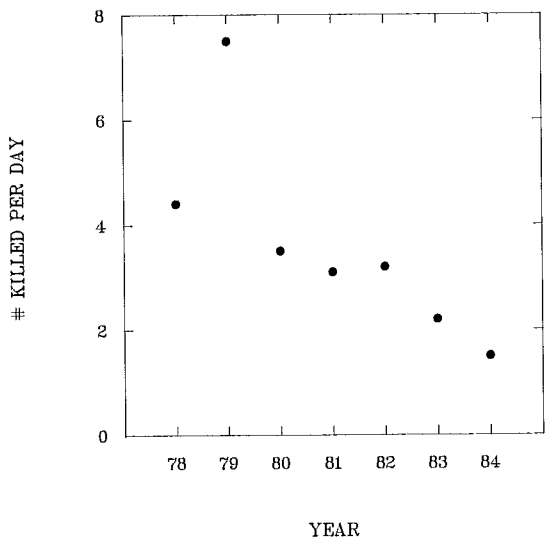


Fig. 18. Number of ravens killed per hunting day at Húsavík, North Iceland, 1978-84. The annual kill ranged from 60 (in 1984) to 483 (in 1979); the number of annual hunting days were relatively constant, 50-64 per year, except 39 in 1984 (Árni L. Sigurbjörnsson, pers. comm.)

CONCLUSIONS

Ravens in Iceland reproduce well; they have high nest success, relatively large brood size, and the breeding population is apparently stable. So far, we have only been able to tentatively conclude that the persecution levels during 1981-85 did not seem to have reduced numbers of breeding ravens. However, large-scale control programs began only recently. Whether the raven population would increase in the absence of persecution is speculative.

In Northeast Iceland, where ravens were persecuted more severely than in either the Southwest or East during 1981-85, ravens differed significantly in many of their life history characteristics: they had lower occupancy rates of territories and lower nest success; nestlings were recovered at higher rates, at an earlier age, and after dispersing shorter distances.

Raven depredation is usually hard to predict and varies both with time and location. Measures, therefore, must be aimed to control depredation locally, rather than by merely reducing overall raven numbers. Also, emphasis on preventive measures, e.g., preventing access by ravens to organic waste by adequate disposing of offal and other garbage, and using deterrents, will probably prove more effective than the culling approach. In some areas of Iceland where raven control measures have been taken annually, their abundance, and thus their alleged depredation, has not been reduced. Numbers of birds present in the overall environment, however, may be temporarily decreased when management is performed within short time periods and at the population level (cf. Van Vessem et al. 1985).

Accurate estimates of breeding and non-breeding populations and raven survival rates must be obtained to permit a proper assessment of the impact of control measures on raven numbers. Finally, information on alleged raven damage is far from being satisfactory, and the effectiveness of control measures on raven depredation remain largely unknown.

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APPENDICES

Appendix 1. Number and regional distribution of ravens banded in Iceland, 1928-87.[a]

Years	Southwest	West	Northwest	North	Northeast	East	Southeast	All
1928-30				11				11
1931-40	22			10	4			36
1941-50								0
1951-60	3	8		2 (1)				13 (1)
1961-70		21 (17)		4			4 (1)	29 (18)
1971-80	16 (1)[b]	8	1 (1)	3		3		31 (2)
1981					42	57 (1)		99 (1)
1982	36	10			57	38 (1)		141 (1)
1983	30	3		4	91	50		178
1984	12			1	65	70 (16)		148 (16)
1985			7 (3)	18	25 (5)	37		87 (8)
1986		1		6		10		17
1987	5				9	35	2	51
All	124 (1)	51 (17)	8 (4)	59 (1)	293 (5)	300 (18)	6 (1)	841 (47)

[a]For geographic boundaries of regions employed, see Fig. 2.
[b]Figures in parenthesis indicate the number of full-grown birds in the sample.

Appendix 2. Observations of ravens in nesting territories in Northeast Iceland, 1983–85.[a]

Nesting territory	1983					1984							1985			
	Breeding	S	O	N	D	J	F	M	Breeding	S	O	N	D	J	F	M	Breeding
1	4 young	–	2	–	0	0	X	0	Failed	0	0	0	0	2T	1T	2T	Failed
2*	Ad shot	X	–	–	–	–	X	–	Bred	X	X	X	X	–	2	2	Bred
3	Failed	–	0	–	–	–	0	0	Failed	–	–	–	–	–	–	–	–
4	Ad shot	3	–	–	–	–	–	3	0	0	0	3	1	0	0	0	Bred
5	0	–	–	–	0	–	–	X	Failed	0	0	0	0	0	X	–	Bred
6	Failed	–	1	–	–	–	–	–	Failed	–	–	–	–	–	–	–	–
7	0	0	0	0	–	–	–	–	0	–	2	–	–	–	–	–	0
8	0	–	–	–	–	–	2	P	X	X	–	–	–	–	2	Bred	
9	Bred	–	0	–	–	–	–	–	Bred	–	–	–	–	–	–	–	–
10	5 young	2	–	–	–	–	–	0	5 young	0	0	0	0	0	0	2	Failed
11	0	–	–	–	–	2	0	0	0	–	–	–	–	–	–	–	–
12	1 young	0	0[b]	0	0	0	2[c]	0	Failed	–	–	–	0	–	–	–	3 young
13*	Failed	–	–	–	–	–	X	2	Failed	–	–	–	–	–	–	–	–
14	Bred	–	–	2	–	0	–	0	0	–	–	–	–	–	–	–	–
15	P	–	0	–	0	0	0	–	P	–	0	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	Bred	–	–	–	–	–	–	2	Bred
17	Bred	–	–	–	–	X	–	–	Bred	–	–	–	–	–	–	–	–
18	0	0	0	–	–	–	–	0	P	0	0	0	0	0	0	0	0
19	0	–	2	–	–	–	–	–	P	–	–	–	–	–	–	–	–
20	3 young	–	2	–	–	0	–	–	2 young	–	–	–	–	–	–	–	–
21	0	–	0	–	0	0	0	2T	P	0	–	–	–	–	–	0	0
22	P	–	1	0	1	0	0	–	Bred	2	2	1	2	–	–	0	Bred
23*	Bred	–	–	–	–	–	X	–	Bred	–	–	–	–	–	–	–	–
24*	Bred	–	–	–	–	–	2	–	Bred	–	–	–	–	–	–	–	–
25	Bred	–	–	–	2	–	–	–	Bred	–	–	–	–	–	–	–	–
26	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	
27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2T	–	–
28	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1T	–	–

Legend: [a]Figures in the month columns refer to number of ravens observed in the territories.
[b]Raven pair was frequently seen near this site, according to a local inhabitant.
[c]Raven pair came to roost at the nest site after dark.
* Coastal sites (<10 km from the coast); all other sites were inland.
P Territory was occupied by a non–breeding pair.
0 No birds observed.
– No information.
X Signs of occupancy, e.g. fresh pellets, fresh white-wash or freshly molted feathers.
T Territorial behavior, e.g. mobbing observer, vocalizations, aerial displays.

Appendix 3. Densities and spacing of breeding ravens in Europe and North America, for areas >100 km^2. Figures from Iceland are given in Table 5.

Location and study period	Area (km^2)	Number of pairs present	Pairs/ 100 km^2	Percent of territories occupied	Mean internest distance (km)	Source
Northern Germany						
Southern Angeln with Schleswig, 1951	440	24	5.5			Looft 1965
Schleswig, 1951/64	1058	30/21	2.8/2.0	[a]		–
„Ostholst", 1957/60	1220	23/15	1.9/1.2	[a]		–
Westmecklenburg, 1956	1800	37	2.1			–
Northern Schleswig-Holstein, 1950/80	2280	49/17	2.1/0.7	[a]		Looft 1983
Mecklenburg, around 1975[b]	11606	(1250)	4.7	[a]		Prill 1981
Switzerland (Wallis), 1977-85(?)	2500	72-76	2.9-3.0	89-94%		Oggier 1986
Britain						
NW-England (Lake District), 1945-61	1142	67[c]	5.9		2.7	Ratcliffe 1962, Dare 1986
N-Wales (Sowdonia), 1950-61	671	38[c]	5.7		2.7	– –
SW-Scotland (Galloway), 1946-61	440	23[c]	5.2		2.7	– –
S-Scotland (Moffat Hills), 1949-61	502	11[c]	2.2		4.6	– –
Central-Wales, 1975-79	475	63-68[d]	13.3-14.2	80-86%[e]		Newton et al. 1982
N-Wales (Snowdonia), 1978-81	926	84-93[d]	9.4-10.4	87-97%[a]	2.0	Dare 1986
Wales (Migneint-Hiraethog), 1978-81	477	18[d]	3.8	92%[a]	3.6	–
Orkney, 1972-77	523	21-25	4.0-4.8	84-93%		Booth 1979
Shetland, 1982-83	1440	161-184[f]	11.2-12.8		1.8-2.5[g]	Ewins et al. 1986
Isle of Man, 1941	587	35[h]	6.0	72%		Cowin 1941
North America						
Virgina (Ridge Valley), 1973-74	466	12	2.6	85%	5.0	Hooper et al. 1975
Utah (Eastern Great Basin), 1967-70	207	4	1.9			Smith & Murphy 1973
Idaho (Snake River), 1975-78	130[i]	46-56	35-43			US Dept. of Interior 1979
– – –	3387	99-128	2.9-3.8	71-100%[k]		– –
Oregon (Malheur), 1976-77	732	29-32	4.0-4.6	75-80%		Stiehl 1978, 1985
NWT (central arctic Canada), 1983-86	2000	7-12[l]	0.35-0.6		14.0	Poole & Bromley 1988
Alaska (Colville), 1967-69					5.6-164	White & Cade 1971

[a]Raven population not stable in the study area.
[b]Based on density figures during 1969-80 (0.6-12.5 pairs/100 km^2) from 24 subareas (100-1243 km^2); Sellin (1987) reported densities of up to 18.7 pairs/km^2 in a 107 km^2 study area within this region.
[c]Maximum number of pairs known to have been breeding in the study areas in any one year.
[d]Calculated by us using the total number of known raven territories in the area and annual occupancy rates.
[e]If seven territories are excluded which were never occupied during the study period, occupancy rates became 91-100%. The general impression was of a stable or slightly declining breeding population.
[f]Figures refer to raven territories that were regularily occupied by breeding pairs throughout the study (n = 161), and total number of territories in which breeding occurred (n = 184).
[g]Figures refer to raven territories <5 km from a large dump (1.8 km) and >5 km from a large dump (2.5 km), respectively.
[h]Calculated by us using the number of known raven territories (n = 48), number of territories visited (n = 45), and number of territories occupied (n = 33).
[i]The boundaries of this high density area (Birds of Prey Natural Area) were arbitrarily drawn.
[k]Numbers refer to sample of raven territories in the Snake River area that were checked during 1974-79 (Kochert et al. 1979).
[l]Number refer to terriories occupied by ravens in the study area in the central Northwest Territories (11-12, except 7 in 1983).

Appendix 4. Some parameters of raven breeding biology for samples >10.

Location and study period	Mean clutch size	Mean number of young fledged/ successful nest	Mean nest success	Mean percentage of pairs breeding	Source
Iceland					
Southwest, 1982-84	5.1	3.5	82%	95%	This study; Tables 1,5,6
Northeast, 1981-85	4.5	3.2	77%	87%	This study; Tables 2,5,6
East, 1981-85	4.6	3.3	89%	90%	This study; Tables 3,5,6
Sweden, 1913-76		3.6[a]			Strandberg 1980
Germany, Mecklenburg	4.3	3.1			Prill 1982
Britain					
N-Wales, 1946-67	5.2	3.3	80%		Allin 1968
N-Wales, 1978-81		2.5	73%		Dare 1986
Central-Wales, 1975-79	4.5	2.8	67%	89%	Newton et al. 1982
Scotland (coastal), 1961-62		3.0			Mearns 1983
Scotland (inland), 1981		3.2	74%		–
Northumberland and S-Scotland, 1974-76	5.1	2.7			Marquiss et al. 1978
Orkney, 1972-77	5.1	3.1			Booth 1979
Shetland, 1982-85	4.7[b]	3.2[b]	52%		Ewins et al. 1986
Isle of Man, 1941		3.2			Cowin 1941
Britain, 1945-61	4.6	2.6[c]			Ratcliffe 1962
Britain	5.2				Holyoak 1967
North America					
Nova Scotia	5.0				Tufts 1961
Virgina, 1972-74		2.5	63%		Hooper 1977
Wyoming (Jackson Hole), 1971	5.4	3.0	58%		Dorn 1972
– – 1975			64%		Craighead & Mindell 1981
Idaho (Snake River), 1974-81	5.0	4.0	72%	91%	Kochert et al. 1980, 1981
– – 1984		3.9	88%		– 1984
Oregon (Malheur), 1976-77	6.0	3.9[d]	60%		Stiehl 1985

[a]Brood size of young banded.
[b]Including figures from Fetlar 1967-83 which did not differ significantly from breeding attempts in the whole of Shetland.
[c]Number of young >3 days old.
[d]Calculated by us using the mean nest success (60%) and the mean number of young fledged per nest in 1976 (2.2; n = 25) and 1977 (2.5; n = 28).

Appendix 5. Dispersal of raven young from their parents' territories and development of independence in Iceland, 1982-85.

Location[a]	Date	Minimum distance from nest (km)	Number of young	Were adults nearby?[b]
Mýrar, NW	10/6 85	2	2+	Yes
Holt, NW	11/6 85	2	1	No
Klaustursel	26/6 82	0.5	2	1 NT
Breidamörk	2/7 84	1.5	2	2 NT
Grindavík, SW	10/7 85	1.5	2	No
Kvoslækur, SW	11/7 82	1	4	2
Hlíd, W	13/7 85	0	4	? NT
Egilsstadir	13/7 84	2.5	1	No
Valthjófsstadur	13/7 84	0	5	? NT
Hólmanes	15/7 84	0.3	2	? NT
Hörgsnes, NW	15/7 85	0	5	? NT
Grenisalda	16/7 84	5	5	No
Dagverdargerdi	17/7 84	1.5	3	1
Flateyri, NW	18/7 85	3	ca 9	F of 30
Vattarnes	18/7 84	0	4	2 NT
Innri-Thverá	20/7 84	2.5	3	No
Graenafjall	20/7 84	5	2	?
Eskifjördur	22/7 84	5	1	begging in F
Eskifjördur	23/7 84	5	4	in F
Eskifjördur	24/7 84	5	4	in F
Reydarfjördur	26/7 84	2	3	No
Eskifjördur	26/7 84	5	2	in F
Reydarfjördur	27/7 84	2	3	No
Merki	28/7 84	1	3	No NT
Reydarfjördur	28/7 84	2	4	No
Eskifjördur	28/7 84	5	2+	in F
Langahlíd	30/7 84	9	2	No
Innri-Fjallgardur	30/7 84	15	2	No
Saudá, Mödrudalur	30/7 84	2	1	No
Merki	1/8 83	2	2	No NT
Deildartún	4/8 84	11	2	?
Reydarfjördur	6/8 84	2	3	No
Reydarfjördur	9/8 84	2	1	No

[a]See Fig. 2 for geographic boundaries employed. All locations are in the East region unless otherwise stated; SW = Southwest, W = West, NW = Northwest.
[b]NT = young definitely on natal territory, F = a group of ravens at a garbage dump.

Appendix 6. Post-fledging behavior of some *Corvus* spp.

Species	Post-fledging behavior of juveniles	Source
C. corax	Young disperse from their natal territories about a month after fledging (e.g., in Iceland, western USA); some young (e.g., northern Germany) apparently stay with their parents for several months	This study; references therein
C. corone	Young disperse during summer and fall and gradually join non-breeding flocks. Some stay in their natal territories until the following spring	Loman 1985
C. brachyrhynchos *C. caurinus*	Young usually disperse during late summer and fall; some do not disperse, but stay in their natal territories for a year or more and help their parents to raise young in the next breeding season	Jollie 1976, Kilham 1989, Verbeek & Butler 1981, R. Knight, pers. comm.
C. capensis	Young may stay with their parents for over 5 months	Skead 1952
C. coronoides	Young disperse 3-4 months after fledging; breeding birds maintain permanent territories	Rowley 1973
C. mellori	Young disperse almost immediately after fledging; breeding birds are nomadic	Rowley 1973
C. macrorhynchos	Young are usually accompanied by parents for 3-4 weeks after fledging; some young may stay with their parents for up to 3 months	Kuroda 1977

Appendix 7. Numbers of ravens banded and recovered in some banding schemes.[a]

Country (scheme)	Years	Number banded	Percent recovered	Percent killed by humans	Source
Iceland (Reykjavík)	1928-80	120	13	56	This study; Table 9, App. 1
Iceland (Reykjavík)	1981-87	721	38	87	– – –
USSR (Moskva)	1925-82	1038	2		Euring: annual reports
Estonia (Matsalu)	1970-85	343	1		–
Poland (Gdansk)	1931-83	102	10		–
Yugoslavia (Zagreb)	1910-82	358	1		–
Finland (Helsinki)	1913-86	4202	16	65[b]	–
Sweden (Stockholm)	1960-83	2889	8		–
Norway (Oslo)	1914-80	215	11		–
Norway (Stavanger)	1914-82	664	9		–
Germany-GFR (Helgoland)	1909-88	1395	5		–
The Netherlands (Arnhem)	1911-83	174	16		–
Spain (Madrid)	1957-82	336	1		–
Spain (Madrid-Icona)	1973-85	206	1		Asensio 1987
Sweden (several schemes)[c]	1913-76	1610	12	55	Strandberg 1980
Germany-GDR (Hiddensee)	1964-85	3203	6		Knoche 1985; Siefke, in litt.
Switzerland (Sempach)	1924-87	1664	10		L. Jenni, in litt.
Britain & Ireland (London)	1909-88	5843	8	25[d]	Mead & Clark 1989
Greenland (Copenhagen)	1946-74	118	37	39	Salomonsen 1972, 1979
USA & Canada (Washington)	1913-81	6707	7		Clapp et al. 1983

[a]Figures from schemes where <100 ravens have been reported banded were omitted from the table.
[b]From Saurola (1977).
[c]Includes ravens banded in the Stockholm scheme mentioned above.
[d]From Hickling (1983: 264).

Appendix 8. Results of raven banding from several banding schemes.

Country or area	Recovered ≤1 year after banding[a]	Most recovered during	Recovered < 80 km from banding locations	Maximum distance travelled (km)	Dispersal pattern	Source
Iceland	62%	Aug-Oct (45%), Apr-May (24%)	77%	386	Variable among the study areas; median dispersal = 40 km	This study
Finland[b]	ca 56%	Aug-Nov (ca 64%)	ca 76%[c]	379	Random dispersal	Saurola 1977
Sweden[b]	68%	Sept-Oct of first year (36%)	72%	508	Mostly random dispersal; southerly oriented in late fall and winter	Strandberg 1980
Latvia				200	Most travelled 15-75 km	Bergmanis 1963
Germany (northern)[b]			ca 80%	>300	Mostly random dispersal; mean = 55 km	Prill 1983, Schultz-Soltau 1962
Britain & Ireland[b]	61%	March-May, during lambing & nesting season; 20% in May shortly after fledging		306	Ca 50% dispersed <32 km; one bird crossed the Irish Sea	Holyoak 1971
Wales[d]	ca 50%	April – May		317	Median dispersal = 23 km	Dare 1986
Greenland[b]	60%	August – December (62%), with 21% in August alone		1150[e]	36% dispersed >100 km; juv. tended to move south	Salomonsen 1967
Nova Scotia[f]			78%		No recocoveries beyond the Maritime Provinces; mean dispersal = 112 km	Coldwell 1972 Boersma 1978 Crawford 1978

[a]Figures refer to June – May, except Britain and Ireland (April – March).
[b]Some parameters calculated by us using data given by the author(s).
[c]Figure refers only to young recovered before March of their first year.
[d]Includes some of the recoveries analysed by Holyoak (1971).
[e]This is the longest movement reported for ravens along with a similar distance (about 1080 km) travelled by a raven banded in northern Labrador (Cooke 1938). Both birds were recovered in early winter of their first year.
[f]Mostly full-grown birds banded during winter.

Busse (1969) combining raven recoveries from throughout northern Europe, found that 75% of the recoveries came from within 100 km from the banding place and there was no pronounced direction in movements. Zink (1981), partly updating that same banding material, came to similar conclusions, but pointed out that movements >200 km from the banding place tended to be in southerly direction.

Appendix 9. Sightings of color-marked ravens in Iceland, 1982-87[a].

Band number	Banding region	Date	Age when banded	Where sighted	Date (s) sighte	Days between sighting and banding	Distance travelled (km)	Notes
211553	East	2/6 83	Nestling	East	1/8 83	60	0	
211554	–	–	–	–	1/6 84-1/5 87	365-1428	0	Female; occupied natal territory as a yearling; bred and raised young when two, three and, four years old.
211558	–	3/6 83	–	–	5/2 84	247	58	In a non-breeding flock in a coastal town.
211567	–	7/6 83	–	North	30/3 84	297	138	In a non-breeding flock in a coastal town; shot 15 days later 139 km to the northeast.
211568	–	–	–	–	9-19/2 85	613-623	138	Sibling to the above bird and seen at the same place.
227121[b]	–	2/6 81	–	East	17/6 84	1111	53	In a non-breeding flock in a coastal town.
227176	–	29/5 82	–	–	28/7 82	60	0	
227177	–	–	–	–	–	–	0	Siblings; No 227177 shot 63 days later 97 km to the northwest at Lake Mývatn.
227178	–	–	–	–	–	–	0	
227307	SW	4/6 82	–	SW	19/9 82	107	41	In a coastal suburb.
227350	East	6/6 83	–	NE	28/2 85	633	134	In a coastal town; shot 413 days later 52 km to the east in another coastal town.
233712	SW	27/5 84	–	SW	31/3-4/4 85	308-312	97	In a non-breeding flock in a coastal town.
233713	East	2/6 84	–	East	4/8 84	63	14	Shot 51 days later 9 km to the northeast.
233744[c]	–	18/6 84	2+ years	–	24/7 84	36	0	
				–	2/4 85	288	0	Paired.
233745[c]	–	–	–	–	22/7 84	34	0	
233746[c]	–	–	–	–	25/6 84	7	0	
233749[c]	–	22/6 84	–	–	–	3	0	
233750[c]	–	–	1 year	–	22-28/7 84	30-36	0	
233777	–	3/6 85	Nestling	–	31/1 86	242	62	In a non-breeding flock in a coastal town.
233901[c]	–	22/6 84	2+ years	–	25/6 84	3	0	
				–	24/2 85	247	0	
233902[c]	–	22/6 84	–	–	7-22/7 84	15-30	0	
				–	19/7 84	27	9	Seen at a garbage dump in a nearby town.
				–	11-12/3 85	262-263	0	Paired; male according to size and behavior.
233905[c]	–	25/6 84	1 year	–	16-24/7 84	21-29	0	
233907[c]	–	25/6 84	–	–	12/3 85	260	0	
238501	NW	23/5 85	1+ years	NW	28/5 85	5	6	Banded in a eider colony; seen in a nearby town.

[a]Included are only those birds that could be individually identified.
[b]This bird was caught and released after the band number had been positively identified.
[c]Banded at a garbage dump in the coastal town of Eskifjördur in the East.

Appendix 10. Age composition of ravens killed in non-breeding flocks in Iceland, 1982-85.

Place	Region[a]	Date	Killing method[b]	Number aged	Percent≤ 1-year-old	Percent subadults[c]
Mývatn	NE	Aug 82	S	7	100	
Breiddalsvík	SE	Oct 82	P	55	44	
Selfoss	SW	Nov 82	S	12	42	17
Nordfjördur	E	Nov 83	P	33	54	
Hornafjördur	SE	Dec 84	P	25	92	
Eskifjördur	E	Feb 83	P	34	50	9
Hafnarfjördur	SW	Feb 84	P	29	17	
Reykjavík	SW	Feb 84	P	24	29	
Húsavík	NE	Feb 85	P	9	56	
Selfoss	SW	Mar 82	S	8	62	
Hreppar	SW	Mar 84	P	178	53	
Eskifjördur	E	Mar 85	S	5	20	
Hreppar	SW	Apr 84	P	114	32	
Mývatn	NE	A/M 84	S	74	69	
Jökulsárhlíd	E	May 84	S	3	33	
Önundarfjördur	NW	May 85	P	68	46	18
Eskifjördur	E	Jun 84	P	32	28	9

[a]For geographic boundaries of regions employed, see Fig. 2.
[b]S = shot, P = poisoned.
[c]In some cases subadults could not be separated from adults.

Appendix 11. Registered raven kill in Iceland, 1981-85[a].

Area and location[b]	1981	1982	1983	1984	1985
Southwest, total	*198*	*439*	*312*	*528*	*112*
Rangárvallasýsla	0	0	46	94	0
Hreppar	0	0	0	292	79
Selfoss	87	340	111	73	0
Reykjavík area	51	99	87	69	29
Other	60	0	68	0	4
West (Breidafjördur)*	*0*	*332*	*57*	*275*	*553*
Northwest (Vestfirdir)*	*0*	*198*	*0*	*100*	*101*
North, total	*717*	*1101*	*999*	*1081*	*1156*
Midfjördur	608	850	907	724	1131
Blönduós	60	105	14	0	0
Skagafjördur	0	48	42	40	0
Hörgárdalur*	49	18	30	20	25
Akureyri	0	76	6	251	0
Other	0	4	0	46	0
Northeast, total	*239*	*332*	*279*	*258*	*213*
Húsavík	160	158	116	60	64
Lake Mývatn*	79	132	163	198	149
Thistilfjördur	0	42	0	0	0
East, total	*283*	*404*	*112*	*361*	*354*
Nordfjördur	68	14	36	4	0
Eskifjördur	95	35	76	113	0
Breiddalsvík	0	199	0	0	0
Berufjördur*	0	53	0	149	1
Other	120	103	0	95	353
Southeast, total	*144*	*165*	*14*	*353*	*187*
Hornafjördur	144	49	0	65	0
Kirkjubaejarklaustur	0	84	0	97	52
Mýrdalur	0	32	14	191	135
All areas[b]	*1581*	*2971*	*1773*	*2956*	*2676*

[a]Based on information from the Wildlife Damage Control Unit and some local controllers (marked by *). In 1986 and 1987 the total registered kill was 2670 and 2294 ravens, respectively.
[b]For geographic boundaries of regions employed, see Fig. 2.

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