GRIT INGESTION AND CEREAL CONSUMPTION IN FIVE CORVID SPECIES

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ABSTRACT Grit use in five corvid species has been studied in a cereal-producing plain area where cereal is an important dietary component. Grit size differed significantly between species. Almost all of the pellets examined contained grit, principally quartz. We found strong support for the hypothesis that grit helps to break down the ingested food in Jackdaws, Carrion Crows and Ravens. Only the Jackdaw and the Carrion Crow data significantly support the hypothesis that calcareous grit is a necessary source of calcium for eggshell formation. In the case of the Raven, other studies had recorded vegetable matter only rarely, and grit almost never in either stomach or pellet contents. On the basis of the grit size selection pattern found in our study, and of the lack of grit ingestion reported in other studies, we suggest that the Raven is currently adapting its diet to cereal consumption.

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INTRODUCTION

Grit has frequently been reported in the stomach contents of birds. Grit is especially abundant in granivorous bird diets (Mathiasson 1972, Myrberget *et al.* 1975, Grigera & Aliotta 1976, Alonso 1985), but also is present, although in smaller quantity, in birds with other diets, such as waders (Lifjeld 1984, Moksnes 1988), frugivorous species (Tejero *et al.* 1983, Soler *et al.* 1988, Pérez-González & Soler 1990), and insectivorous species (Herrera 1977, Walton 1984, Martínez-Cabello *et al.* 1991). It is generally accepted that stomach stones enable a more effective break down of ingested food, serving the functional role of teeth (Farner & King 1972). However, grit may also represent a valuable source of minerals (Walton 1984), especially of calcium, which would be important throughout the year (Lienhart 1953, McCann 1961), and particularly during eggshell formation (Harper 1964, Kopischke 1966).

We have studied grit ingestion and cereal consumption in five sympatric species of corvids: the Jackdaw, *Corvus monedula*, the Magpie, *Pica pica*, the Chough, *Pyrrhocorax pyrrhocorax*, the Carrion Crow, *Corvus corone*, and the Raven, *Corvus corax*. All five species are generally omnivorous (Coombs 1978), though the importance of vegetable matter differs among species. Vegetable matter, especially cereals, is very important to the Jackdaw (Lockie 1956, Holyoak 1968, Folk 1967), the Carrion Crow (Holyoak 1968, Houston 1974, Jollet 1984) and the Magpie (Högstedt 1980, Reebs & Boag 1987). In our study area, however, volumetric percentages of vegetable matter (mainly cereals) in the pellet contents of these five species are higher than reported elsewhere: 78% (mineral fraction = 8.5%) in the Jackdaw (Soler *et al.* 1990) 50.3% (mineral fraction = 39.5%) in the Carrion Crow and 59.3% (mineral fraction = 15.3%) in the Magpie (Soler & Soler 1991). In other study areas the diet of the Chough consists almost entirely of invertebrates (Roberts 1982, 1989), and the Raven's diet is mainly carrion and small vertebrates (Holyoak 1968, Temple 1974, Marquiss & Booth 1986, but see Engel & Young 1989). For these two species vegetable matter normally has little importance. Nevertheless, in our study area, cereal is the most important component of both the Raven (%V = 74.4%, mineral fraction = 13.6%; Soler & Soler 1991) and Chough diets (%V = 37.3%, mineral fraction = 9.5%; Soler 1991).

Three main hypotheses attempt to explain the function of gizzard grit: (1) Grit aids in the tritura-

Received 11 March 1993, accepted 14 July 1993.

tion and digestion of hard vegetable matter (Farner & King 1972, May & Braun 1973, Myrberget *et al.* 1975), (2) Calcareous grit is a valuable source of nutritional calcium (McCann 1961) and (3) In Spring, during eggshell formation, calcareous grit represents a necessary source of calcium (Sadler 1961).

In the present paper, we analyze grit use in five corvid species, discuss hypotheses of the functions of grit in bird gizzards, and present evidence supporting the generally accepted hypothesis that the stomach stones aid in breaking down ingested food.

STUDY AREA AND METHODS

This work was carried out in the Hoya de Guadix (Southern Spain), a cereal-producing plain at 900-1100 m above sea level. This area has many gullies with clay cliffs with abundant crevices and holes, where Jackdaws, Ravens and Choughs nest. Magpies and Carrion Crows nest mostly in holm oaks *Quercus rotundifolia* and almond trees *Prunus dulcis*.

In 1984 and 1985 we collected a total of 140 pellets of Jackdaws, 185 of Magpies, 140 of Choughs, 231 of Carrion Crows and 208 of Ravens. Approximately 40 of each species during each of the months November, January, April, and August which are assumed to be representative of autumn, winter, spring and summer respectively. All pellets in each season were collected on the same or two consecutive days from only one communal roosting site for every species. Only fresh looking pellets were selected.

For each pellet we estimated: (a) volume of the vegetable fraction; (b) volume of the animal fraction; (c) volume of the mineral fraction (volumes were used to avoid overestimating the importance of the grit); (d) number of stomach stones (only those larger than 0.2 mm were counted); and (e) breakdown fragmentation level of the cereal remains. We distinguished six levels of fragmentation which can be listed in ascending order: (1) most of the remains are whole kernels; (2) most kernels are broken but some intact; (3) grain fragments exist, but separated from their largely intact coats; (4) most of the remains are largely undamaged coats; (5) seed coats are quite fragmented, though large pieces remain; and (6) all vegetable remains are thoroughly triturated.

The longest dimension of each grit particle, from 60 pellets selected at random (12 for each species) was measured to the nearest 0.01 mm with a digital caliper. Grit composition was determined by examining the particles under a zoom binocular microscope, dividing the grit into two groups: calcareous and non-calcareous.

Grit availability was sampled in the seven habitats most frequently used by corvids in our study area (according to information from Soler 1991). The sampling method, which was repeated a total of 96 times, consisted of tossing a 25x25 cm metal

Table 1. Grit, vegetable and animal fractions of the pellets of the five corvid species in Spain. *SE* = Standard error.

Species	Pellets compositions (mean ± *SE* of % of volume) Vegetable	Animal	Grit	Number of grit particles per pellets (mean±*SE*)	Frequency of occurrence of grit (%)	Trituration level	N[1]
Jackdaw	46.0±1.70	9.0±0.87	45.0±1.67	60.9± 4.64	100	4.5±0.01	140
Carrion Crow	49.7±1.16	10.9±0.71	39.4±1.21	133.1± 6.40	100	4.5±0.06	231
Raven	71.3±1.73	13.6±1.34	14.1±0.13	250.8±22.8	96.6	3.0±0.07	208
Magpie	61.2±1.54	25.9±1.61	12.9±0.70	25.8± 3.11	98.9	3.6±0.08	185
Chough	36.1±1.58	51.7±1.78	12.2±0.82	25.3± 4.76	99.3	4.0±0.08	140

[1] for trituration level N=: 131, 226, 203, 181 and 138 respectively.

frame on the ground, then counting the number of pebbles of appropriate size (0.2-7 mm) within the frame, distinguishing calcareous from non-calcareous pebbles. For each species we used results obtained in its preferred foraging habitats (see Soler 1991).

Size of grit particles and volumes of mineral fraction and vegetable matter were not normally distributed and therefore had to be transformed in order to obtain approximately normal distributions. In the analyses, size of grit was log-transformed and percentages of volumes were transformed to arcsine values.

Values given are mean ± *SE*. Statistics follow Siegel (1972), Sokal & Rohlf (1981) and Zar (1984).

RESULTS AND DISCUSSION

Grit use in the five corvid species

Grit appeared in almost all the pellets of the five species, with percent occurrence ranging from 97 in the Raven to 100 in the Jackdaw and the Carrion Crow (Table 1). The Raven and the Carrion Crow had the largest number of grit per pellet, while the Jackdaw and the Carrion Crow had the greatest percentage of grit per volume, probably owing to the size difference between the grit found in the Raven and the Jackdaw pellets (Fig. 1). The Magpie and the Chough, which had the least grit, both in number per pellet and percentage of volume, had the highest animal fractions (Table 1).

Size and mineral composition of selected grit

Significant differences exist between species and pairs of species in the size of grit selected ($F_{4,2761}$ = 126.5, P < 0.00001; Fig. 1), except between the Magpie and the Chough and between the Chough and the Raven (Tukey LSD test $P > 0.10$; Fig. 1).

The Raven, as opposed to the other four species, appears not to select grit size, but instead plunges its beak into the sand and indiscriminately swallows pebbles of all sizes (pers. obs.) which may account because the Raven was the only species in which, after removing all the grit larger than 0.2 mm, a large amount of sand remained.

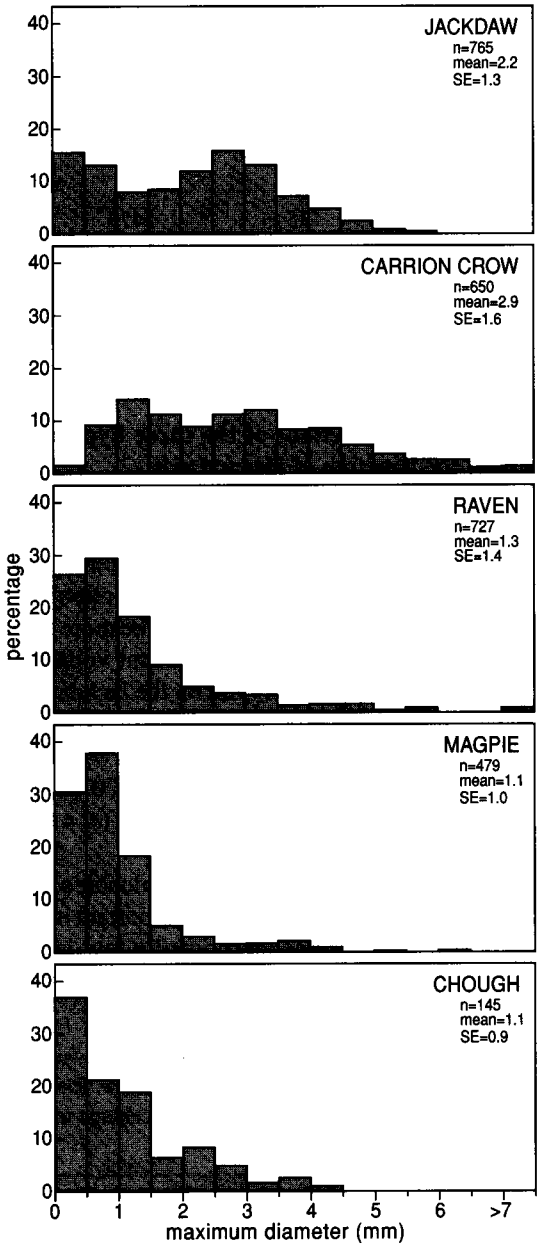

Fig. 1. Size distribution of grit particles found in the five corvid species. *n* = number of grit.

Siliceous grit outnumbered significantly calcareous grit in the pellets of the Chough, Raven and Jackdaw (Table 2).

Table 2. Mineralogical composition of grit in the five corvid species. More than 95% of the non-calcareous grit was quartz particles and values of non-calcareous grit are complementary with calcareous grit values.

Species	Number of pellets	Number of grit particles	Percentage of calcareous grit (mean±*SE*)	Wilcoxon test *p*	Mean of calcareous grit per pellet
Jackdaw	35	1479	35.3±4.95	0.0013	14.9
Carrion Crow	33	1393	46.8±4.33	0.46	19.7
Raven	28	748	15.3±4.20	0.00002	4.0
Magpie	25	550	50.3±7.74	0.86	9.0
Chough	30	159	19.3±4.47	0.00017	1.0

Test of the predictions of the three hypotheses about the function of gizzard grit

We shall discuss our results in relation to the predictions of each hypotheses cited above.

- **Hypothesis 1**: Grit aids in the trituration and digestion of hard vegetable matter. **Prediction**: The vegetable remains of the pellets will be more triturated when the percentage of mineral volume is greater. This prediction is valid for the Jackdaw ($r_s = 0.41$, $P < 0.0001$, $n = 138$), the Carrion Crow ($r_s = 0.45$, $P < 0.0001$, $n = 226$), the Raven ($r_s = 0.20$, $P < 0.005$, $n = 203$), the Magpie ($r_s = 0.18$, $P < 0.05$, $n = 181$), but not for the Chough ($r_s = 0.09$, $P > 0.25$, $n = 138$).

- **Hypothesis 2**: Calcareous grit is a valuable source of nutritional calcium, especially important in granivores because grains are normally low in calcium. **Prediction**: Calcareous grit will be preferentially selected throughout the year. According to samplings in our study area (see methods), calcareous grit predominates in foraging areas of all species, except in the almond habitat, favoured by the Magpie, where siliceous grit is much more abundant (Table 3). Comparing these grit availability data (Table 3) with the percentage of calcareous grit in the pellets of each species, we found significant differences in all cases ($t = 3.42$, $df = 81$, $P < 0.01$ in Jackdaw; $t = 3.10$, $df = 90$, $P < 0.01$ in Carrion Crow; $t = 6.42$, $df = 33$; $P < 0.001$ in Raven; $t = 6.42$, $df = 33$, $P < 0.001$ in Magpie; and $t = 4.57$, $df = 85$, $P < 0.01$ in Chough). In the Magpie the average percentage of the calcareous grit is significantly greater in pellets than in the environment. In the other four species the opposite is true -the average percentage of calcareous grit is significantly less in pellets than in the environment. Al-

Table 3. Mineralogical composition of grit availability in the foraging habitat. We have sampled 3, 4, 4, 1 and 4 different habitats for Jackdaw, Carrion Crow, Raven, Magpie and Chough respectively, taking a mean of 15 samples of every habitat. The means of percentage of non-calcareous grit are complementary for every species. *SE* = Standard error.

Species	Number of samples	Number of grit particles	Grit availability Percentage of calcareous grit (mean±*SE*)
Jackdaw	48	4375	60.7±5.6
Carrion crow	58	7630	67.2±5.0
Raven	68	6558	43.1±5.2
Magpie	10	1080	0.5±0.3
Chough	57	12734	51.6±4.5

Table 4. Comparison between mean percentage (± standard error) of calcareous grit in the pellets from the egg-shell formation period and the rest of the year. We test the null hypothesis of equal means. Number of pellets and number of grit particles respectively in parentheses.

	Percentage of calcareous grit (mean ± *SE*)		One-tailed *t*-test		
	Period of egg-shell formation	Rest of the year	*t*	*df*	*P*
Jackdaw	64.4 ± 8.02 (12, 307)	23.6 ± 4.38 (25, 441)	5.10	18	<0.0001
Carrion Crow	52.8 ± 4.23 (8, 430)	44.9 ± 5.54 (25, 963)	1.86	14	<0.05
Raven	16.41 ± 7.74 (12, 307)	14.41 ± 4.76 (16, 441)	0.26	18	>0.3
Magpie	60.1 ± 17.65 (5, 222)	47.8 ± 8.75 (20, 328)	0.69	8	>0.2
Chough	23.64 ± 9.43 (8, 43)	17.75 ± 5.14 (22, 116)	0.62	14	>0.2

though the Magpie pellets have a high proportion of calcareous grit (Table 2), the total amount of grit in its pellets is relatively low (Table 1). Therefore, in the Carrion Crow and the Jackdaw, the most important granivorous corvid species, the absolute quantities of calcareous grit per pellet is higher than in the Magpie (Table 2).

- **Hypothesis 3**: In Spring, during eggshell formation, calcareous grit represents a necessary source of calcium. **Prediction**: A species will ingest a greater percentage of calcareous grit during the eggshell formation period than during the rest of the year. In all five species there was an increase in the ingestion of calcareous grit during the egg-forming period, but the increase was significant only in the Jackdaw and in the Carrion Crow (Table 4). This difference between species may be due to the fact that the Jackdaw and the Carrion Crow are the two species where grains are more important (Soler 1991). The Raven and Magpie, in our study area, consume carrion and small vertebrates (Soler & Soler 1991) and the Chough ingests a large percentage of insects (Soler & Soler 1993).

Therefore, we conclude that Hypothesis 1 best explains our results concerning the grit use in our five corvids, while Hypothesis 3 is supported only by the Jackdaw and the Carrion Crow, which selects calcareous grit during the egg-forming period.

Grit consumption and adaptation to cereal ingestion

Grit size appears to be important to trituration, since in the two species with the largest size of grit, the Jackdaw and the Carrion Crow, the vegetable remains are noticeably more triturated.

In agreement with previous studies, our data indicate that Ravens are omnivorous generalists. Only two studies, however, have cited vegetable matter as being a significant food for Ravens (Harlow *et al.* 1975, plants = 20.1% of total volume, and Engel & Young 1989, cereal grains = 69.3% of total weight). Only these two works report inorganic material in Raven pellets (2.2% of total volume in Harlow *et al* 1975; 4.4% of total weight of inorganic material in Engel & Young 1989). In our study area carrion and small mammals are very scarce, but

there is an abundance of cereals (particularly barley), that make up the most important component of the Raven diet (Soler & Soler 1991). Here Ravens ingested grit but did not select grit of a particular size, perhaps because selection would be costly for a bird with such a large beak, whereas it is easier to swallow pebbles and sand together. The absence of grit ingestion in other studies, and the lack of grit-size selection in our study, could indicate that Ravens in our study area are in process of adapting to cereal consumption.

ACKNOWLEDGMENTS

We thank M. Díaz, P. Jordano and A.P. Møller for constructive comments on earlier version of this paper.

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SAMENVATTING

Bij vijf kraaiachtigen, Kauw, Zwarte Kraai, Raaf, Ekster en Alpenkraai werd onderzocht in hoeverre steentjes werden gebruikt als onderdeel van het dieet. De studie werd verricht in de Hoya de Guadix (in het zuiden van Spanje), een gebied waar graan wordt verbouwd, en waar graan ook een belangrijke component vormt van hun voedsel.

De grootte van de gegeten steentjes, bepaald aan de hand van braakballen, verschilde van soort tot soort (Fig. 1). In vrijwel alle braakballen werden steentjes gevonden, vooral kiezeldeeltjes. De gegevens van Kauw, Zwarte kraai en Raaf ondersteunen de hypothese dat steentjes bijdragen aan de vermaling en vertering van hard plantaardig materiaal (Tabel 1).

De hoeveelheid steentjes nam toe naarmate de braakballen meer resten van plantaardig materiaal bevatten. Bovendien nam de grootte van de plantaardige deeltjes af met de hoeveelheid steentjes.

In veel braakballen kwamen kalksteentjes voor (Tabel 2), maar bij de meeste soorten ging de voorkeur uit naar kiezeldeeltjes (Tabel 3). Alleen de Ekster die vooral in kalkarme gebieden voorkomt, bleek een voorkeur te hebben voor kalksteentjes. De hypothese dat het gebruik daarvan noodzakelijk is voor de vorming van de eischaal, wordt alleen ondersteund bij de Kauw en de Zwarte Kraai. Bij die twee soorten neemt de fractie kalksteentjes toe in de periode dat de eischalen worden gevormd (Tabel 4). De gegevens van de Raaf verdienen speciale aandacht, omdat deze soort in het algemeen slechts zelden plantaardig voedsel gebruikt en ook bij uitzondering steentjes consumeert. In het studiegebied lijkt de Raaf zich echter aan te passen aan een dieet met granen, mede dankzij de consumptie van steentjes. - JvR