IBIS 136: 441–447

Interinsular variations in the spring and summer diet of the Raven *Corvus corax* in the Canary Islands

M. NOGALES[1] & E. C. HERNANDEZ[2]

[1] *Departamento de Biología Animal (Zoología), Universidad de La Laguna, 38206, Tenerife, Canary Islands, Spain*

[2] *Museo Insular de Ciencias Naturales, Aptdo. de Correos 853, 38080, S/C de Tenerife, Canary Islands, Spain*

This paper presents the first data on the diet of the Raven *Corvus corax* in the Canary Islands, based on analysis of 2315 pellets collected from all of the islands and islets in the archipelago. The Ravens on three groups of island showed differences in diet, but in all cases the diet was clearly omnivorous, both in its qualitative and quantitative composition. It is evident that a broadening of the Raven's trophic niche has occurred in comparison with those living in continental areas. While the diet has a strong plant component on the wetter islands (frequency of occurrence >87%), an appreciable animal component in the diet (principally vertebrates) is more frequent on the drier islands of the archipelago (frequency of occurrence >96%). The composition of the plant component of the diet varied markedly from one island to another. Remains of refuse are more commonly found in the Raven's diet on the central and western islands. We concluded that while the animal diet is essential from the bioenergetic point of view, the vegetation diet is only a complementary food source. The Raven plays an important role in seed dispersal among the different habitats within each island.

The diet of the Raven *Corvus corax* has been the subject of relatively few studies, despite its wide distribution. The diet has been investigated in depth by a few authors (Temple 1974, Ewins *et al.* 1986, Engel & Young 1989, R. B. Stiehl, pers. comm.), and there are a large number of short notes dealing with specific trophic issues (e.g. MacManus 1935, Maser 1975, Mallory 1977, Schaber 1983). Nevertheless, the vast majority of these studies have been carried out in continental zones or on islands very close to such zones, and there are no studies of the diet of the Raven in oceanic island ecosystems. The Raven is markedly omnivorous in the vast majority of the habitats it occupies (e.g. Harlow 1922, Géroudet 1980, Cugnasse & Riols 1987), although this conclusion would appear to be based on qualitative and not quantitative estimates. In the greater part of the Raven's range, its behaviour corresponds to a bird that feeds primarily on animals (frequently vertebrates and arthropods).

The Raven has the ability to take advantage of a range of trophic niches and uses a wide variety of methods to search for and obtain food. A number of researchers have observed feeding at rubbish tips (Houston 1977, Huber & Pfister 1986), scavenging (Feilden 1909, Watson & O'Hare 1980), predation (Holyoak 1968, White & Cade 1971, O'Gara *et al.* 1983) and kleptoparasitism (Conner *et al.* 1975, Latscha 1979, Kilham 1985). This high degree of flexibility in obtaining food is one of the factors that may explain the Raven's wide geographic distribution, ranging from arctic zones to desert regions.

The principal purpose of the present study was to examine the spatial variation in the Raven's feeding patterns on the islands and islets of the Canarian Archipelago in terms of the various habitats on these islands. The study also investigated the question of whether the island-dwelling Raven has extended its trophic niche in an oceanic island ecosystem in comparison with its continental counterparts, a situation well documented in the literature for other island-inhabiting birds (Grant 1965, MacArthur *et al.* 1972).

STUDY AREA AND METHODS

The Canarian Archipelago is situated in the Atlantic Ocean some 100 km (at the closest point) from the African continent, lying between 27°37′–29°25′N and 13°20′–29°25′W. The Canary Islands are volcanic in origin and are made up of seven islands and four major islets (Fig. 1). The climate of the Canarian Archipelago is determined by a complex of factors such as latitude, altitude, direction and humidity level of the winds, degree of incline and orientation, proximity to the sea and topography (Bravo 1954). The average annual rainfall on the dry islands (Lanzarote, Fuerteventura and the offshore eastern islets) is less than 250 mm, while on the central and western islands, which are higher in altitude and longitudinally more oceanic, it is over 600 mm. The average annual temperature is 23°C in the coastal areas and 10°C in the mountains (Marzol Jaén 1988). Because of these climatic characteristics, sparse xerophyte scrub covers the greater part of the surface of the islands closest to Africa

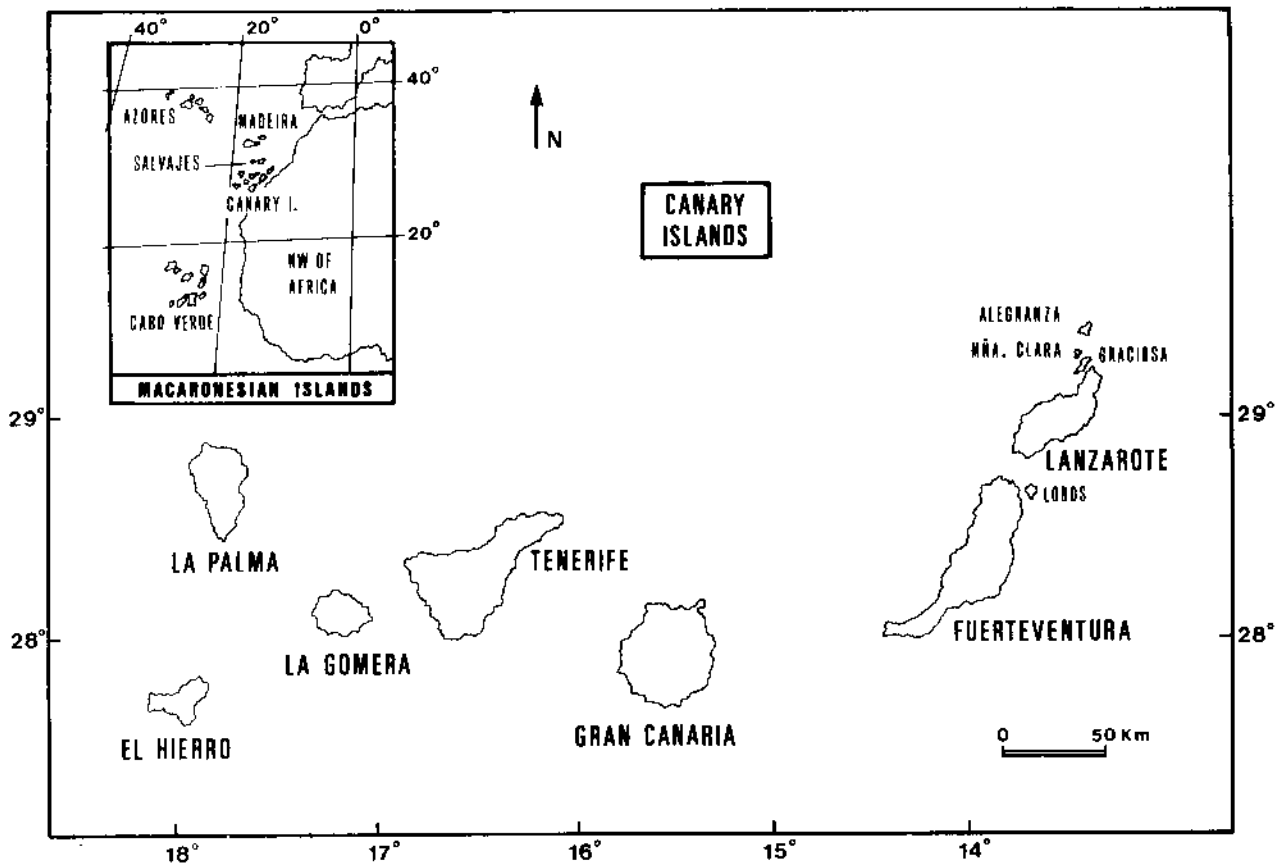

Figure 1. Location of the Canary Islands and the other Macaronesian archipelagoes.

(Fuerteventura, Lanzarote and the offshore eastern islets). The central and western islands have areas of forest.

Field work was carried out from July 1986 to September 1987. Study material was collected in the summer months (June–August). During this period, visits were made to each of the islands and islets.

The study material, made up of 2315 pellets, came from all of the islands and islets in the Canarian group (El Hierro, 679 pellets; La Palma, 13; La Gomera, 352; Tenerife, 69; Gran Canaria, 491; Fuerteventura, 296; Lobos 40; Lanzarote, 248; Graciosa, 69; Alegranza, 30; Montaña Clara, 28). Pellets were collected mainly at rubbish tips, communal roosts and from nests. Judging by the high degree of disintegration in pellets produced during the winter, the food described was most probably consumed in the spring and summer months.

The pellets were individually wrapped in aluminium foil *in situ* in an effort to maintain the unit of regurgitation, which is basic to the analysis of dietary results in the present study. Analysis of the material was carried out under ×16 magnification after the pellets had been soaked in water. Identification was achieved by comparison with previously prepared collections, which included various types of mammal hair, seeds and insects. The identification of remains also used data in Errington (1930) and Day (1966).

Analysis of the Raven's pellets is complicated by the differing degrees of digestibility of food items, which affect the presence or absence of certain remains (Engel & Young 1989). At the same time, because of the Raven's tendency to scavenge and the fact that it does not always eat the whole carcass of its prey, calculation of the biomass ingested is not possible. Analysis of the pellets provides only a rough idea of their qualitative composition. It is extremely difficult to estimate the composition quantitatively (Marquiss *et al.* 1978, Marquiss & Booth 1986). For this reason, in most studies of the Raven's diet, parameters such as the percentage of each food item per pellet are normally used together with the number of specimens of each element observed in the pellet. In the cases of invertebrate prey and that of fruits and seeds, it was possible to estimate their relative importance with reasonable precision.

Table 1 shows that the variation in vertebrate and invertebrate food between the islands is small, and in most cases, clear variations occurred only in seeds. For this reason, a decision was made to use the frequency of occurrence as the basic comparative unit, thus emphasizing the quantitative component only in those cases in which important variation was recorded in the number of specimens of prey or seeds consumed.

The methodological review of diet studies by Reynolds &

Aebischer (1991) suggests that on some islands, such as La Palma, Tenerife and the islets, our samples were too small to arrive at consistent statistical inferences but elsewhere they are, at least, adequate.

The chi-square values have been calculated by utilizing frequencies of occurrence in pellets for each food item.

RESULTS

Table 1 shows the quantitative results of the number of prey or seeds detected in the pellets analysed from each island or islet. While in the majority of pellets with vertebrate remains only a single prey is recorded, in those in which insects or seeds were found, a greater number of individual food items occurred. The presence of small mammals (basically mice *Mus* cf. *musculus*) and reptiles (*Tarentola* spp. and *Gallotia* spp.) among the vertebrates is particularly noteworthy, while among the invertebrates the Orthoptera (grasshopper) and Coleoptera (beetles) were important. In the plant component of the diet, seeds of *Opuntia ficus-barbarica*, *Ficus carica*, *Rubia fruticosa* and *Lycium intricatum* played an important role.

Frequencies of occurrence of food items in the pellets are shown in Table 2. The diet is omnivorous, and there are high frequencies of occurrence recorded for both animal and vegetable matter.

From Figure 2 it is possible to discern three clearly distinct groups of islands based on the animal and vegetable diet: the central and western islands, the eastern islands and Montaña Clara, and the offshore eastern islets. In the first group, the Raven consumes significantly more vegetable than animal food ($\chi^2_1 = 61$, $P < 0.001$), while on the eastern islands and offshore islets the opposite was the case ($\chi^2_1 = 133$, $P < 0.001$). No significant differences in terms of animal diet were found between the eastern islands and the offshore islets ($\chi^2_1 = 0.22$, n.s.), but there were significant differences in the vegetable component of the diet ($\chi^2_1 = 144$, $P < 0.001$). Montaña Clara was excluded from the analysis of the offshore eastern islets since the composition of the diet (maize, livestock remains, etc.) of the only breeding pair was not typical of this group of offshore islets, as the birds frequently moved between Lanzarote and the islet.

In terms of the relative consumption of invertebrates and vertebrates, the Ravens on the eastern islands and offshore islets consumed invertebrates more frequently than they did on the central and western islands ($\chi^2_1 = 48$, $P < 0.001$). This was also the case for the consumption of reptiles ($\chi^2_1 = 134$, $P < 0.001$) and birds ($\chi^2_1 = 29$, $P < 0.001$) on the offshore eastern islets in comparison with the major islands. No significant differences were found between the various categories of mammal used as food among the major islands.

Molluscs were more abundantly consumed on the eastern islands and offshore islets than on the western group ($\chi^2_1 = 698$, $P < 0.001$). In El Hierro, Orthoptera and Coleoptera (weevils, Curculionidae) were important, in terms of both frequency and abundance.

The important qualitative and quantitative differences detected in the vegetable diet (mainly seeds) reflect the distinct vegetation types in the various ecosystems that the Raven occupied in the Canaries.

Inorganic remains appeared more frequently in the central and western islands ($\chi^2_1 = 48$, $P < 0.001$) than in other parts of the study area. No significant differences were observed between the eastern islands and offshore islets ($\chi^2_1 = 0.01$, n.s.).

DISCUSSION

The frequency of occurrence of plant material was greater than that of animal material in the diet of the Raven in the western islands, and this contrasts with the results from the eastern islands and offshore islets. The western islands are characterized by habitats with lusher vegetation compared with the eastern islands. Because of this, the Ravens had access to and used a series of plant foods that were unavailable in the eastern sector of the archipelago.

The food of Ravens of the continental zones is more like that on the eastern islands and offshore islets than that on the central and western islands. Ravens on the continent generally tend to consume food of animal origin (basically vertebrates) (Harlow *et al.* 1975, Newton *et al.* 1982, Marquiss & Booth 1986, Amat & Obeso 1989) and very little vegetable matter. Only a few studies mention an important plant component (Soler & Soler 1987, Engel & Young 1989).

It is probable that the absence or low availability of vegetable matter on the eastern islands caused the Ravens there to depend on animal prey. It is also likely that these prey animals were not often found as carrion and that the Ravens were compelled to develop predatory habits in contrast to their usually passive and, therefore, less energetically demanding methods of obtaining food. A clear indication of this is the fact that a pair of Ravens were seen to capture a Rabbit *Oryctolagus cuniculus* on the islet of Alegranza. An important source of carrion on Fuerteventura and Lanzarote are medium-sized and small mammals (mainly rabbits and a few Hedgehogs *Atelerix algirus*) killed by cars.

Invertebrates, despite the high percentage of occurrence in pellets on almost all of the islands, cannot be an important component of the diet because only small numbers of specimens were found in the pellets (see Table 1). Only on the island of El Hierro were large numbers of Orthoptera and Coleoptera found in the pellets.

Inorganic remains reached a maximum frequency of occurrence on Gran Canaria and La Gomera (58% on each). This is probably explained by the fact that both have inland rubbish tips where Ravens frequently fed.

In the Canaries and in other studies carried out in continental areas, a high number of insects and vertebrates have been reported in both spring (Marquiss *et al.* 1978, Amat & Obeso 1989, J. L. Dorn, pers. comm.) and summer (Engel & Young 1989). The plant diet, however, does not play such an important role in most of the continental studies as it

Table 1. *Mean values of the number of each food item identified per pellet of Raven collected on the Canary islands and islets. L, Lanzarote; G, Graciosa; M, Montaña Clara; A, Alegranza; F, Fuerteventura; Lo, Lobos; C, Gran Canaria; T, Tenerife; Go, La Gomera; P, La Palma; H, El Hierro*

	Mean number of prey/seeds										
	L	G	M	A	F	Lo	C	T	Go	P	H
Vertebrates											
Crocidura canariensis	—	—	—	—	1.1	3.0	—	—	—	—	—
Atelerix algirus	—	—	—	—	1.0	—	—	1.0	—	—	—
Mus cf. *musculus*	1.0	1.3	1.5	1.3	1.0	1.8	1.0	1.0	1.0	1.0	1.0
Rattus sp.	1.1	—	—	—	1.1	1.0	1.0	1.0	1.0	—	1.0
Atlantoxerus getulus	—	—	—	—	1.0	1.0	—	—	—	—	—
Oryctolagus cuniculus	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Capra hircus	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Ovis aries	1.0	—	1.0	1.0	1.0	—	1.0	1.0	1.0	1.0	1.0
Unidentified livestock	1.0	1.0	1.0	—	1.0	1.0	1.0	1.0	1.0	—	1.0
Unidentified birds	1.1	1.1	1.0	1.1	1.1	1.0	1.0	1.1	1.0	—	1.0
Gallotia spp.	1.6	1.1	1.0	2.0	1.0	6.0	1.0	1.6	1.0	1.0	1.0
Chalcides spp.	—	—	—	—	—	—	—	—	—	—	1.0
Tarentola spp.	1.0	2.1	1.0	2.5	1.0	1.0	1.0	3.3	1.0	—	—
Invertebrates											
Mollusca	2.5	2.5	1.8	2.2	1.1	1.1	1.1	1.0	1.1	1.0	1.0
Diplopoda	1.0	—	—	—	1.0	—	1.0	1.0	1.0	1.0	1.0
Dermaptera	—	—	—	—	—	—	—	1.0	1.0	—	2.0
Acrididae	1.8	2.1	1.3	1.0	1.0	3.0	1.3	1.8	1.0	1.0	25.0
Tettigonidae	11.0	—	—	—	1.0	—	2.9	2.8	1.0	—	5.0
Curculionidae	5.9	10.3	1.9	2.3	1.4	3.4	1.7	1.8	1.1	—	1.0
Scarabaeidae	1.1	1.3	1.0	—	—	29.5	1.1	—	1.0	—	2.0
Tenebrionidae	1.0	3.4	1.0	1.0	1.1	1.7	1.3	2.0	1.0	—	2.0
Staphylinidae	1.0	—	—	—	—	—	1.0	1.5	—	—	5.0
Lepidoptera	3.5	1.0	—	—	—	1.0	1.0	1.7	—	—	1.0
Other Arthropoda	1.5	2.2	2.7	1.0	2.4	1.7	1.5	2.1	1.0	1.0	3.0
Vegetation											
Opuntia ficus-barbarica	169.0	30.0	299.0	—	13.0	—	67.0	124.0	79.0	29.0	130.0
Opuntia dillenii	69.0	—	—	—	31.0	—	28.0	76.0	—	49.0	124.0
Ficus carica	162.0	73.6	46.0	—	2.0	—	116.0	117.0	1.0	7.0	64.0
Lycium intricatum	11.0	16.7	22.7	163.0	41.0	2.0	23.0	—	—	—	—
Asparagus pastorianus	—	—	—	—	27.0	—	—	—	—	—	—
Plocama pendula	—	—	—	—	—	—	23.0	1.0	14.0	—	—
Phoenix spp.	—	9.0	—	—	—	—	5.0	8.0	6.0	1.0	—
Rubus cf. *inermis*	—	—	—	—	—	—	—	—	11.0	—	—
Ilex canariensis	—	—	—	—	—	—	—	3.0	—	—	57.0
Laurus azorica	—	—	—	—	—	—	—	—	—	14.0	—
Myrica faya	—	—	—	—	—	—	—	—	53.0	—	38.0
Visnea mocanera	—	—	—	—	—	—	—	—	—	—	11.0
Pinus canariensis	—	—	—	—	—	—	1.0	2.0	2.0	3.0	2.0
Juniperus phoenicea	—	—	—	—	—	—	1.0	—	1.0	—	25.0
Juniperus cedrus	—	—	—	—	—	—	—	—	—	10.0	—
Rubia fruticosa	3.0	—	2.0	—	2.0	—	23.0	25.0	3.0	—	77.0
Cosmopolitan herbaceous plants	18.0	23.0	41.0	6.5	34.0	2.5	2.0	8.0	5.0	—	12.0
Cereals	1.0	—	1.0	—	1.0	—	2.0	5.0	2.0	—	8.0
Total number of pellets	248	69	28	30	296	40	491	69	352	13	679

Table 2. *Frequencies of occurrence found in the analysis of the pellets of the Ravens collected in Canary islands. L, Lanzarote; G, Graciosa; M, Montaña Clara; A, Alegranza; F, Fuerteventura; Lo, Lobos; C, Gran Canaria; T, Tenerife; Go, La Gomera; P, La Palma; H, El Hierro*

	Percentage frequency of occurrence										
	L	G	M	A	F	Lo	C	T	Go	P	H
Animals											
Mammalia											
Crocidura canariensis	—	—	—	—	0.3	2.5	—	—	—	—	—
Mus cf. *musculus*	2.0	4.3	7.1	13.3	5.1	15.2	1.2	5.8	0.6	7.7	0.9
Rattus sp.	13.3	—	—	—	1.3	—	1.6	27.5	2.0	—	4.1
Atlantoxerus getulus	—	—	—	—	8.4	2.5	—	—	—	—	—
Total small mammals	17.7	4.3	7.1	13.3	15.2	15.0	2.9	30.4	2.6	7.7	5.0
Oryctolagus cuniculus	19.8	7.2	10.7	66.6	25.6	15.0	13.2	11.6	4.3	23.0	9.4
Atelerix algirus	—	—	—	—	0.3	—	—	1.5	—	—	—
Total medium size mammals	19.8	7.3	10.7	66.6	25.9	15.0	13.2	11.6	4.3	23.0	9.4
Capra hircus	4.9	4.3	10.7	13.4	12.0	7.5	4.5	8.7	15.6	23.0	2.8
Ovis aries	1.0	—	1.0	3.3	2.0	—	13.2	1.5	2.0	7.7	7.4
Unidentified livestock	1.0	5.8	6.2	—	5.5	2.5	1.2	1.4	2.6	—	1.5
Total livestock	6.9	10.1	17.9	16.7	19.5	10.0	18.9	11.6	20.2	30.7	11.7
Total mammalia	41.1	15.9	35.7	83.3	56.9	35.0	33.8	46.4	27.0	61.5	22.0
Birds											
Birds	27.0	34.8	50.0	33.3	8.1	50.0	22.4	11.6	1.7	—	4.7
Eggshells	3.2	2.9	10.7	3.3	2.0	—	17.7	8.7	21.0	23.0	10.0
Total birds	29.4	37.7	53.6	36.7	9.8	50.0	32.8	15.9	22.7	23.0	13.9
Reptilia											
Gallotia spp.	12.1	11.6	3.8	23.3	2.0	2.5	1.8	26.1	4.3	7.7	1.5
Chalcides spp.	—	—	—	—	—	—	—	—	—	—	0.2
Tarentola spp.	0.4	42.0	7.1	13.3	1.0	7.5	0.2	13.0	2.3	—	—
Total Reptilia	12.1	46.4	10.7	26.7	2.7	7.5	2.0	36.2	6.5	7.7	1.6
Total fishes	12.1	10.1	21.4	3.3	—	5.0	7.7	18.8	15.6	—	1.6
Total Vertebrata	74.2	78.3	82.1	100.0	65.0	80.0	62.9	71.0	55.4	61.5	34.4
Insecta											
Acrididae	2.4	26.1	10.7	10.0	28.3	2.5	9.2	15.9	16.5	15.4	28.2
Tettigonidae	0.4	—	—	—	1.0	—	4.7	18.8	5.1	—	19.9
Curculionidae	25.8	52.2	57.1	13.3	50.2	22.5	12.6	31.9	22.4	—	3.5
Scarabaeidae	2.8	11.6	3.8	—	—	5.0	1.4	—	0.6	—	11.7
Tenebrionidae	1.6	24.6	3.8	3.3	3.7	7.5	1.2	5.8	2.6	—	11.7
Staphylinidae	0.4	—	—	—	—	—	—	1.5	—	—	2.8
Lepidoptera	1.6	1.5	—	—	—	5.0	1.2	4.4	—	—	3.1
Total Insecta	25.8	53.4	57.1	14.0	51.2	22.5	13.5	33.8	22.4	15.4	30.4
Other Invertebrata											
Mollusca	67.4	76.8	92.9	50.0	55.5	60.0	11.2	8.7	16.2	7.7	6.6
Diplopoda	0.4	—	—	—	0.3	—	0.2	11.6	2.0	15.4	4.1
Other Arthropoda	13.7	17.4	21.4	6.7	7.7	7.5	10.0	23.2	16.8	23.0	12.4
Total Invertebrata	80.2	98.6	100.0	63.3	87.5	70.0	38.7	66.7	52.8	38.5	65.5
Total animal diet	96.8	98.6	100.0	100.0	98.3	97.5	78.4	85.5	78.4	69.2	81.3
Plants											
Opuntia ficus-barbarica	14.9	5.8	3.8	—	4.7	—	21.2	24.6	11.9	7.7	35.7
Opuntia dillenii	2.0	—	—	—	1.0	—	1.0	36.2	—	23.0	4.0
Ficus carica	64.5	10.1	17.9	—	58.3	—	15.1	24.6	9.9	23.0	16.5
Lycium intricatum	10.5	13.0	64.3	23.3	13.1	7.5	1.4	—	—	—	—
Asparagus pastorianus	—	—	—	—	17.1	—	—	—	—	—	—
Plocama pendula	—	—	—	—	—	—	5.3	1.5	0.6	—	—
Phoenix canariensis	—	—	—	—	—	—	0.6	5.8	12.2	7.7	—

Table 2. *Continued*

	Percentage of occurrence										
	L	G	M	A	F	Lo	C	T	Go	P	H
Rubus cf. *inermis*	—	—	—	—	—	—	—	—	0.3	—	—
Ilex canariensis	—	—	—	—	—	—	—	1.5	—	—	0.2
Laurus azorica	—	—	—	—	—	—	—	—	—	7.7	—
Myrica faya	—	—	—	—	—	—	—	—	0.3	—	1.5
Visnea mocanera	—	—	—	—	—	—	—	—	—	—	5.3
Pinus canariensis	—	—	—	—	—	—	7.3	4.4	0.3	15.4	6.8
Juniperus phoenicea	—	—	—	—	—	—	0.2	—	0.3	—	6.6
Juniperus cedrus	—	—	—	—	—	—	—	—	—	69.2	—
Rubia fruticosa	0.4	—	3.8	—	0.3	—	5.7	14.5	0.6	—	28.3
Total wild seeds	79.4	33.3	78.6	33.3	75.8	25.0	59.1	85.5	58.0	84.6	78.8
Cosmopolitan herbaceous plants	12.9	8.7	14.3	16.7	30.6	17.5	22.6	27.5	29.5	—	14.5
Cereals	3.6	—	3.8	—	4.0	—	8.4	5.8	11.4	—	14.5
Vegetative parts of plants	63.7	21.7	39.3	26.7	56.2	10.0	73.1	68.1	79.3	69.2	59.7
Total plant diet	87.5	40.6	85.7	46.7	87.5	32.5	88.0	95.6	93.2	100.0	88.2
Inorganic remains	15.7	31.9	25.0	—	29.3	22.5	58.2	20.3	58.2	23.0	14.5
Grit	96.0	94.2	82.1	93.3	72.1	87.5	72.5	78.3	81.0	46.2	60.5
Total number of pellets	248	69	28	30	296	40	491	69	352	13	679

does in the Canarian ecosystem. The diet of the Raven in the last half of the nineteenth and the first half of this century may have been characterized by a greater presence of carrion than it is today. This is supported by the fact that in locations where carrion is still abundant, as in Wales (where there is a large Raven population), it is the species' principal source of food, and a very high frequency of occurrence of carrion in the pellets is maintained throughout the year (Newton *et al.* 1982).

According to data provided by Garcia (1984), the free-grazing livestock population of the Canaries has declined markedly since the end of the nineteenth century. This reduction in numbers of free-grazing livestock and the trend towards the progressive stabling of livestock in recent years, as well as the improvements in sanitary conditions in which animals are kept, have resulted in a drastic reduction in the amount of carrion available to Ravens.

An animal component in the diet was important on all of the islands and islets in the Canaries. The lowest frequency for this component was at La Palma (69%). Plant food would not appear to be so important for this species, judging by the low frequencies of occurrence found on the offshore islets with impoverished xeric vegetation.

From the bioenergetic point of view, the daily energy requirement for an animal in the wild correlates closely with its body size and is 17 times greater in homeothermic animals (Nagy 1987). A bird such as the Raven, therefore, with a body weight of 750–1300 g will require a high-energy diet to maintain its body temperature and to perform vital daily activities. For this reason, a high protein level in the diet is probably crucial. Furthermore, Berthold (1976) believes that omnivorous birds prefer an animal diet, when it is readily available, over vegetable foods, since the latter are relatively poor from the nutritional point of view.

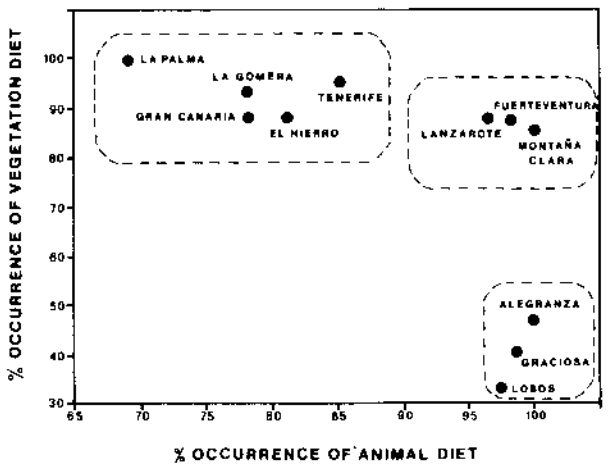

Figure 2. Distribution of the islands and islets in relation to the frequencies of occurrence of animal and vegetable food types recorded in pellets from Ravens.

This paper had its origins in a chapter from the PhD dissertation of the first author of this paper. We would therefore like to express our thanks to the supervisors of that study, Aurelio Martín and Pedro Jordano, for reading and providing valuable comments on the manuscript. D. C. Houston revised and made helpful comments on the text.

REFERENCES

Amat, J.A. & Obeso, J.R. 1989. Alimentación del Cuervo (*Corvus corax*) en un ambiente marismeño. Ardeola 36: 219–224.

Berthold, P. 1976. The control and significance of animal and vegetable nutrition in omnivorous songbirds. Ardea 64: 140–154.

Bravo, T. 1954. Geografía General de las Islas Canarias. I Goya, Santa Cruz de Tenerife.

Conner, R.N., Prather, I.D. & Adkisson, C.S. 1975. Common Raven and Starling reliance on sentinel Common Crows. Condor 77: 517.

Cugnasse, J.M. & Riols, C. 1987. Note sur le régime alimentaire du Grand Corbeau, *Corvus corax*, dans le sud du Massif Central. Oiseaux 39: 57–65.

Day, M.G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. J. Zool. Lond. 148: 201–217.

Engel, K.A. & Young, L.S. 1989. Spatial and temporal patterns in the diet of Common Ravens in southwestern Idaho. Condor 91: 372–378.

Errington, P. 1930. The pellet analysis method of raptor food habits study. Condor 32: 292–296.

Ewins, P.J., Dymond, J.N. & Marquiss, M. 1986. The distribution, breeding and diet of Ravens *Corvus corax* in Shetland. Bird Study 33: 110–116.

Feilden, H.W. 1909. Ravens as scavengers. Br. Birds 3: 57–58.

García, J. 1984. La ganadería. *In* Geografía de Canarias III: 182–206. Santa Cruz de Tenerife: Interinsular Canaria.

Géroudet, P. 1980. Les Passereaux. I: du Coucou aux Corvidés. Neuchâtel-París: Delechaux et Niestlé.

Grant, P.R. 1965. The adaptive significance of some size trends in island birds. Evolution 19: 355–367.

Harlow, R.C. 1922. The breeding habits of the Northern Raven in Pennsylvania. Auk 39: 339–410.

Harlow, R.F., Hooper, R.G., Chamberlain, D.R. & Crawford, H.S. 1975. Some winter and nesting season foods of the Common Raven in Virginia. Auk 92: 298–306.

Holyoak, D. 1968. A comparative study of the food of some British Corvidae. Bird Study 15: 147–153.

Houston, C.S. 1977. Changing patterns of Corvidae on the prairies. Blue Jay 35: 149–156.

Huber, B. & Pfister, V. 1986. Kolkrabenschwärme. Vogel Heimat 56: 152–153.

Kilham, L. 1985. Sustained robbing of American Crows by Common Ravens at a feeding station. J. Field Ornithol. 56: 425–426.

Latscha, H. 1979. Kolkraben jagen wanderfalken seine Beute ab. Ornithologische Mitt. Gottingren 31: 225.

MacArthur, R.H., Diamond, J.M. & Karr, J.R. 1972. Density compensation in island faunas. Ecology 53: 330–342.

MacManus, R. 1935. Feeding habits of the Raven in winter. Auk 52: 99.

Mallory, F.F. 1977. An ingenious hunting behaviour in the Common Raven (*Corvus corax*). Ont. Field Biol. 31: 53.

Marquiss, M. & Booth, C.J. 1986. The diet of Ravens *Corvus corax* in Orkney. Bird Study 33: 190–195.

Marquiss, M., Newton, I. & Ratcliffe, D.A. 1978. The decline of the Raven, *Corvus corax*, in relation to afforestation in southern Scotland and northern England. J. Appl. Ecol. 15: 129–144.

Maser, C. 1975. Predation by Common Ravens on feral Rock Doves. Wilson Bull. 87: 552–553.

Marzol Jaén, M.V. 1988. La lluvia: Un recurso natural para Canarias. Santa Cruz de Tenerife: Servicio de Publicaciones de la Caja General de Ahorros de Canarias.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111–128.

Newton, I., Davis, P.E. & Davis, J.E. 1982. Ravens and buzzards in relation to sheep farming and forestry in Wales. J. Appl. Ecol. 19: 681–706.

O'Gara, B.W., Brawley, K.C., Muñoz, J.R. & Henne, D.R. 1983. Predation on domestic sheep on a western Montana ranch. Wildl. Soc. Bull. 11: 253–264.

Reynolds, J.C. & Aebischer, N.J. 1991. Comparison and quantification of carnivore diet by faecal analysis: A critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. Mammal Rev. 21: 97–122.

Schaber, S. 1983. Cas de prédation sur des Canards domestiques par le Grand Corbeau. Oiseaux 37: 41–42.

Soler, J.J. & Soler, M. 1987. Importancia de los cereales en la dieta invernal de la Corneja y el cuervo en un hábitat estepario cerealista. *In* I Congreso Internacional de Aves Esteparias: 233–239. León 1987. Junta de Castilla-León.

Temple, S.A. 1974. Winter food habits of Ravens on the Arctic Slope of Alaska. Arctic 27: 41–46.

Watson, A. & O'Hare, P.J. 1980. Dead sheep and scavenging birds and mammals on Mayo Bog. Irish Birds 1: 487–491.

White, C.M. & Cade, T.J. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. Living Bird 10: 107–150.

Submitted 22 April 1993; revision accepted 3 October 1993